**REVIEW ARTICLE**

**Myxozoan genera: definition and notes on taxonomy, life-cycle terminology and pathogenic species**

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Key words: Myxozoa, definition of genera, taxonomy, terminology, phylogeny, pathogenic species

Abstract. A list of myxozoan genera is presented in the current taxonomical scheme. These genera are defined; their type species and most important pathogens along with their hosts are listed. Simultaneously, definitions of actinospore stages representing sexual stages of the myxosporean life cycle are given; altogether, 17 actinospore collective groups with 180 types have been described. Life cycles of the two classes of the phylum Myxozoa, Malacosporea and Myxosporea, are briefly outlined with specification of the appropriate terms. Up to now, 4 malacosporean and 2,180 myxosporean species assigned to a total of 62 genera, have been established. The surviving classification of myxosporeans, based on spore morphology, is discussed in the context of the still fragmentary data resulting from SSU rDNA sequence analyses. The main task for the future is a rigorous, detailed morphological description combined with molecular techniques in establishment of new species and in revision of the existing ones. Establishment of a classification acceptable from morphological, biological and phylogenetical viewpoints is necessary.

Myxozoa enjoy increasing attention not just because new myxosporean pathogens are continually emerging and threatening the development of pisciculture. New findings on life cycles, the discovery of the new class Malacosporea and the dispute on myxosporean phylogeny and origin provide additional stimuli for their study. Although in recent research the experimental approach prevails, descriptions of new myxosporean genera have not fallen behind.

In the first, “discovery decade” 1890 to 1900, ten genera were established; in the following decades, until 1980, the number of newly described genera fluctuated between one and five, while in the decade 1980–1990 the number of genera newly established increased to 14, and in 1991–2000 nine new genera were discovered.

Classification of the phylum has a long history since the discovery of Myxosporea by Jurine (1825) and subsequent observation by Müller (1841) and actually began when Otto Bütschli (1882) classified Myxosporida (along with Sarcosporida) as a subclass of the then class Porozoa. The subsequent twists and turns in classification of this group can be followed in detail in publications by Balbiani (1883), Gurley (1893, 1894), Thélohan (1895), Doflein (1898), Štolc (1899), Auerbach (1910), Kudo (1919, 1933), Hartmann (1923–1925), Tripathi (1948), Shulman (1966), Grassé (1960, 1970), Lom and Noble (1984), Donets and Shulman (1984), and Kent et al. (1994a).

A groundbreaking discovery was the recognition that the enigmatic creature Buddenbrockia living within bryozoans was a primitive myxozoan (Canning et al. 1996). After more than one hundred years of alleged protozoan nature and disputes on their possible metazoan affinities, Myxozoa were finally transferred to Metazoa. Cavalier-Smith (1998) considers them to be a subkingdom of Animalia; Hausmann et al. (2003) list them as a superclass of infraphylum Metazoa within the phylum Opisthocoonta (Empire Eukarya). The majority of molecular studies (Smothers et al. 1994, Schlegel et al. 1996, Anderson et al. 1998, Okamura et al. 2002, Zrzavý and Hypša 2003) assign Myxozoa to Bilateria or their sister group. The controversial finding of Kelley et al. (2004) that Myxobolus cerebralis branches with its actin gene sequence outside both opisthokonts and Amoebozoa warrants further phylogenetic analysis. The simple body form, especially in Myxosporea, is viewed as the result of large-scale reduction due to adaptation to parasitism. Extensive discussion of the putative processes leading to present-day myxozoan cell structure and equipment with polar capsules can be found in Canning and Okamura (2004).

A short summary of the phylum is in Kent et al. (2000b). The rather recent state is presented in Kent et al. (2001) and the last outline of the framework of the phylum’s classification can be found in Canning and Okamura (2004).

In this review we attempt to summarise the present rather neglected state of classification of myxozoan genera and of actinospore stages of Myxosporea. In each genus, we draw attention to the most important pathogenic species currently recognised.

**PHYLUM MYXOZOA**

Grassé, 1970

Parasites of invertebrates and vertebrates characterised by spores composed of several cells transformed into one to seven spore shell valves, one to many amoe-
boid infective germs (sporoplasts) and one to several nematocyst-like polar capsules (in Kudoa permucicap- 
sula up to 15). The capsules contain an extrudible fila-
ment with an anchoring function. The typically eu-
karyotic cells lack centrioles and flagella. Mitochondria 
have tubular, flat or discoid cristae. Cell junctions are 
commonly found. Vegetative (trophic) stages in the 
form of a primitive bilateral worm-like organism or in 
the form of a closed sac (class Malacosporea) have been 
in most representatives (class Myxosporea) reduced to a 
spore-producing multicellular, often amoeboid plasmo-
dium.

In the class Myxosporea, vegetative stages may be 
coelozoic (in body cavities or cavities of body organs) 
or histozoic, intercellular (wedged between tissue cells), 
or often intracellular. The life-cycle pattern —supposed 
to be present in most of the species— involves alternate-
tion of hosts, one of them, in which the sexual process 
has been proven, being the definitive one (an inverte-
brate), the second (a vertebrate) serving mainly for parasite multiplication. The cell-in-cell organisation 
is typical of stages in vertebrates.

References: Grassé and Lavette (1978), Uspenskaya 
(1984), Lom (1990), Siddall et al. (1995), Kent et al. 

CLASS MALACOSPOREA Canning, Curry, Feist, 
Longshaw et Okamura, 2000

Life cycle, structure and terminology

Parasites of freshwater bryozoans (Phylum Bryozoa, 
Class Phylactolaemata). The trophic, proliferative stages 
live within bryozoan body cavity in the form of closed 
multicellular sacs or worm-like organisms (also termed 
vermiform bodies).

Trophic stages are preceded by cryptic stages in the 
host epithelium —they may persist there for a period of 
up to six weeks and develop first in loose clusters with-
out cell junctions, then rearrange themselves to form the 
trophic stages, i.e., simple sac-like or vermiform organ-
isms. The worm-like organism (up to about 3.6 × 0.1 
mm) of Buddenbrockia plumatellae has an outer wall 
formed by a layer of flat mural cells, bound together by 
cell junctions. The outer wall encloses four longitudi-
nal muscle blocs and an inner layer of cells. This layer 
consists of more dense type B cells separated by larger, 
less dense —perhaps secretory— type A cells. In more 
advanced vermiform stages, B cells proliferate and pile 
up in several layers and then disperse in the lumen of the 
“worm”. These pre-spore cells will become spores 
after completion of meiosis. Then they divide to form 
compact groups of ten, which mature as typical spheri-
cal malacospores with eight unhardened shell valves 
topped by four polar capsules, including two sporop-
plasms with inner (secondary) cells inside them. Sporopl-
asms have electron-dense bodies with lucent invagina-
tions, sporoplasmosomes. Polar capsules and sporo-
plasms are encased with valvogenic cells, which in ma-
lacospores do not cover the exit point of the polar fila-
ment. Polar capsules at the anterior pole of the spore 
have their mouths covered by a dense cap overlain by a 
structure of fibrous components. During capsulogenesis,

external tube of the capsular primordium is not always 
observed but has been proven in some populations. In 
some malacosporean populations spores arise in the 
layer of mural cells (Morris et al. 2002).

The ellipsoid, sac-like stages or sacs of Tetracapsu-
loides bryosalmonae are simpler: there is an outer layer 
of mural cells subtended by an incomplete layer of B 
cells destined to become spores. Deeper from the wall 
there is a mass of free cells; a group of distinctive stel-
late cells aggregate around a sporoplasmogenic cell 
which undergo meiosis. A spherical malacospore is then 
produced from this aggregation.

In T. bryosalmonae there is a stage infecting sal-
onid fish, primarily kidney, as the so-called PKX 
stage, the agent of proliferative kidney disease (PKD). 
These stages are composed of an enveloping cell with 
sporoplasmosomes of a special form and contain an 
inner, secondary cell that in turn may contain tertiary 
cells. Sporogenesis is mostly missing. However, Hed-
rick et al. (2004) found mature spores in the urine of 
Oncorhynchus mykiss, different from bryozoan malaco-
spores, for which the term fishmalacospores was pro-
posed. These spores have two shell valves enclosing 
two polar capsules and one sporoplasm.

No complete malacosporean life cycle has been un-
ravelled thus far. As Tops et al. (2004) reported, there is 
no evidence for bryozoan-to-bryozoan transmission and 
there might be another malacosporean host still uniden-
tified. Transmission of Tetracapsuloides from fish to 
bryozoans still requires further investigation. Taticchi et 
al. (2004) suggested that T. bryosalmonae might be 
transmitted within bryozoan statoblasts. T. bryosal-
monae is not transported through fisheries activities (Henderson and Okamura 2004).

The genus representing the class, Buddenbrockia, 
may well be taken for a missing link between bilaterian 
ancestors and highly derived myxosporeans that have 
lost all ancestral features.

References: Anderson et al. (1998), Canning et al. 
(2005).

ORDER MALACOVALVULIDA Canning, Curry, Feist, 
Longshaw et Okamura, 2000

With characters of the class.

Sac sporidae Canning, Okamura et Curry, 1996

With characters of the order. All uninucleate cells within 
the sac are potential spores.

Buddenbrockia Schröder, 1910 Fig. 1 Synonym: Tetracapsula Canning, Okamura et Curry, 1996

Trophi stages in form of both sac-like and worm-like or-
ganisms of triploblast organisation. Cells produced by division 
of one sporogenic cell into ten cells are needed to constitute
the spore (four valvogenic, four capsulogenic and two sporoplasms, each of the latter with one secondary cell inside). Spherical spores have at their anterior pole four polar capsules. Buddenbrockia can probably not be transmitted directly from bryozoan to bryozoan. Vertical transmission occurs by colony fragmentation and further growth of the offspring thus produced.

Type species Buddenbrockia plumatellae Schröder, 1910 (syn. Tetracapsula bryozoides Canning, Okamura et Curry, 1996) described from the coelomic cavity of Plumatella fungosa from Belgium, found later in six other species, is cosmopolitan. Vermiform forms are up to 3.6 mm long. Spores are spherical, 19 µm in size when fresh (Fig. 1). Tops et al. (2005) have announced discovery of two more species.

References: Schröder (1910), Canning et al. (1996).

Tetracapsuloides Canning, Tops, Curry, Wood et Okamura, 2002

Differs from the preceding in that the trophic stages are in form of a closed sac formed by a simple layer of cells. Spores develop from an aggregate of distinctive stellate cells, probably diploid, around a sporoplasmonic cell that undergoes meiosis. The 18S rDNA sequence differs by 20% from that of Buddenbrockia (Anderson et al. 1999a, b). It also occurs in other bryozoan species (Okamura and Wood 2002, Canning and Okamura 2004). Mature subspherical fishmalacospores with two soft valves, two polar capsules and a single sporoplasm (Fig. 2) were reported from the urine of Oncorhynchus mykiss (Hedrick et al. 2004). Based on development to an immature stage in salmonid fish, Kent et al. (2000a) described the species as Tetracapsula renicola Kent, Khattra, Hedrick et Devlin, 2000, which is a junior synonym of Tetracapsuloides bryosalmonae.

Tetracapsuloides bryosalmonae (Canning, Curry, Feist, Longshaw et Okamura, 1999) Canning, Tops, Curry, Wood et Okamura, 2002 was first identified from Cristatella mucedo, Pectinatella magnifica and Plumatella rugosa from Ohio and Michigan, USA (Anderson et al. 1999a, b). It also occurs in other bryozoan species (Okamura and Wood 2002, Canning and Okamura 2004). Mature subspherical fishmalacospores with two soft valves, two polar capsules and a single sporoplasm (Fig. 2) were reported from the urine of Oncorhynchus mykiss (Hedrick et al. 2004). Based on development to an immature stage in salmonid fish, Kent et al. (2000a) described the species as Tetracapsula renicola Kent, Khattra, Hedrick et Devlin, 2000, which is a junior synonym of Tetracapsuloides bryosalmonae.

Tetracapsuloides bryosalmonae is the agent ("PKX") of proliferative kidney disease of cultured (and wild) salmonid fishes of the genera Salmo, Oncorhynchus, Thymallus and also pike (Esox) in North America and Europe, sought since the 1970’s.

According to Morris et al. (2000), the portal of entry of infectious sporoplasms are the gills, while Longshaw et al. (2002) found it to be mucous cells in the skin. In renal interstitium of the fish the "PKX" cell complexes appear. Stages proliferating in the interstitium provoke a vigorous defence reaction of the host and hereby the actual disease. Mortality in susceptible fish, especially fry, may fluctuate from 30 to 50%. It has been widely speculated that salmonids are accidental, facultative or dead-end hosts for T. bryosalmonae. Phylogenetic network using molecular methods implies that southern European was colonised by immigration of the parasite from North America and that this colonisation substantially pre-dated fisheries activities (Henderson and Okamura 2004).


CLASS MYXOSPorea Bütschli, 1881

Life cycle, structure and terminology

Following the basic discovery of Wolf and Markiw (1984), it has been accepted that as a rule the life cycle takes place in two hosts. The term myxosporean covers both life-cycle phases, the myxospore and actinospore one. The generally better known myxospore phase, resulting in production of myxospores, takes place in lower vertebrates, typically in fish, rarely in amphibians and reptiles, exceptionally perhaps in birds and mammals. Hosts of the actinospore phase, involving a sexual process and resulting in production of actinospores, are annelids, rarely sipunculids. The myxospores are as a rule hard-shelled, with two (sometimes more) shell valves and are produced in small or large sporogonial plasmodia. A typical feature in developmental stages is the cell-in-cell condition, when the endogenously produced (secondary) cells persist inside the primary (mother) cells. Myxosporea lack centrioles and display a closed mitosis. The microtubules of the spindle often persist as a coherent bundle long after karyokinesis. Mitochondrial cristae are of variable shape, plate-like, tubular or discoid.

The actinospore, discharged from an annelid into water, randomly encounters the fish (intermediate) host. Upon contact with the skin or gill epithelium, polar capsules discharge their polar filaments, fastening the spore to the host. Then the spore shell valves open and the sporoplasm enters the skin generally through the openings of epidermal and epithelial mucous cells. A series of presporogonic stages follows, which may be intra- or intercellular. They migrate to the site where the sporogonic stage—a plasmodium or a pseudoplasmodium—develops. Both may develop temporary cytoplasmic projections, pseudopodia, and may divide by plasmodotomy, i.e., cleavage in two or more daughter parts. Plasmodia can be taken for an extremely reduced sac- or worm-like stage of Malacosporea; their cytoplasm may include a variety of cytoplasmic inclusions. Plasmodial stages may be histozoic, situated in the tissue and often appearing as “cysts”; or coelozoic, in cavities of body organs (mainly urinary tract or gall bladder). The plasmodium may be a large body with many vegetative nuclei of its own and with endogenously produced generative cells. These may be of one type, sporogenic cell, each of which produces a spore by division and differentiation, or of two types, sporogenic cell and pericyte. These two latter cells engage in spore formation, sporogony. The pericyte envelopes the sporogenic cell which divides into differentiated capsulogenic, valvogenic and sporoplasmogenic cells. Corresponding numbers of these cells develop into two sporoblasts and consequently mature into two myxospores inside the pericyte. Myxospores generally have a hard shell. The pericyte with the progeny of the sporogenic cell represents the pansporoblast. Plasmodia may also enclose lobocytes, large cells of presumably scavenging function within the plasmodium. Large plasmodia produce as a rule many spores, are poly- sporic. Pseudoplasmodia are rather small, contain one nucleus and generative cells necessary to compose one.
Fig. 1. Malacospore of Buddenbrockia plumatellae; two of the polar capsules are beyond the plane of the drawing; note the two uninucleate sporoplasm, each with a uninucleate secondary cell. Sporoplasm contain sporoplasmomes (courtesy of Dr. E.U. Canning et al. 1996 and Folia Parasitol.). Figs. 3–27. Line drawings of myxosporean spores. Fig. 3. Sphaeromyxa balbianii in frontal view (a) with polar filament (PF) incorrectly drawn as a spiral (from Thélohan 1895), (b) enlarged polar capsule of
or two spores (are monosporic or disporic). Sometimes, even when the sporogonic stages have been developed, extrasporeonic stages persist, serving for additional parasite proliferation. The myxospore consists mostly of one to four polar capsules, one or two sporoplasms (the actual infective germs), all these being encased with two to seven shell valves. Capsulogenesis involves regularly production of an external tube associated with the capsular primordium. Shell valves adhere together along the line of dehiscence, the suture line, and also cover the apex of polar capsule. Sporoplasm contains sporoplasmosomes, without the central lucent invagination known in malacosporeans. Under certain conditions, the development in the fish may be arrested before the onset of sporogenesis (Higgins et al. 1993).

When ingested by the definitive host (typically an oligochaete) in which the sexual phase takes place, the sporoplasm of the myxospore initiates a merogony phase. Resulting uninucleate cells produce a tetrane- cleate stage, two sporogonial cells enveloped by a pair of pericyetes, the future pansporocyst. During further development of these cells the two (or more) enveloping cells harbour inside them eight pairs of gametic cells (α and β cells) which, having undergone meiosis with the occurrence of synaptonemal complexes, fuse to produce eight zygotes. The zygotes develop by cell division and differentiation into eight triradiate actinospores. In most of these actinospores there is an anterior spore body containing always three polar capsules and three shell valves that leave an opening for the apex of polar body the shell valves extend in most actinospores into very long, hollow and mutually caudal projections, inflate osmotically by water into full length when the spore is released from the host. In some actinospore stages, the three projections, prior to diverging from each other, fuse to form a style. The cycle is repeated when the spore encounters a fish host. In a few species, a direct transmission from fish to fish has been proven (e.g., Enteromyxum).


Hosts

Most representatives of the myxospore phase live in freshwater and marine fishes; 3 species have been reported in Agnatha, 35 species in Chondrichthyes, and the rest in Ostechthyes. Thirteen myxosporean species have been described from amphibians, and six from reptiles. Nothing has been reported about their possible actinospore phase of the non-fish myxosporeans.

Recently, myxosporean or developmental stages resembling those occurring in the fish hosts were also discovered in homeothermic vertebrates. Myxosporean-like developmental stages, causing xenoma formation, have been found in the brain of a mole (Talpa europaea) in Austria (Friedrich et al. 2000). Developmental stages and unassigned spores were surprisingly found in inflammatory lesions of hepatic ducts in ducks (Lowenstein et al. 2002). There have been also repeated findings of Myxobolus spores in the faeces of humans suffering from intestinal disorders or infected with the HIV virus (e.g., Boreham et al. 1998, Moncada et al. 2001, Hessen and Zamzame 2004). These reports led Canning and Okamura (2004) to postulate that myxozoans may under certain conditions become opportunistic parasites of homeothermic vertebrates.

A few species have been reported to occur in myxospore stage in invertebrates: a Kudoa sp. was found in the muscles of the arm of the giant octopus Paroctopus dobleini (Yokoyama and Masuda 2001). The following are doubtful reports: Chloromyxum diploxy (Gurley, 1893) Thélohan, 1895 was once reported from the abdominal cavity of the lepidopteran Tortrix viridana (Thélohan 1895). It seems to be a myxosporean, but not a Chloromyxum. An alleged myxosporean from an insect, Dactilopitus indicus, described as Symmetrula coxinealis Sundara Rajulu et Radha, 1966, is claimed

S. magna Zhukov, 1964 with PF as a broad folded ribbon (from Lom 1969). Fig. 4. Myxidium lieberkuehni. Fig. 5. Enteromyxum scopthalmi (courtesy of Dr. P. Alvarez-Pellitero and Parasitology). Fig. 6. Zschokkella hildae (after Kudo 1919). Fig. 7. Coccomyxa morovi. Fig. 8. Ortholinea divergens in sutural (a) and frontal view (b) with empty polar capsules after the filaments have been extruded (modified from Kudo 1919). Fig. 9. Neomyxobolus ophiocephalus in frontal (a) and apical view (b). Fig. 10. Cardinomyxum leshanensis in frontal (a) and sutural view (b); modified from Chen and Ma (1998). Fig. 11. Triangularia yankiangensis in frontal view. Fig. 12. Triangularum amazonicum in oblique partly dissected view (courtesy of Dr. C. Azvedo and Eur. J. Protistol.). Fig. 13. Kentmoseria alata in frontal (a) and sutural view (b) (courtesy of Dr. M.L. Kent and J. Eukaryot. Microbiol.). Fig. 14. Simulineola dimorpha (after Kudo 1919). Fig. 15. Davisia diplorheis. Fig. 16. Myxoproteus australis (courtesy of Yoshino and Noble 1974 and J. Parasitol.). Fig. 17. Bipteria admiranda. Fig. 18. Paramyxoproteus rehhardtii in sutural (a) and apical view (b) (after Wierzbicka 1986). Fig. 19. Neobieteria macrouri. Fig. 20. Schulmania ovale. Fig. 21. Noblea admiranda. Fig. 22. Fabespora nana. Fig. 23. Fabespora vernicola (courtesy of Dr. R.M. Overstreet and J. Parasitol.). Fig. 24. Ceratomyxum arcuata (from Meglitsch 1960, courtesy of J. Parasitol.). Fig. 25. Ceratomyxum sparsaraurai (courtesy of Dr. A. Sitjá-Bobadilla and J. Eukaryot. Microbiol.). Fig. 26. Leptotheca agilis (from Kudo 1919). Fig. 27. Meglitschisa insolita. Figs. 3a, 4, 6, 7, 9, 11, 13, 14, 15b, 16, 18–21, 26, 29, 31–35a, b, 36–38, 40–42, 45–54, 56, 58–62 and 64–67 are taken from Lom and Dyková (1992) with kind permission of Elsevier Publishers.
to have spherical, two-valved spore with a single polar capsule, and has trophozoites not corresponding to myxosporean developmental stages (Sundara Rajulu et Radha 1966). Myxobolus labracis Abdel-Aal, Badawy et Gattas, 2001 was reported from a cerambycid beetle (Courtesey of D. R. P. Hedrick and Parasitol. Res.).

The invertebrates known thus far as definitive hosts for actinospores are oligochaetes (mostly tubificids) from freshwater, and some from the marine environment. In marine polychaetes, actinospores of the tetractinomyxon type have been reported (Køie 2005a). A few actinospores have been found in marine sipunculids. The actinospore phases of only 32 myxosporean species from freshwater environment have been known, while only one was found in the genuinely marine environment (Ellipsomyxa gobii with stages in Nereis spp. – Koie et al. 2004).

Classification

The taxonomy which persists until now follows largely Lom and Noble (1984). The drawback is that the main criterion of classification is the spore morphology, namely the number and configuration of shell valves and polar capsules. This spore-based taxonomy is generally artificial, clearly at the family level and with quite vague boundaries between many genera such as Leptotheca and Ceratomyxa, Myxidium and Zschokkella, or between some species of Myxobolus and Thelohanellus. It also does not reflect the life cycle with alternation of hosts, morphology of actinospores within the definitive invertebrate hosts, host and tissue preferences and first of all, phylogenetic relationships as revealed by SSU rDNA analyses. All morphological features important in describing species in the myxospore and actinospore stage are listed in Lom and Arthur (1989) and Lom et al. (1997a).

Designation of a separate class, the Malacosporea, is in agreement with their forming a separate clade in a root-like position from which myxosporean clades diverge. However, in other respects the molecular approach does not in the least support the existing myxosporean taxonomy (Kent et al. 2001; I. Fiala, Inst. Parasitol. AS CR, České Budějovice, pers. comm. – see References). The two main myxosporean clades are not based on similarities of spore morphology of the taxa included but, surprisingly, according to freshwater or marine habitat of their hosts. Thus representatives of several genera (Myxidium, Sphaerospora, Zschokkella) are found within both major clades. These clades are subdivided into subclades, where the grouping of genera and species does not always correspond to spore structure. Several species having similar spores, i.e., belonging to the same genus, are distributed separately in phylogenetic trees, while species from morphologically different genera cluster together. The subclades follow to a great extent the coelozoic vs. histozoic way of life.

It would be beyond the scope of this introduction to deal in detail with all the subclades assigned to the two major clades in the above mentioned papers. We can just briefly mention that within the marine clade, according to Fiala (pers. comm.), Ceratomyxa species group together with Palliatius indecorus. Myxidium species, Auerbachia pulchra and Ellipsomyxa gobii cluster with Zschokkella magilis. Most (not all) of the Kudoa species analysed form what seems a monophyletic clade.

A rather basal phylogenetic position of coelozoic “marine” myxosporeans (e.g., species of the genera Auerbachia, Ceratomyxa, Enteromyxum or Palliatius – Fiala, pers. comm.) reminds of Shulman’s (1966) suggestion that myxosporeans were originally coelozoic in marine teleosts, from which they evolved to parasitize freshwater hosts.

In the large freshwater clade there are also groupings of genera and species opposing their morphology-based relationship. Thus freshwater coelozoic species of the genera Chloromyxum, Zschokkella and Myxidium cluster together with purely marine species of the genus Sphaeromyxa (Fiala, pers. comm.). In the group of Sphaerospora oncorhynchi, Myxidium lieberkuehni and Chloromyxum legeri (Kent et al. 2001; Fiala, pers. comm.) the coelozoic way of life is the unifying element, while spore morphology is different. Interestingly, histozoic species of Myxobolus and Henneguya form branches that are often close to each other (Cone and Easy 2005; Fiala, pers. comm.).

However preliminary the categories indicated in the clades may be, they might suggest the future outlines of the classification. It would be desirable to find some other features, in addition to molecular analysis, to support them. Histozoic parasitism must have evolved several times both in marine and freshwater fishes and it is only to some extent indicative of evolution of pertinent taxa.

The reliability of the cladograms of course depends on correct identification of the species sequenced, which may not be always safe (e.g., sequences of the “marine” species Myxobolus muelleri or M. exigus in GenBank).
The molecular data, being still very incomplete and based on a single gene, are far from being sufficient to launch a well substantiated new classification – a situation similar to that in microsporidia (Vossbrinck and Debrunner-Vossbrinck 2005, Larsson 2005). Future classification of Myxosporea should represent a synthesis of molecular phylogeny and the combined evidence of both life-cycle stages, if known (Xiao and Desser 2000). Taxonomic relationship of a myxosporean should also take into account tissue tropism (Molnár 2002), which may reflect rRNA grouping of the species in question (Andree et al. 1999). Also geographic origin may be decisive, as Hervio et al. (1997) have shown in Kudoa species, which cluster according to such origin rather than by spore morphology. The matter is not yet settled; more recently, Yokoyama and Itoh (2005) have shown that the degree of sequence similarity does not comply with geographic distribution. Andree et al. (1999), working with species of the genus *Myxobolus*, found that morphological features are not necessarily good indicators of true genetic relationship at the species level, which also applies to species of other genera. Host specificity should also be considered; it may be strict in some species but rather wide in others (Nielsen et al. 2002).


Considering this very complicated situation, we retain for the time being the existing classification, preferring it to a merely alphabetical listing of genera compiled under a similarly confusing situation in microsporidians (e.g., Canning and Vávra 2000, Lom 2002). We list in the following text updated definitions of all myxosporean genera with remarks, which might be relevant for better understanding the organisms, and add some references, which can serve as sources of further information. In most genera, in addition to the type species, we list pathogenic species important in contemporary pisciculture and for sport fisheries in freshwater or sea. Names of the fish hosts follow Froese and Pauly (2005).


**Myxosporean genera**

According to Shulman (1966), there were 731 species of myxosporeans; as of October 2005, 60 genera with 2,180 species have been recorded, many of them regrettably established without complete morphological or molecular data. In this current classification only named species are considered. Most of these species can not be properly revised until there is sufficient resolution provided both by detailed morphological study and molecular analysis, so that numbers given for each genus may eventually be lower or perhaps even higher. Certainly, a large number of species still remain to be discovered.

**ORDER BIVALVULIDA** Shulman, 1959

Spore shell is composed of two valves meeting in one circumsporal line of dehiscence or suture. Spore contains two, sometimes four or rarely one polar capsule, and one, rarely two sporoplasms.

**SUBORDER SPHAEROMYXINA** Lom et Noble, 1984

Polar filament is short, and at variance with all other Myxosporea, not tube-like but flat, being very broad at the base and gradually tapering to the end. In the polar capsule it is folded several times instead of being spirally wound. Plasmodia are coelozoic in the gall bladder of marine fishes. The separateness of this suborder has thus far not been confirmed by SSU rDNA analysis.

*Spheromyxa* Thélohan, 1892

With characters of the family. Number of species: 39

References: fine structure – Lom (1969), list of species – Lom (2004). Type species *Spheromyxa balbiana* Thélohan, 1892 (Fig. 3); originally recorded hosts (without specification of the type host) are *Gaidropsarus vulgaris* (syn. *Motella tricirrata* and *M. maculata*), *Cepola macrophthalmalma* (syn. *C. rubescens*); later found also in other host species in the Mediterranean Sea and in the Atlantic Ocean off European coasts.

**SUBORDER VARIISPORINA** Lom et Noble, 1984

Polar capsules —one or two, sometimes four—are in various positions in the spore. When they are located at one pole of the spore they do not lie solely in the sutilar plane or they may lie in a plane perpendicular to it. Mostly coelozoic, most of the genera live in marine fishes.

*Myxidiidae* Thélohan, 1892

Spores mostly elongated, spindle-shaped, sigmoid or crescent-shaped, some are almost semicircular in valvular view. Generally two polar capsules in opposite ends discharge terminal or more or less laterally. The longitudinal sutilar line is straight, curved or sigmoid. As a rule coelozoic, rarely histozoic parasites in marine and freshwater fishes.
Myxidium Bütschli, 1882

Synonym: Cystodiscus Lutz, 1889

Sporo- cores are generally fusiform, straight or slightly crescent or even sigmoid, with more or less pointed ends. Shell valves smooth or with ridges, suture line bicuspid the spore. Two polar capsules, mostly pyriform, lie one at each end of the spore. Capsular foramina are situated in the sutureal plane, at or near the end of the spore and open as a rule in opposite directions. The bimuculeate sporoplasm lies between the capsules. The species are typically coelozoic (rarely histozoic), forming small or large trophozoites, mono- or polysporic, the latter with pansporoblast formation. The heterogeneity of the genus is illustrated by representation in different phylogenetic clades and by development into actinospores of different collective groups. A total of 205 species infect marine and freshwater fishes with 8 species in amphibians and 4 in reptiles.

In only one species has the complete developmental cycle been experimentally revealed: in Myxidium giardi the actinospore stage is aurantiactinomyxon (Benajiba and Marques 1993). Molecular analysis identified a raabea type with M. truttae (Holzer et al. 2004).

References: species reported from eels in Hine (1980); list of species in Jayasri and Hoffman (1982); fine structure in Benajiba et al. (1993) and Canning et al. (1999a).

Type species: Myxidium lieberkuehni Bütschli, 1882 (Fig. 4); type host Esox lucius, site of infection is the urinary tract; in the whole Holarctic region with prevalence often up to 100% (Lom et al. 1989).

Pathogenic species: Myxidium truttae Léger, 1931 causes serious infections of bile ducts and liver of salmonoids in Eurasia (McGeorge et al. 1996a, b).

Enteromyxum Palenzuela, Redondo et Alvarez-Pellitero, 2002

Fig. 5

Sporo- cores slightly crescent-shaped; very large and elongated polar capsules taper to their distal side and open at the ends of the spore. They discharge in opposite directions relative to the longitudinal plane, bisecting the spore in top or bottom view. The rather inconspicuous suture line is nearly transversal. One, binucleate sporoplasm. Spores develop in disporic pseudoplasmodia. Histozyotic parasites in epithelia of digestive tract (including sometimes the gall bladder) of marine fishes causing acute enteritis, cachexia and death in susceptible fish. Number of species: 3.

Type species Enteromyxum scophthalmi Palenzuela, Redondo et Alvarez-Pellitero, 2002 (Fig. 5) causes enteritis and death of turbot Psetta maxima (syn. Scophthalmus maximus) cultured in Spain. Experimental direct transmission was successful (Redondo et al. 2004).

Pathogenic species: Enteromyxum fugu (Tun, Yokoyama, Ogawa et Wakayabashi, 2002) Yanagida, Nomura, Kimura, Fukuda, Yokoyama et Ogawa, 2004 (syn. Myxidium fugu) and Enteromyxum sp. described by the later authors are agents of emaciation disease in maricultures of Takifugu rubripes in Japan. They can also be transmitted directly from fish to fish in sea cages (Yasuda et al. 2002). E. leei (Diamant, Lom et Dykova, 1994) Palenzuela, Redondo et Alvarez-Pellitero, 2002 (syn. Myxidium leei), a pathogen in the intestine of Sparus aurata and many other sparid fishes (Padros et al. 2001), has according to Diamant (1997) a unique, direct transmission from fish to fish, in which, however, not spores but proliferative stages releasing infective cells may be instrumental (Branson et al. 1991).

Zschokkella Auerbach, 1910

Synonym: Parazschokkella Kalavati et Narasimhamurti, 1987

Sporo- cores ellipsoidal in sutural view and slightly bent or semi-circular in valvar view, with rounded or bluntly pointed ends. Shell valves smooth or with ridges. The suture is straight, curved or sinuous. Polar capsules almost spherical, open slightly subterminally and both to one side; the sporoplasm is binucleate. Trophozoites disporic to polysporic, the latter with pansporoblast formation. The genus with species represented in different phylogenetic clades is heterogeneous in forming different actinospore stages. In the future it may be split in several genera. Morphological distinction between the genera Myxidium and Zschokkella is sometimes extremely difficult; e.g., some important diagnostic features of Myxidium triangulum Shulman, 1962 or M. monstruosum Shulman, 1962 assign it to Zschokkella, while e.g., Zschokkella costata Kashkovsky, 1965 has features of Myxidium. Molecular analysis does not help too much thus far – some species of both genera cluster together, some are wide apart (Fiala, pers. comm.). The total of 68 species (mostly coelozoic, exceptionally histozyotic) in marine and freshwater fishes, 2 additional species in amphibians and 2 in reptiles.

In two species only the complete developmental cycle was revealed: in Zschokkella nova the actinospore stage is a siedleckiella (Usponskaya 1995) and in Zschokkella sp. an echinactinomyxon (Yokoyama et al. 1991).


Type species Zschokkella hildae Auerbach, 1910 (Fig. 6) described originally from the urinary bladder of Physic bien- noides, Gadus morhua (syn. G. callarias) and Pollachius virens (syn. Gadus virens) without specification of the type host was also found in some other gadid fishes in North European seas and the Atlantic.

Pathogenic species: Zschokkella ictericia Diamant et Pappena, 1992 causes cholestasis and bile duct breakdown in Siganus luridus from the Red Sea. It may also invade liver parenchyma (Diamant and Pappena 1992).

Coccomyxa Léger et Hesse, 1907

Fig. 7

Sporo- cores ellipsoidal rounded in transverse section, with a single elongated polar capsule (the second presumably lost), which opens in the suture plane. Sutural line sigmoid, sporoplasm binucleate. Trophozoites are mono- or polysporic. Based on SSU rDNA sequences, species of this genus are phylogenetically closely related to Zschokkella and Enteromyxum (Diamant and Palenzuela 2005). Coelozoic in marine fishes, one species histozyotic (C. hoffmani Cheung et Nigrelli, 1990 in gill cartilage of Platysus anguillaris). Number of species: 13.

Type species Coccomyxa morovi Léger et Hesse, 1907 (Fig. 7) from the gall bladder of Sardina pilchardus from the Mediterranean and Celtic Seas and the English Channel.

Ortholineidae Lom et Noble, 1984

Sporo- cores to irregularly ellipsoidal and bilaterally symmetrical along the straight sutural line. Two anteriorly located polar capsules shifted widely sidewise in the sutural plane. Capsular foramina are directed away from each other at a certain angle. Binucleate sporoplasm in the posterior part of the spore. Coelozoic, mono- to polysporic plasmodia, in marine and freshwater fishes. The assignment of the genera Neo- myxobolus and Triangula to the family is rather tentative.
Ortholinea Shulman, 1962

Sporangia have a single spore, which may be slightly flattened parallel to the sutural plane or may be pointed posteriorly. Polar capsules are suberophilous to parapyriform. Coelozoic, in the urinary system of marine fishes. Number of species: 12.

Type species Ortholinea divergens (Thélohan, 1895) Shulman, 1962 (Fig. 8) in the urinary system of Lipophrys pholis (syn. Bliennius pholis) and Symphodus melops (syn. Crenilabrus melops) from the northern coast of France, also infects other marine fishes.

Neomyxobolus Chen et Hsieh, 1960

Sporooids, in valvular view wider than long. Anterior end flattened, posterior semicircular, flattened parallel to the sutural plane. Binucleate sporoplasm may contain an idionophilous vacuole. In the urinary tract of freshwater fishes. Number of species: 3.

Type species Neomyxobolus ophiocephalus Chen et Hsieh, 1960 (Fig. 9) in the urinary system of the freshwater fish Channa argus (syn. Ophiocephalus argus) and C. maculata (syn. O. maculatus) in China.

Cardimyxobolus Ma, Dong et Wang, 1982

Sporangia in the frontal view oval, with one side very vaulted and with sutural markings along the posterior border; spindleshaped in sutural view. Suberophilous polar capsules. Shell valves are smooth, in the sporangium is an idionophilous vacuole. Polysporic plasmodium is histozoic. Number of species: 2. A thorough differentiation from Neomyxobolus is still needed.

Type species Cardimyxobolus leshanensis Ma, Dong et Wang, 1982 (Fig. 10) in the gills of Garra imberba (syn. G. pingi) in China.

Triangula Chen et Hsieh, 1984

Sporangia triangular but very rounded, anterior end wider; they are flattened parallel to the sutural plane. Their surface is smooth, polar capsules suberophilous, binucleate sporoplasm contains an idionophilous vacuole. Histozoic, polysporic plasmodium in freshwater fishes. Number of species: 3.

Type species Triangula yangiokangensis Chen et Hsieh, 1984 (Fig. 11) in the skin and gills of Rhinogobius gurinus and Rhodeus lighti (syn. Pseudoperilampus lighti) in China (Chen and Hsieh 1984a).

Azevedo et al. (2005) proposed a new genus Triangulamyxa with a single species T. amazonica Azevedo, Corral et Matos, 2005 (Fig. 12) forming coelozoic plasmodia attached to the surface of the intestine of Amazonian freshwater fish Sphaeroides testudineus. The differences from Triangula are, however, not very pronounced (histozoic vs. coelozoic plasmodia, smooth vs. wrinkled spore surface so that the independence of Triangulamyxa warrants confirmation.

Kentmoseria Lom et Dyková, 1995


Elongated spores, wider anteriorly than posteriorly, slightly flattened parallel to the straight suture. Pointed projections extend backwards from the posterior half of the smooth shell valves. Pyriform polar capsules open laterally. Plasmodia mono- to disporic, coelozoic in the urinary tract of marine fishes.

Type and only species Kentmoseria alata (Kent et Moser, 1990) Lom et Dyková, 1995b (syn. Paraortholinea alata Kovaleva, 1997) (Fig. 13) described from lumina of renal tubules and collecting ducts of the marine fish Chaetodon rainfordi from the Great Barrier Reef off Australia.

Sinuolineidae Shulman, 1959

Sporangia have a single spore, which may be oval or inversely pyramidal, may have caudal or lateral projections. Two spherical or suberophilous polar capsules are anteriorly located and set apart, sometimes even at opposing sides of the spore; the plane connecting them is perpendicular to the mostly sinuous or meandering sutural line which often appears as a figure “8”. Plasmodia mono- to polysporic, located in the urinary system of marine fishes.

Sinuolina Davis, 1917

Sporangia have a single spore, which may be oval or inversely pyramidal, may have caudal or lateral projections. Two spherical or suberophilous polar capsules are anteriorly located and set apart, sometimes even at opposing sides of the spore; the plane connecting them is perpendicular to the mostly sinuous or meandering sutural line which often appears as a figure “8”. Plasmodia mono- to polysporic, located in the urinary system of marine fishes.

Davisia Laird, 1953

Sporangia have a single spore, which may be oval or inversely pyramidal, may have caudal or lateral projections. Two spherical or suberophilous polar capsules are anteriorly located and set apart, sometimes even at opposing sides of the spore; the plane connecting them is perpendicular to the mostly sinuous or meandering sutural line which often appears as a figure “8”. Plasmodia mono- to polysporic, located in the urinary system of marine fishes.

Myxoproteus Doflein, 1898

Synonym: Conispora Sakurathi, 1977

Sporangia have a single spore, which may be oval or inversely pyramidal, may have caudal or lateral projections. Two spherical or suberophilous polar capsules are anteriorly located and set apart, sometimes even at opposing sides of the spore; the plane connecting them is perpendicular to the mostly sinuous or meandering sutural line which often appears as a figure “8”. Plasmodia mono- to polysporic, located in the urinary system of marine fishes.

Bipteria Kovaleva, Zzhchenko et Krasin, 1983

Sporangia have a single spore, which may be oval or inversely pyramidal, may have caudal or lateral projections. Two spherical or suberophilous polar capsules are anteriorly located and set apart, sometimes even at opposing sides of the spore; the plane connecting them is perpendicular to the mostly sinuous or meandering sutural line which often appears as a figure “8”. Plasmodia mono- to polysporic, located in the urinary system of marine fishes.

Paramyxoproteus Wierzbicka, 1986

Like Bipteria, but with pointed projections are shaped like stiff, keel-like, meridionally running membranes. The suture line runs obliquely to the plane of the two polar capsules; in the original description, its course cannot be unambiguously discerned, so that the status of the genus warrants further study.

Type species *Paramyxoproteus reinhardtii* Wierzbia, 1986 (Fig. 18) described from the urinary bladder of *Reinhardtus hippoglossoides* in the Atlantic off Labrador and in the Barents Sea.

**Neobipteria** Kovaleva, Gaevskaya et Krasin, 1986  
Like *Bipteria*, but with keel-like extensions running meridionally along the sutural line. Type and only species *Neobipteria macrouri* Kovaleva, Gaevskaya et Krasin, 1986 (Fig. 19) in the urinary bladder of *Coryphaenoides acrolepis* in the Bering Sea and in the Pacific off Kuril Islands.

**Schulmania** Kovaleva, Zubchenko et Krasin, 1983  
Differs from *Bipteria* in having sometimes straight sutural line, mono- or disporic trophozoites and mainly four longitudinal, keel-like, stiff membranes. Two of them run along the sutural line, two others extend along the middle line of each shell valve. Number of species: 10.

Type species *Schulmania ovale* Kovaleva, Zubchenko et Krasin, 1983 (Fig. 20) described from the urinary bladder of marine fish *Lycodes esmarkii* in the Atlantic Ocean off the Newfoundland and Labrador coasts.

**Noblea** Kovaleva, 1989  
Spores inversely pyramidal and rounded. Two keel-like membranes extend along the slightly wavy sutural line; two thickening adheres to but are slightly raised off the apex of the spore. Wide ends of the thickenings cover the polar capsules and the tapering ends extend backwards along the spore surface. Plasmodia mono- or disporic.

Type and only species *Noblea admiranda* Kovaleva, 1989 (Fig. 21) described from the urinary bladder of freshwater fish *Lycodes esmarkii* in the Atlantic Ocean off the Canadian Atlantic coast at Sable Island.

**Fabesporidae** Naidenova et Zaika, 1969  
Spores have valves elongated in the direction perpendicular to the plane of the central transverse sutural line. Two polar capsules in the opposite spore ends discharge terminally or laterally. Coelozoic in marine fishes. There are at least five species from freshwater hosts, obviously derived from marine ancestors: *Ceratomyxa angulata* Tuzet et Ormières, 1957 from the gall bladder of *Anguilla anguilla* from Mediterranean brackish waters, *C. hilsae* Chakravarty, 1943 from the gall bladder of the anadromous Indian fish *Tenualaosa ilisha* (syn. *Hilsa ilisha*), *C. hongkongensis* Hsieh et Chen, 1984 from the gall bladder of *Pelteobagrus eupogon* (syn. *Pseudobagrus eupogon*) from China, *C. hungarica* Molnár, 1992 from Bowmann’s capsules and renal tubules of freshwater goby *Proterorhinus marmoratus* from the Danube river basin, and *C. shaeta* Noble, 1950. The latter is a dangerous pathogen of North American salmonids, histozoic in the digestive tract (Margolis and Evelyn 1975, Bartholomew 1998). Although it adapted to a freshwater fish, phylogenetic analysis based on the SSU rDNA places it in the clade of marine myxosporidians (Kent et al. 2001). Its action stage, a tetractinomyxon, lives in a benthic freshwater polychaete, *Manyunkia speciosa* (Bartholomew et al. 1997). Number of species: 172.

References: Bartholomew et al. (1989); partial list of species – Aseeva (2003), ultrastructure and development of the piscine phase – Cho et al. (2008).

Type species *Ceratomyxa arcuata* Thélohan, 1892 (Fig. 24) originally described from the gall bladder of *Gaidropsarus vulgaris* (syn. *Motella tricirrata*), *Symphodus melops* (syn. *Crenilabrus melops*), *Pagellus bogaraveo* (syn. *P. centrodontus*), *Scorpaena porcus* and *S. scrofa* in the Mediterranean.

Other pathogenic species: *Ceratomyxa sparsaurati* Sitjà-Bobadilla, Palenzuela et Álvarez-Pellitero, 1995 (Fig. 25) inflicts damage in the gall bladder of cultured *Sparus aurata* (Palenzuela et al. 1997).

**Leptotheca** Thélohan, 1895  
Spores oval, ellipsoid, sometimes arcuate. The length of the individual laterally prolonged shell valve — as measured from the midpoint of the suture to the most distant point of the valve — does not exceed the axial diameter of the spore (i.e., a difference from *Ceratomyxa*) but significantly exceeds one half of this diameter. In some cases, the distinction between *Ceratomyxa* and *Leptotheca* is quite problematic. Sporoplasm often fills the spore cavity completely; usually one binucleate but sometimes two uninucleate sporoplasmic stages. Trophozoites generally disporic. Species coelozoic in the gall bladder or urinary system in marine fishes, rarely histozoic. Number of species: 56, one of which in the urinary system of amphibians and one in reptiles.

Type species *Leptotheca agilis* (Thélohan, 1892) Thélohan, 1895 (Fig. 26) originally described from the gall bladder of marine fish *Dasytis pastinaca* (syn. *Trygon pastinaca*) and of a species of the genus *Scorpaena* along the French coast.
Sphaerospora Davis, 1917

Spores generally spherical or sub-spherical, sometimes rounded pyramidal with tapering anterior end or slightly elongated, often with appendages. Two polar capsules open at the anterior tip and are situated in a plane perpendicular to the straight sutural line. Trophozoites mono- or disporic, less often polyosphoric. Mostly coelozoic in marine and freshwater fishes, sometimes histozoic.


Sphaerospora Thélohan, 1892

Synonym: Podospora Chen et Hsieh, 1984

Spherical or sub-spherical spores, valvar diameter equals and only in a few species significantly exceeds the sutural diameter. Valves smooth or ridged, often with posterior or lateral protuberances or bumps, like in S. plagiognathopsis (Chen et Hsieh, 1984). The sutural ridge often prominent, polar capsules sub-spherical or pyriform. Two uninucleate sporoplasms. Mono- or disporic trophozoites are coelozoic, mainly in the urinary system of freshwater and marine fishes, some are histozoic. In its present conception, the genus is polyphyletic, with species distributed in different freshwater and marine clades. Coelozoic species from the urinary system usually seem to be host specific and have easy to find pre- and extrasporegonic stages in definitive hosts, polychaetes of the genus Nereis (Kie et al. 2003a, Kie et al. 2004).

Polysporoplasma Sitjá-Bobadilla et Alvarez-Pellitero, 1995

Diffsers from Sphaerospora in having many uninucleate sporoplasms; 4 to 12 are observed in one plane of section. Disporous pseudoplasmodia in urinary tract and kidney tissue.

Number of species: 2.

Type species Polysporoplasma sparis Sitjá-Bobadilla et Alvarez-Pellitero, 1995 (Fig. 31), a serious pathogen in glomeruli, tubuli or connective tissue of trunk kidney of Sparus aurata in fish farms at the Atlantic and Mediterranean coasts of Spain (Palenzuela et al. 1999).

Hoferrhut Berg, 1898

Synonyms: Hoferia Dolefin, 1898; Mitrasporsa Fujita, 1912

Spores in valvar view pointed, mitre-like or completely rounded, with many stiff filaments at the posterior end. Polar capsules pyriform, sporoplasmin binucleate, trophozoites polysporic, without pansporoblast formation. Complete life cycle revealed in two species. Coelozoic in the urinary system of freshwater fishes, some with conspicuous intracellular development. Number of species: 25, one of which is pathogenic in frogs (Mutschmann 2004).

The taxonomy of Hoferrhut, as based on Kudo (1919), is a puzzle: how could have Berg (1898) in a short note in Buenos Aires established a genus without marking out as a type species, the only species, of the genus known at that time (1919)? To avoid further confusion, let us consider the genus as proposed by Kudo (1919) for the time being a nomen conservandum.

References: discussion on taxonomy – Lom (1986); fine structure – Lom et al. (1986).

Type species Hoferrhut cyprini (Dolefin, 1898) Mercier, 1908 (Fig. 32) is a common pathogen in the urinary system of common carp, Cyprinus carpio in Eurasia. Actinosporofase represented by aurantiactinomyxon stage (Grosheider and Körtig 1992). Hoferrhut carassii Khmerov, 1960 in the kidney of Carassius auratus auratus in Eurasia and North America. In Asia and USA it is the agent of goldfish kidney enlargement disease, known as “kidney bloater” (Ahmed 1974, Molnár et al. 1989, Trouillier et al. 1996). Actinosporofase phase found to be an aurantiactinomyxon (according to El-Matbouli et al. 1992a) or neoactinosporus stage (Yokoyama et al. 1993); this indicates the uncertain identification of this species.
**Wardia** Kudo, 1919

Spores oval in valvular view but resemble a double isosceles triangle with two convex sides in sutural view and flattened perpendicularly to the sutural plane. Fine ridges on the surface of the valves run into fringe-like processes at the posterior end. Large polar capsules in the central part of the spore open at the anterior tip of the spore. Large, histoizic polysporic plasmodia appear like cysts. The status of the genus has to be re-examined to exclude identity with *Sphaerospora*. Number of species: 3 in freshwater fishes.

Type species *Wardia ovinocuca* Kudo, 1919 (Fig. 33) described from oocytes and connective tissue in ovaries of *Leptomis humilis* in Illinois, USA.

**Palliatus** Shulman, Kovaleva et Dubina, 1979

Spores subspherical, with anteriorly prominent sutural ridge and enveloped in a membranaceous veil, which in immature spores is twisted in two cords around the spore. Polar capsules pyriform, sporoplasm bincnucleate. Coelozoic trophozoites in the gall bladder of marine fishes produce 1 to 6 disporic pansporoblasts. Contrary to morphology of spores, phylogenetic analysis showed the genus as closely related to *Ceratomyxa* (Fiala, pers. comm.). Number of species: 6.

Type species *Palliatus mirabilis* Shulman, Kovaleva et Dubina, 1979 (Fig. 35) in the gall bladder of the marine fish *Xenodermichthys copei* (syn. *X. socialis*) off Guinea-Bissau. Unpublished data suggest the existence of more species.

Subspherical spores with smooth valves, each extending into a stout, tapering caudal projection. Plasmodia polysporic with pansporoblast formation. One species was observed in kidneys of freshwater fishes, one in the amphibian *Mobige cristata*. Unpublished data suggest the existence of more species.

Type species *Caudomyxum nanum* Bauer, 1948 (Fig. 38) described from renal tubules of *Lota lota* in rivers of the European and Siberian part of the former USSR.

**Agarella** Dunkerly, 1915

Spores elongate ovoid, very slightly flattened parallel to the sutural line. Each valve extends into a caudal projection. Four pyriform polar capsules, of which two are larger with a long, narrow anterior neck and two smaller, shorter ones, with one of each in each shell valve. Histoizic polysporic plasmodia in freshwater fishes.

Type and only species *Agarella gracilis* Dunkerly, 1915 (Fig. 39) described from the testes of the freshwater fish *Lepidosiren paradoxa* in Brazil. One unidentified species was found in a Surinam frog.

**Auerbachia** Evdokimova, 1973

Spores have asymmetrical unequal smooth shell valves and a single elongated polar capsule with a filament making a few longitudinal turns. Coelozoic, polysporic plasmodia in the gall bladder of marine fishes.

**Auerbachia** Meglitsch, 1968

Spores club-like, with a broad anterior part and a narrow caudal part. The two unequally large shell valves are asymmetrical, dissimilar in form and meet along a curved, very indistinct suture; the larger valve is drawn into a wide caudal projection. Polar capsule opens at the anterior end of the spore. Sporoplasm binucleate. Large polysporic plasmodial. Number of species: 3.

Type species *Auerbachia anomala* Meglitsch, 1968 (Fig. 40) in the gall bladder of the deep-sea fish *Gymnopus bla-codes* off the coast of New Zealand.
Figs. 28–49. Line drawings of myxosporean spores. Fig. 28. *Ellipsomyxa gobii* in apical (a) and sutural view (b) (courtesy of M. Koie and Folia Parasitol.). Fig. 29. *Sphaerospora elegans*, pitted spore surface (a), sutural view (b) (courtesy of Dr. S.W. Feist and Eur. J. Protistol.). Fig. 30. *Sphaerospora renicola* in sutural view. Fig. 31. *Polysporoplasma sparis* in sutural view (courtesy of Drs. Sitjà-Bobadilla and Alvarez-Pellitero and Eur. J. Protistol.). Fig. 32. *Hoferellus cyprini* in sutural view. Fig. 33. *Wardia ovinoca*. Fig. 34. *Myxobilatus gasterostei* in sutural view. Fig. 35. *Palliatus mirabilis* in sutural view. Fig. 36. *Chloromyxum leydigii* in sutural (a) and frontal view (b). Fig. 37. *Chloromyxum cristatum* in apical view. Fig. 38. *Caudomyxum nanum*. Fig. 39. *Agarella gracilis*. Fig. 40. *Auerbachia anomala* (from Meglitsch 1968, courtesy of Proc. Iowa Acad. Sci.). Fig. 41. *Globospora sphaerica*. Fig. 42. *Alatospora samaroidea*. Fig. 43. *Pseudoulatospora scombri*. Fig. 44. *Renispora simae* (courtesy of Dr. C. Kalavati et al. and Syst. Parasitol.). Fig. 45. *Parvicapsula asymmetrica* (modified from Shulman and Shulman-Albova 1953). Fig. 46. *Neoparvicapsula ovalis*. Fig. 47. *Myxobolus muelleri*. Fig. 48. *Spirosuturia carassii* in frontal (a) and apical view (b). Fig. 49. *Unicauda clavicaua*. 
**Globospora** Lom, Noble et Laird, 1975  
Subspherical spores have unequal smooth shell valves meeting along a curved, delicate suture. Capsular opening at some distance from sutural line.

Type and only species *Globospora sphaerica* (Evdokimova, 1973) Lom, Noble et Laird, 1975 (Fig. 41) lives in *Odontesthes incisa* (syn. *Austroatherina incisa*) off Argentina coast. Sporogenic plasmodium was not observed.

**Alatosporidae** Shulman, Kovaleva et Dubina, 1979

Spores in sutural view shaped like a double isosceles flat triangle. The long tips are set perpendicularly to the central sutural line, short tips are oriented in continuation of the suture. Two polar capsules are set in a plane perpendicular to the suture. Shell valves bear conspicuous wing-like projections. Coelozoic in gall bladder of marine fishes.

**Alatospora** Shulman, Kovaleva et Dubina, 1979  
Fig. 42

Spores extremely elongated in plane perpendicular to the central straight suture line. Shell valves bear wing-like membranaceous projections adhering along their posterior half. Polar capsules small. Disporic to polysporic trophozoites in the gall bladder. Number of species: 17.

Type species *Alatospora samaroides* Shulman, Kovaleva et Dubina, 1979 (Fig. 42) in the gall bladder of *Chlorophthalmus atlanticus* off the Atlantic coast of Africa.

**Pseudoalatospora** Kovaleva et Gaevskaya, 1983  
Fig. 43

Spores similar to *Alatospora* differ in having their valve projections doubled to form parachute-like pockets. Trophozoites mono- to disporic. Number of species: 12.

Type species *Pseudoalatospora scombrii* Kovaleva et Gaevskaya, 1983 (Fig. 43) was described from the gall bladder of *Scomber japonicus* from the South-Eastern Pacific.

**Renispora** Kalavati, Longshaw et MacKenzie, 1996  
Fig. 44

Reniform spores have a transverse sutural line. Shell valves have laterally extending alate processes adhering all around the valves. Pyriform polar capsules situated close to sutural line in a plane perpendicular to it. Polysporic plasmodia, coelozoic in gall bladder.

Type and only species *Renispora simae* Kalavati, Longshaw et MacKenzie, 1996 (Fig. 44) in *Patagonotothen sima* from the Atlantic Ocean off the Falkland Islands.

**Parvicapsulidae** Shulman, 1953

Spores asymmetrical, thin-walled, elongated roughly in sutural plane. Unequal shell valves meet in a curved suture. Two or four conspicuously small polar capsules in the suture apex. Trophozoites disporic to tetrasporic. Coelozoic in the urinary system or histozoic in marine and anadromous fishes.

**Parvicapsula** Shulman, 1953  
Fig. 45

Spores elongated, asymmetrical, somewhat curved. Two small pyriform polar capsules located anteriorly but discharge sideways. One relatively large binucleate sporoplasm. Disporic trophozoites coelozoic in the urinary system or histozoic in kidneys. Number of species: 10. A survey of species was published by Koe (2003b).

Type species *Parvicapsula asymmetrica* Shulman, 1953 (Fig. 45) in the urinary bladder of *Cyclopterus lumpus* in the White Sea.


**Neoparvicapsula** Gaevskaya, Kovaleva et Shulman, 1982  
Fig. 46

The main difference from *Parvicapsula* is the presence of four small pyriform polar capsules in a cross-like arrangement in the suture apex. Trophozoites di- to tetrasporic, coelozoic in the urinary system of marine fishes. Number of species: 2.

Type species *Neoparvicapsula ovalis* Kovaleva, Gaevskaya et Shulman, 1982 (Fig. 46) in the urinary system of *Gobionotothen giberifrons* (syn. *Notothenia giberifrons*) from the South Atlantic.

**SUBORDER PLATYSPORINA** Thélohan, 1892

The suture forms an elevated ridge and may be drawn out as long posterior projections. One of the two polar capsules may be smaller or disappear completely. Spores in most species have a spherical polysaccharide inclusion (iodinophilous vacuole) in the sporoplasm.

**Myxobolus** Bütschli, 1882  
Fig. 47

Synonyms: *Myxosoma* Thélohan, 1892; *Lentospora* Plehn, 1905; *Disparospora* Akhmerov, 1954; *Facieplatycauda* Wyatt, 1979; *Rudicapsula* Kalavati et Narasimhamurti, 1984

Spores in valvular view ellipsoid, ovoid or rounded, in sutural view biconvex. Shell valves as a rule smooth. Two polar capsules mostly pyriform, sometimes unequal, exceptionally one seems to be missing. The sutural ridge may extend posteriorly onto a crescentic ledge. Sporoplasm binucleate, often with an iodinophilous vacuole. Trophozoites as a rule large, with formation of numerous pansporoblasts and appear in the tissue-like cysts. Generally histozoic in freshwater fishes. About 30 species live in marine (mostly estuarine) fishes, some of them have coelozoic plasmodia of far less compact structure than histozoic trophozoites (e.g., *M. conei* Lom et Dyková, 1994). Future research may assign—at least partly—marine and freshwater species to different genera. Many species seem to be host- and tissue-specific, while others have been reported to indiscriminately infect many hosts and various tissues, an issue, which has to be verified. Number of species: 792, including 7 in amphibians.

Description of the monotypic genus *Gyrospora* Qadri, 1962 is not complete enough to permit a safe differentiation from *Myxobolus*; it was described as having polar filaments.
with a very thick basal part (Qadri 1962b). Thus far, complete developmental cycles have been described for 14 species. In Myxobolus cerebralis (discovered by Wolf and Markiw 1984), M. cotti (El-Matbouli and Hoffmann 1989), M. carassii (El-Matbouli and Hoffmann 1993), M. arcticus (Kent et al. 1993, Urawa 1994), M. drjagini (El-Mansy and Molnár 1997a), M. portucaleensis (El-Mansy et al. 1998), M. hungaricus (El-Mansy and Molnár 1997b), M. pseudodispars (Szkely et al. 2001), M. branae (Esztuberger et al. 2000), M. macrocapsularis (Szkely et al. 2002) and M. parviformis (Kallert et al. 2005b) the actinospore stage is a triactinomyxon. In M. pavlovskii it is a hexactinomyxon (Ruidisch et al. 1991), in M. cul tus (Yokoyama et al. 1995) and in M. dispar it is raabeia (Molnár et al. 1999a, Holzer et al. 2004). The diversity of actinospore stages confirms the heterogeneity of the genus and should be reflected in its taxonomy in near future. Curiously, M. dispar and M. pavlovskii, with differing actinospore stages, cluster together in SSU rDNA phylograms (Fiala, pers. comm.).

References: list of species – Landsberg and Lom (1991); recent synopsis – Eiras et al. (2005), 49 species are missing in this list; list of North American species – Cone and Raesly (1995); molecular analysis – Cone and Easy (2005); molecular kinship vs. tissue specificity – Esztuberger (2004).

Type species Myxobolus muelleri Bütschli, 1882 (Fig. 47) originally described from gills and fins of Leuciscus cephalus from Germany. This name probably covers a conglomerate of more species, as evidenced by the great variability of spores, most varied tissues which it was claimed to infect, and especially a great number of hosts (more than 80 can be found in the literature!), mostly cyprinids from the whole Eurasia.


Spirosuturia Chen et Hsieh, 1984

Fig. 48

Differens from Myxobolus only by a strongly sinuous sutural line, slightly diverging from the plane in which the two polar capsules lie. A molecular revision is warranted. Histozoic in freshwater fish. Number of species: 3.

Type species Spirosuturia carassii Chen et Hsieh, 1984 (Fig. 48) lives in the wall of the urinary bladder of Carassius auratus in China.

Unicauda Davis, 1944

Fig. 49

Sporos similar to those of Myxobolus have a single caudal appendage. This, unlike in Henneeguya, is no prolongation of the shell valves but a structure made up from different, not yet precisely specified material and adheres to the shell valve along a distinct boundary. Strictly histozoic in freshwater fishes. Twenty-seven species, of which in about 16 is not known whether the appendage really corresponds to the definition of the genus.


Type species Unicauda clavicauda (Kudo, 1934) Davis, 1944 (Fig. 49) in subcutaneous tissue of Notropis gunnius from Illinois, USA.

Dicauda Hoffman et Walker, 1978

Fig. 50

It differs from Unicauda by two caudal appendages, extending in opposing directions.

Type and only species Dicauda atherinoidei Hoffman et Walker, 1978 (Fig. 50) in subcutaneous tissue of freshwater fish Notropis atherinoidei from USA.

Phlogospora Qadri, 1962

Fig. 51

Drop-like, flattened spores have a bifurcated caudal process fitted to the posterior end along a distinct boundary. There is a single, elongated polar capsule. Binucleate sporoplasm with polysaccharide reserves in form of a spherical inclusion. Vegetative stages unknown. Number of species: 3.

Type species Phlogospora mysti Qadri, 1962 (Fig. 51) is a histozoic parasite of the gills of freshwater fish Mystus bleekeri from India (Qadri 1962a).

Laterocaudata Chen et Hsieh, 1984

Fig. 52

Sporos similar to those of Myxobolus are ellipsoid in val-

ular view and have a long, thin and curved process split at the end. The process originates posterior laterally from the sutural edge of the valves. Plasmodium was not described.

Type and only species Laterocaudata mastacembala Chen et Hsieh, 1984 (Fig. 52) was described from the gills of freshwater fish Macragnostus aculeatus (syn. Mastacembelus acu- leatus) from China.

Henneeguya Thelohan, 1892

Fig. 53

Sporos ellipsoid, spindle-shaped or rounded in valcular view, biconvex in sutural view. Each valve continues as a caudal projection, both projections may be apposed. Shell valves smooth. Two polar capsules are as a rule very elongated. In the binucleate sporoplasm is usually a spherical polysaccharide inclusion. Polysporic plasmodia with paraphroblast formation usually large, appearing like cysts. Histo-
zoic in freshwater, sometimes marine fishes. Number of species: 204. The assumption of Kent et al. (2001) and Bahri et al. (2003) that Henneeguya is an invalid taxon is probably legiti- mate, since the distinguishing character, the two caudal pro-
jections, had probably arisen several times in the evolutionary
history of Myxobolus. This is supported by many species of both genera clustering together in SSU rDNA phylograms (Yokoyama et al. 2005, Eszterbauer et al. 2005).


Complete life cycle is known in three species: in Henneguya exilis the actinospore is an aurantiactinomyxon earlier described as A. janiiszewskai (Lin et al. 1999), in H. icatula the aurantiactinomyxon was earlier named as A. icatuli (Pote et al. 2000), in H. nuestini Schuberg et Schröder, 1905 it is a triactinomyxon (Kallert et al. 2005a). In the recent phylogenetic tree (Fiala, pers. comm.), H. exilis clusters separately from two other species mentioned above.

Type species Henneguya psorospermica Thélohan, 1892 (Fig. 53), common parasite in the gills of Esoc lucius and Perca fluviatilis, perhaps also Sander lucioperca (syn. Stizostedion lucioperca) in Eurasia (Dyková and Lom 1978).


Hennegoides Lom, Tonguthai et Dyková, 1991 (Fig. 54).

Unlike Henneguya the spores are asymmetrical with non-axially attached caudal appendages. Polar filament anisofilar, wound longitudinally in the polar capsules. Polysporic, without ponsporoblast formation. Number of species: 4.

Type species Hennegoides longitudinalis Lom, Tonguthai et Dyková, 1991 (Fig. 54) infects subepithelial layer in the intestine of cultured Osphronemus goramy in Thailand (Lom et al. 1991b).

Tetrauronema Wu, Wang et Jiang, 1988 (Fig. 55).

Sporos resemble those of Myxobolus, are posteriorly tapered and bear four thin, symmetrically arranged projections, one inserted at each side of the shell valve near the posterior end. Histozoic in freshwater fishes. Number of species: 2.


Type species Tetrauronema macropodus Wu, Wang et Ji-ang, 1988 (Fig. 55) in gill filaments of Macroopus opercularis (syn. M. chinensis) in Fujian province, China.

Thelohanellus Kudo, 1933 (Figs. 56, 57).

Sporos tear-shaped, pyriform to broadly ellipsoidal in valvular view, being more slender in sutural view. Always with smooth valves. A single polar capsule, either pyriform, tear-shaped with a single coil of polar filament, or subpherical with a second, inner coil. Thus the genus might well be split in two according to differences in spore morphology. Species of the genus Myxobolus with one capsule extremely stunted indicate the possible closeness of both genera, also suggested in some phylograms (Fiala, pers. comm.). Sporoplasm binucleate, mostly with a spherical polysaccharide inclusion. Polysporous plasmodia with ponsporoblast formation are mostly large. Histozoic parasites of freshwater fishes. Number of species: 75.

The complete life cycle is known in two species: in both T. hovorkai and T. nikolskii, aurantiactinomyxon stages occur (Yokoyama 1997 and Székely et al. 1998, respectively).

Type species Thelohanellus pyriformis (Thélohan, 1892) Kudo, 1933 (Fig. 56) was described from blood vessels of gills, spleen and kidney of Tinca tinca; also occurs in Rutilus rutilus, Abramis brama and some other cyprinids (Soltyńska 1967, Dyková and Lom 1987).

In Thelohanellus jiroveci Kundu et Haldar, 1981 from the gills of Labeo batá in India were reported macro- and microspores in the same plasmodium, a unique feature in myxospora.

Pathogenic species: Thelohanellus hovorkai Akhmerov, 1960 (Fig. 57), common in Cyprinus carpio of up to two years of age in Eurasia, forming plasmodia of up to 3 mm in size in connective tissue of various organs (digestive tract, kidney, swimbladder, subcutis and even brain); agent of haemorrhagic thelohanelliosis (Molnár and Kovacs-Gayer 1986a, Yokoyama et al. 1998 Liyanage et al. 2003). T. kitaei Egusa et Naka-jima, 1981 produces giant plasmodia in submucosa of the intestine of common carp in Japan (Rhee et al. 1990). T. nikolskii Akhmerov, 1954 (syn. T. cyprini Hoshina et Hoshoda, 1957) common in carp (Cyprinus carpio) fingerlings in Eurasia. Rounded, cyst-like plasmodia up to 2 mm in size appear as bunch-of-grape-like structures on the fins, developing in close associations with cartilaginous fin rays. The relation of T. hovorkai and T. nikolskii warrants revision.


Neothelohanellus Das et Haldar, 1986 (Fig. 58).


Sporos in frontal view oval or egg-shaped with a wider anterior end; longitudinal suture line. A single elliptical polar capsule at the anterior end opens laterally or subapically. Large polysporous plasmodia. Histozoic in freshwater fish. The genus does not differ essentially from Thelohanellus and careful analysis may show it to be a synonym of Thelohanel- lus. Number of species: 3.

Type species Neothelohanellus catiae Das et Haldar, 1986 (Fig. 58) in kidney tissue of the freshwater fish Catla catla in West Bengal, India.

Neohenneguya Tripathi, 1953 (Fig. 59).

Sporos spindle-shaped in valvular view and flattened spindleshaped in sutural view. Two fine, equal prolongations attach to the shell both at anterior and posterior end. Two spherical polar capsules are in tandem position, at some distance from the anterior end. Large polysporous plasmodia histo- zoic in freshwater fishes.

Type and only species Neohenneguya tetradiata Tripathi, 1953 (Fig. 59) is histozoic in the gills of Odontamblyopus rubicundus in India.
Figs. 50–66. Line drawings of myxosporean spores. Fig. 50. Dicauda atherinoidi, aspect of the whole spore (a), spore body in frontal view (b). Fig. 51. Phlogospora mysti. Fig. 52. Laterocaudata mastacembala. Fig. 53. Henneguya psorospermica. Fig. 54. Hennegoides longitudinalis. Fig. 55. Tetrauronema macropodes in frontal (a) and sutural view (b). Fig. 56. Thelohanellus pyriformis (modified from Soltynska 1967). Fig. 57. Thelohanellus hovorkai. Fig. 58. Neothelohanellus catlae (modified from Das and Haldar 1986). Fig. 59. Neohenneguya tetraradiata. Fig. 60. Trigonospores acanthogobii. Fig. 61. Octospina tongrensis (modified from Hsieh and Xiao 1993). Fig. 62. Trilospora californica in side (a) and apical view (b). Fig. 63. Unicapsula seriola. Fig. 64. Kudoa clupeidæ in side (a) and apical view (b). Fig. 65. Kudoa permulticapsula in side (a) and apical view (b) (courtesy of Dr. M.L. Kent and J. Parasitol.). Fig. 66. Kudoa paniformis in side (a) and apical view (b).
**Trigonosporus** Hoshina, 1952

Spores broadly triangular, with rounded anterior and flattened posterior ends. Each shell valve is drawn out into two long filamentous processes on each side, each pair being connected by a filament. Two pyriform polar capsules, binucleate sporoplasm has a spherical polysaccharide inclusion. Polysporic plasmodia, histozoic in marine fishes. Number of species: 3.

Type species *Trigonosporus acanthogobii* Hoshina, 1952 (Fig. 60) in subepithelial tissue of the gills of *Acanthogobius flavimanus* (a marine fish that also lives in brackish and freshwater environment) from the coast of Japan.

**ORDER MULTIVALVULIDA** Shulman, 1959

Spores are radially symmetrical, posterior face is flat or semispherical, the shell consists of three to seven shell valves; the sutures lines are often indistinct. Polar capsules are situated at the apex of spores, their tips are covered by the shell valve and they discharge apically. Their number corresponds to the number of valves. Plasmodia as a rule intracellular in the muscle tissue of marine fishes; pansporoblast formation has not been observed. No actinospore stages have been observed thus far.


Whipp et al. (2003) described a multivalvulid species with 13 polar capsules as *Kudoa multicapsula*, based on SSU rDNA sequence analysis. This resulted in the requirement to change the diagnosis of *Kudoa* and, eventually, classification of multivalvulids in general, which was proposed by Whipp et al. (2004). In their phylogenetic analysis of SSU and LSU rDNA, members of the genera *Pentacapsula*, *Hexacapsula* and *Septemcapsula* rooted within the clade of *Kudoa* species, with *Unicapsula* as an outliner to these genera. They proposed an altered diagnosis of the family Kudoidae. The genus *Kudoa*, the only one within the family Kudoidae Meglitsch, 1960, would accommodate all marine myxosporeans with four or more shell valves and polar capsules. However, the results of Whipp et al. (2004) are important and in this paper they are used in support of demise of the families Pentacapsulidae, Hexacapsulidae and Septemcapsulidae, leaving the order Multivalvulida Shulman, 1959 only with the families Trilosporidae and Kudoidae. However, although reasoning of Whipp et al. (2004) seems convincing, it may be preferable to preserve the existing genera pending future research in molecular analysis, biology and structure which will accumulate decisive data.

**Trilosporidae** Shulman, 1959

Spore with three polar capsules and three shell valves, appearing in apical view as a triradiate star with rounded points. Sporoplasm in the central cavity of the spore. Trophozoites mono- and disporic, in gall bladder or in muscle of marine fishes.

**Trilospora** Noble, 1939

With characters of the family. Number of species: 4.

Type species *Trilospora californica* Noble, 1939 (Fig. 62) was described from the gall bladder of marine fishes *Gibbonsia elegans* and *Typhlogobius californiensis* from California waters.


**Unicapsula** Davis, 1924

Type species *Unicapsula muscularis* Davis, 1924; spores closely similar to *U. seriola*. Plasmodia appear as worm-like structures in muscle fibres of Pacific halibut, *Hippoglossus stenolepis*, from the North-East Pacific; it is the agent of “wormy halibut”.

Pathogenic species: *Unicapsula seriola* Lester, 1982 (Fig. 63) in muscles of *Seriola lalandi* along the Australian coast.

**Kudoa** Meglitsch, 1947

Spores with four shell valves and four polar capsules; two sporoplasm cells, one inside the other.

**Kudoa clupeidae** (Hahn, 1917) Meglitsch, 1947 (Fig. 64) described from *Clupea harengus* (also infects *Alosa pseudoharengus* and two more clupeids) from the Atlantic Ocean. In young *C. harengus*, heavy infections may induce mortalities. Lesions in *Brevoortia tyrannus* were studied by Reimschuessel et al. (2003).
Kudoa permulticapsula Whipps, Adlard, Bryant et Kent, 2003 (Fig. 65), an unusual Kudoa species with 13, sometimes 14 or even 15 polar capsules arranged in a ring, often with 1 or 2 additional capsules located centrally. The reason why it was assigned to Kudoa and not to a new genus is that the neighbour-joining analysis of SSU rDNA placed it within a Kudoa clade, with close relation to K. thyrsites and K. quadricornis. If the view of Whipps et al. (2003) is accepted, it will be the first case when in myxozoan taxonomy molecular analysis prevailed over spore morphology. It is left in the genus Kudoa until final solution of the classification. It lives in somatic muscle of Scomberomorus commerson from the Great Barrier Reef off Australia.

Pathogenic species eliciting mushy flesh or myoliquefaction: Kudoa histolytica (Pérand, 1928) Meglitsch, 1960 in the mackerel Scomber scombrus in the Atlantic Ocean and the Mediterranean Sea (Shukgalter 2004, Hoffmann 2005). K. megacapsula Yokoyama et Itoh, 2005 in the food fish red barracuda Sphyraena pinguis from the China Sea (Yokohama and Itoh 2005). K. musculoliquefaciens (Matsumoto et Arai, 1954) Meglitsch, 1960 in the swordfish Xiphias gladius from the Pacific coast of Japan (Matsumoto and Arai 1954). K. paniformis Kabata et Whitaker, 1981 (Fig. 66) is a deleterious parasite of the Pacific hake, Merluccius productus, in which the total prevalence, single or in infections mixed with K. thyrsites, is up to 90% (Kabata and Whitaker 1981, Patashnik et al. 1982). K. thyrsites (Gilchrist, 1924) Meglitsch, 1960 described from Thyrsites atun off South African coast has been known now as a cosmopolitan parasite infecting many species of marine fishes, such as Pacific hake, Merluccius productus, and including salmonids, such as Salmo salar and Oncorhynchus kisutch (Stehr and Whitaker 1986, Whitaker and Kent 1991, Morán et al. 1999b).

Species damaging the muscle tissue by proliferation of a mass of trophozoites: Kudoa amamiensis Egusa et Nakajima, 1978 in cultured Seriola quinquergadiata in Japan (Egusa and Nakajima 1978).

A unique, non-piscine Kudoa sp. was found to cause post-mortem myoliquefaction of arm muscles in the cephalopod Paroctopus dofleini in the North Pacific (Yokoyama and Masuda 2001).

**Pentacapsula** Naidenova et Zaika, 1970

Spores in apical view stellate, pentaradiate, in frontal view therefore of a flat conical. There is a polar capsule to each valve. Histozoic parasites of marine fishes. Number of species: 4.

Type species *Pentacapsula shulmani* Naidenova et Zaika, 1970 (Fig. 67) in skeletal muscles of Nemipterus japonicus from the Pacific.


**Hexacapsula** Arai et Matsumoto, 1953

Spores have six polar capsules and six shell valves. Parasites in muscles of marine fishes.

Type and only species *Hexacapsula neothunni* Arai et Matsumoto, 1953 (Fig. 68) develops in skeletal muscles of marine fish *Thunnus albacares* (syn. *Neothunnus macropterus*) from seas around Japan. No data on sporogenic plasmodia were given. The parasite induces “jellied condition” of the flesh (Arai et Matsumoto 1953). Such fish are unmarketable.
plan quite different from that of other multivalvulids. Hsieh and Xiao (1993) established this family for the genus Octospina and then suggested tentatively a new order Tetravalvulidea to accommodate it, which of course would also include Kudoa. This order was then proposed by Chen, Ma, Wu and Lei in the book of Chen and Ma (1998). Until future revision, Octospina has to be regarded as incertae sedis.

**Octospina** Hsieh et Xiao, 1993  
With characteristics of the family, sporoplasm with an iodinophilous vacuole.

Type and only species Octospina tongrenensis Hsieh et Xiao, 1993 (Fig. 61) attached to swimbladder and gall bladder walls and floating in the bile of Ctenopharyngodon idella in China. Plasmodia were not described.

**ACTINOSPORE STAGES AND THEIR DIVERSITY**

Thirteen zoological genera and 44 species of actinospores were described until 1984, when these organisms were still considered to constitute a separate class Actinospora. Recently, some 136 new types of actinospore collective groups have been described and two genera and four types were still established as independent zoological categories. The counts given for separate collective groups below include only described types; in addition, many types were only mentioned without any description. Experimental infections identified 33 actinospore types as developmental stages of determined myxosporeans. It is up to further research to assign the other types to their fish-infecting myxospore stages.

Since actinospores are nothing more than sexual developmental stages in myxosporean life cycle (Wolf and Markiw 1984), it is not possible to consider them as independent genera and species. They should be named only in the vernacular, using the former genera as collective group names, i.e., a finding should be termed e.g., actinospore triactinomyxon stage, type 2 of Smith 1999 (Kent et al. 1994a, 2001, Lom et al. 1997a, Kent and Lom 1999). One can assume that the development of actinospores into myxospores is a general rule; the direct fish-to-fish transmission can only be taken as a unique exception. A recent finding suggests that also marine myxosporeans may have actinospore stages (Köie et al. 2005). Consequently, also former actinospore genera of which no myxospore counterpart has yet been found can be taken as developmental stages (e.g., Guenotia, Ormieractinomyxon). Moreover, even the recently erected actinospore genera (Endocapsa, Tetraspora) should be taken for such collective groups and treated as vernacular names. It is possible that they belong to an already described myxospore with a nomenclatural priority. In the case that they would be associated with a myxospore of a still undescribed myxosporean species, a petition would have to be placed with the International Commission on Zoological Nomenclature to waive their nomenclatural priority to avoid havoc in the existing taxonomy.

Actinospore stages have spores with triradiate symmetry. Their spores develop in groups of eight within a pansporocyst except for tetraspora, in which groups of four develop in the pansporocyst. The stages are classified according to spore morphology; developmental phases have not been reported to have reliable differentiating features. However, spore morphology may be fallacious; Hallett et al. (2002) proved that a single aurantiactinomyxon genotype might have different phenotypes. In addition, reliability of morphometric data in establishing separate spore types was put in doubt by Hallett et al. (2004). The vast discrepancy between the huge number of myxosporean species and of the relatively few actinospore types lead Longshaw and Feist (2005) to propose that actinospore morphology may be a function of the environment and that each actinospore type will not necessarily have a specific corresponding myxospore stage.

In view of the general agreement with the proposal of Kent et al. (1994a) to abolish the class Actinospora, different actinospore collective groups are listed alphabetically, irrespective of the generic system proposed by Janiszewska (1955, 1957) and Marques (1984). The authority is given to each group. Characters important in describing actinospore stages are given in Lom et al. (1997a).

In individual forms of actinospore stages listed below, the first number indicates number of findings described earlier as a regular zoological species (RZS), the second refers to proven or putative myxospore developmental stages (DS).

**Antonactinomyxon** Janiszewska, 1957  
Ellipsoidal spore body with protruding tips of polar capsules and a plasmodial sporoplasm with many infectious cells. The valves do not form any style below the spore body and extend into caudal projections diverging from each other, which with their thickened ends contact the ends of caudal projections of other spores. Thus a three-dimensional, cube-like group of all eight spores of the pansporocyst is formed. In freshwater oligochaetes; known as developmental stage of the life cycle of *Chloromyxum auratum*. Original type *Antonactinomyxon antoni* Janiszewska, 1957 (syn. Siedleckiella antoni Janiszewska, 1954) described from freshwater oligochaete *Limnodrilus claperadeanus*, from the Oder River at Wroclaw, Poland.  
RZS: 1, DS: 2.

**Aurantiactinomyxon** Janiszewska, 1952  
Three stout, semicircularly curved, leaf-like caudal projections are attached to an ellipsoidal spore body with protruding tips of polar capsules and a plasmodial sporoplasm with many infectious cells. In freshwater oligochaetes. Known as developmental stage in the life cycle of species of the genera *Henneguya*, *Haferellus*, *Thelohannelus*, *Myxidium* and *Chloromyxum*. Original type *Aurantiactinomyxon raebei* Janiszewska, 1952 described from freshwater oligochaete *Limnodrilus hoffmeisteri* from southern Carpathians, Poland.  

**Echinactinomyxon** Janiszewska, 1957  
An ovoid spore body with slightly protruding polar capsules and a plasmodial sporoplasm with many infectious cells has mutually divergent straight caudal projections, tapering to sharp tips. In freshwater oligochaetes; known as developmen-
Figs. 70–79. Spores of actinosporean stages. Fig. 70. Antonactinomyxon (type antonii Janiszewska, 1955–57), a group of eight spores (a), spore with its thick caudal projections (b). Fig. 71. Aurantiactinomyxon (type raabeiioris Janiszewska, 1957) in side (a) and apical view (b). Fig. 72. Echinactinomyxon (type radiatum Janiszewska, 1957). Fig. 73. Endocapsa (type rossulata Hallett, Erséus et Lester, 1999) in apical (a) and side view (b) (courtesy of Dr. S.L. Hallett and Syst. Parasitol.). Fig. 74. Guyenotia (type sphaerulosa Naville, 1930). Fig. 75. Hexactinomyxon (type psammoreyctis Štolc, 1899). Fig. 76. Neoactinomyxon (type globose Granata, 1922), in apical (a) and side view (b). Fig. 77. Ormieractinomyxon (type racemosum Marques, 1984), single spore (a), spores interconnected to form a large mass (b). Fig. 78. Raabeia (type magna Janiszewska, 1957). Fig. 79. Siedleckiella (type silesica Janiszewska, 1952), single spore (top), group of eight spores from one pansporocyst (bottom).
Subspherical spore slightly flattened in the antero-posterior axis, polar capsules are “embedded” below the spore surface. Valve processes reduced to bulge-like swellings. No data supplied on the sporoplasm. In marine tubificids. Thus far not known as developmental stage in the life cycle of any myxosporean. Original type Endocapsa rosalata Hallett, Erséus et Lester, 1999 described from marine oligochaete Heterodrilus cf. keenani from Great Barrier Reef off Australia.

**Endocapsa** Hallett, Erséus et Lester, 1999  
Fig. 73

Subspherical spore with polar capsules and a cup-shaped plasmodial sporoplasm with many infectious cells. Three stout, slightly divergent and bluntly tipped caudal projections. Not known as developmental stage in the life cycle of any myxosporean. Original and only type G. sphaerulosa Naville, 1930 described from freshwater oligochaete Tubifex tubifex from the Vltava River in Prague, Czech Republic.

**Guyenotia** Naville, 1930  
Fig. 74

The subospherial spore body with polar capsules and a cup-shaped plasmodial sporoplasm with many infectious cells. The shell valves continue posteriorly as a common style, then diverge, each one being split into two sharp-tipped projections. Not known as developmental stage in the life cycle of any myxosporean. Original and only type G. sphaerulosa Naville, 1930 described from freshwater oligochaete Tubifex tubifex from the Calvados region in France.

**Hexactinomyxon** Stolc, 1899  
Fig. 75

Elongated spore body, with protruding tips of polar capsules and sporoplasm plasmodium with many infectious cells. The shell valves continue posteriorly as a common style, then they diverge, each one being split into two sharp-tipped projections. In some types, the projections have subsidiary protrusions. Known as developmental stage in the life cycle of Myxobolus pavlovskii. Original type Hexactinomyxon psammodryctis Stolc, 1899 described from freshwater oligochaete Psammoryctis barbatus from the Vltava River in Prague, Czech Republic.

**Hungactinomyxon** Rácz, Eszterbauer et Molnár, 2005  
Fig. 86

Subspherical spore body similar to echinactinomyxon, with three finger-like, latero-posterior caudal projections of equal size. Their tapered ends are fastened to projection ends of two other spores, so that four spores form a cube-like structure interlaced with another cube made up also of four spores. Thus the eight spores of a pansporocyst form a double cube floating in water. No details on the sporoplasm were provided. Original and only type described from the freshwater oligochaete Branchiura sowerbyi from Šišalombatta, Hungary.

**Neoactinomyxum** Granata, 1922  
Fig. 76

Subspherical spore without caudal projections, with prominent apex and anteriorly protruding tips of polar capsules. Plasmodial sporoplasm with many infectious cells. Spore valves extend to rounded triangular flaps, making the spore to appear rounded triangular in apical view. In freshwater oligochaetaes. Known as developmental stage in the life cycle of Heterocotyle carassii and Chloromyxum sp. Original type Neoactinomyxum globosum Granata, 1922 described from freshwater oligochaete Limnodrilus udekiemianus from the Mugove River, Florence, Italy.

**Ormieractinomyxon** Marques, 1984  
Fig. 77

Similar to echinactinomyxon; the spore body contains a sporoplasm with 16 nuclei (infectious cells?). Long caudal projections taper to a thin rod, at the end of which are small anchor-like structures by means of which the eight spores released from a pansporocyst adhere together. In addition, groups of spores from several pansporocysts also join together to form chains up to several cm long. Not known as developmental stage in the life cycle of any myxosporean. Original type Ormieractinomyxon racemosum Marques, 1984 described from the freshwater oligochaeta Tubifex sp. from the Plaine de Roussillon, France.

RZS: 1, DS: 0.

**Pseudotriactinomyxon** Hallett, Atkinson, Schöl et El-Matbouli, 2003  
Fig. 87

The caudal processes have a prominent longitudinal, axial suture starting already at the base of the spore, like in hexactinomyxon, but unlike it, the processes remain fused longitudinally all their length through, they do not separate in mid-length into two halves. Thus the spore has a triactinomyxon-like appearance. Found in filtrates of water containing freshwater oligochaetaes. Original type not determined.

RZS: 0, DS: 3.

**Raabeia** Janiszewska, 1955  
Fig. 78

An ellipsoidal spore body with protruding tips of polar capsules and plasmodial sporoplasm; caudal projections divergent, long, sharp-tipped and upward curved. In freshwater oligochaetaes. Known as developmental phase in the life cycle of Myxobolus dispers Myxidium truttae. Original type Raabeia goricensis Janiszewska, 1955 described from freshwater oligochaeta Tubifex tubifex from Carpathian rivers in Poland.

RZS: 3, DS: 22.

**Siedleckiella** Janiszewska, 1953  
Fig. 79

Spores similar to those of triactinomyxon with a style beneath the spore body. Sporoplasm with about 100 nuclei (infectious cells?). Caudal projections long and tapering, attach to projections of other spores from the same pansporocyst. This results in a mesh in which all spores are joint between them; this mesh may be irregular or in form of a cube. Known as developmental phase in the life cycle of Zschokkella nova. In freshwater oligochaetaes. Original type Siedleckiella silesica Janiszewska, 1952 described from freshwater oligochaeta Tubifex sp. near the Oder River at Wrocław, Poland.

RZS: 1, DS: 2.

**Sphaeractinomyxon** Caullery et Mesnil, 1904  
Fig. 80

Subspherical spores without projections of shell valves; polar capsules at the spore apex are “embedded” beneath the spore surface. Plasmodial sporoplasm with many infectious cells. In freshwater and marine oligochaetaes. Not known as developmental stage in the life cycle of any myxosporean. Original type Sphaeractinomyxon stolci Caullery et Mesnil, 1904 described from marine oligochaetae species of genera Cli- telllo, Peloscolex and Tubifex at the Atlantic coast of France.

RZS: 8, DS: 0.

**Synactinomyxon** Stolc, 1899  
Fig. 81

Spores with uneven shell valve projections which extend in the same plane: one is short and conical, extending in a direction opposite to the remaining two broadly-based and sharply-tipped projections which run parallel to each other. Sporo-
Lom, Dyková: Myxozoan genera

Figs. 80–84. Spores of actinosporean stages. Fig. 80. Sphaeractinomyxon (type amanieui de Puytorac, 1963); (a) side and (b) apical view. Fig. 81. Synactinomyxon (type tubificis Štolc, 1899), (a) group of eight spores from one pansporocyst, (b) single spores in apical (at left) and side view. Fig. 82. Tetractinomyxon (type intermedium Ikeda, 1912); (a) side and (b) apical view. Fig. 83. Tetraspora (type discoidea Hallett et Lester, 1999); (a) side and (b) apical view (courtesy of Dr. S.L. Hallett and Int. J. Parasitol.). Fig. 84. Triactinomyxon (type ignotum Štolc, 1899), a total view and spore body enlarged.

plasm plasmodium with many infectious cells and polar capsules located at point where the three projections converge; capsules discharge vertically to the plane of the projections. The short conical projections adhere to corresponding projections of other spores from the same pansporocyst, so that a star-like formation is formed. In freshwater oligochaetes; thus far not known as developmental stage in the life cycle of any myxosporean. Original type Synactinomyxon tubificis Štolc, 1899 described from freshwater oligochaete *Tubifex tubifex* in the Vltava River near Prague.

RZS: 2, DS: 6.

**Tetractinomyxon** Ikeda, 1912

Spores rounded tetrahaedroid with polar capsules at the apex of the tetrahaeder; a single binucleate sporoplasm. In body cavity of sipunculids and in freshwater and marine polychaetes. Known as developmental stage in the life cycle of *Ellipsomyxa gobii*; these stages form pansporocysts divided into two halves by a central strangling and some pansporocyst contain less than eight spores. Also known as developmental stage in the life cycles of *Ceratomyxa shasta* and *Parvicapsula minibicornis*. Original type Tetractinomyxon intermedium Ikeda, 1912 described from marine sipunculid *Petalostoma intermedium* from off Plymouth, UK.

RZS: 2, DS: 6.

**Tetraspora** Hallett et Lester, 1999

Spore similar to that of sphaeractinomyxon, may be antero-posteriorly flattened. Sporoplasm with over 100 infectious cells. Pansporocyst only contains four spores. In marine oligochaetes. Known as developmental stage in the life cycle of *Ellipsomyxa gobii*; these stages form pansporocysts divided into two halves by a central strangling and some pansporocyst contain less than eight spores. Also known as developmental stage in the life cycles of *Ceratomyxa shasta* and *Parvicapsula minibicornis*. Original type Tetractinomyxon intermedium Ikeda, 1912 described from marine sipunculid *Petalostoma intermedium* from off Plymouth, UK.

RZS: 2, DS: 0

**Triactinomyxon** Štolc, 1899

Elongated spore body with protruding tips of polar capsules and plasmodial sporoplasm with many infectious cells. Caudal projections continue as a common stem, eventually split into three slightly upwards curved, long arms attenuated as a rule into sharp tips. In freshwater and marine oligochaetes. Known as developmental stage in the life cycle of species of the genus *Myxobolus* and *Henneguya nusslini*. Original type Triactinomyxon ignotum Štolc, 1899 described from freshwater oligochaete *Tubifex* sp. from the Vltava River in Prague, Czech Republic.

RZS: 11, DS: 42.
Heliactinomyxon Bellem in Hanson et al. (2001)

The collective group heliactinomyxon mentioned in the paper by Hanson et al. (2001) has not been published in a regular publication and its description is not accessible; the name is a nomen nudum.

CONCLUSIONS

The classification of Myxozoa is in the state of transition from the surviving mainly spore-based organisation to a new arrangement taking into account molecular characters and other criteria. It may happen that many genera established on minute differences (e.g., Alatospora vs. Pseudoalatospora or Myxobolus vs. Unicauda or Dicauda) will fuse while existing genera will be split.

To establish more appropriate classification will require several prerequisites:

It is necessary to characterise carefully the morphology of new species as well as of the existing ones. For the time being, this requirement applies only to a fraction of the 2,180 species and 60 myxosporean genera described thus far. The number of species listed above in individual genera resulted from a careful registration of all accessible literature. Nevertheless, it cannot be absolutely reliable. While compiling this paper, descriptions in marginal publications may have been missed and of course a complete revision of species and genera could not have been accomplished. However, it is quite certain that only a fraction of all existing species is known.

The existing results of phylogenetic analyses should be completed and made more reliable by adding sequences of a sufficient number of morphologically well characterised species representing most if not all described genera. It is imperative that the description of a new species should include the sequence of the SSU rRNA gene to establish proper their identity and avoid production of synonyms. An attempt to introduce an order at least in some of the Myxobolus species by using SSU rDNA analysis has been published by Cone and Easy (2005). The use of the SSU rRNA gene sequences should be exploited to a maximum while also resorting to other genes. Nevertheless, great caution has to be exerted in interpreting the results.

The impact of life-cycle characteristics has to be assessed in solving relations between species of some genera. This applies to situations e.g., Myxobolus cul tus and M. portucalensis situated side by side in the same clade yet possessing different actinospore stages (raabeia vs. triactinomyxon). This will become more topical as more life cycles become elucidated.

The role of host and tissue preferences in differentiating between closely related species has to be evaluated. The assessment of tissue tropism should be always based on species with well-corroborated site specificity.

The same applies to the value of different geographic distribution in species of certain genera (e.g., Kudoa) in finding differences between the species. With all the above factors considered it would be possible also to investigate the appearance of phenotypic variation among species and thus to expedite the progress in building an improved classification.

Acknowledgement. This study was supported by the research project of the Institute of Parasitology, Academy of Sciences of the Czech Republic (Z60220518).


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