

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

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**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 Sporozoa. 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 meta-

zoan 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 Opisthoconta (Empire Eukaryota). 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 (sporoplasms) and one to several nematocyst-like polar capsules (in *Kudoa permulticap-sula* up to 15). The capsules contain an extrudible filament with an anchoring function. The typically eukaryotic 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 plasmodium.

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 alternation of hosts, one of them, in which the sexual process has been proven, being the definitive one (an invertebrate), 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. (2000b, 2001).

**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 without cell junctions, then rearrange themselves to form the trophic stages, i.e., simple sac-like or vermiform organisms. The worm-like organism (up to about  $3.6 \times 0.1$  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 **longitudinal 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 spherical **malacospores** with eight **unhardened shell valves** topped by four polar capsules, including two **sporoplasms** with inner (secondary) cells inside them. Sporoplasms have electron-dense bodies with lucent invaginations, **sporoplasmosomes**. Polar capsules and sporoplasms are encased with **valvogenic cells**, which in ma-

lacospores do not cover the exit point of the polar filament. 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 *Tetracapsuloides 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 **stellate cells** aggregate around a **sporoplasmodic cell** which undergo meiosis. A spherical malacospore is then produced from this aggregation.

In *T. bryosalmonae* there is a stage infecting salmonid 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, Hedrick et al. (2004) found mature spores in the urine of *Oncorhynchus mykiss*, different from bryozoan malacospores, for which the term **fishmalacospores** was proposed. These spores have two shell valves enclosing two polar capsules and one sporoplasm.

No complete malacosporean life cycle has been unravelled 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 unidentified. 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. bryosalmonae* 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. (2000, 2002), Monteiro et al. (2002), Okamura et al. (2002), Canning and Okamura (2004), McGurk et al. (2005).

**ORDER MALACOVULVULIDA** Canning, Curry, Feist, Longshaw et Okamura, 2000

With characters of the class.

**Saccosporida** 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

Trophic stages in form of both sac-like and worm-like organisms of triploblast organisation. Cells produced by division of one sporogonic 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 Fig. 2

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 sporoplasmodic cell that undergoes meiosis. The 18S rDNA sequence differs by 20% from that of *Buddenbrockia* (Anderson et al. 1999a).

*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 sporoplasmodium (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 analysis using molecular methods implies that southern Europe was colonised by immigration of the parasite from North America and that this colonisation substantially predated fisheries activities (Henderson and Okamura 2004).

References: Bucke et al. (1991), Hedrick et al. (1993), Canning et al. (1999b), Morris et al. (2000), Okamura et al. (2001), Tops and Okamura (2003).

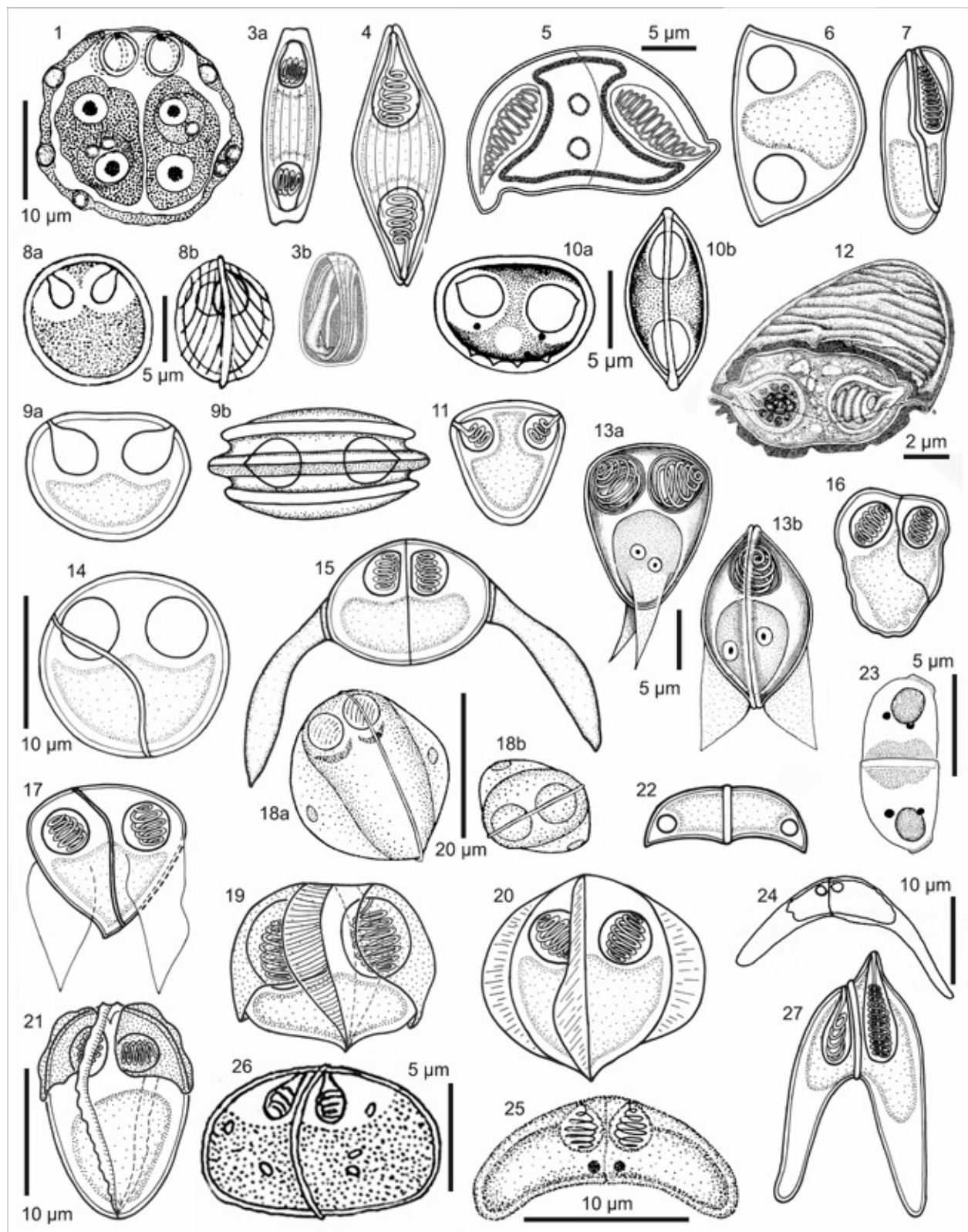
## CLASS MYXOSPOREA Bütschli, 1881

### 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 sporoplasmodium enters the skin generally through the openings of epidermal and epithelial mucous cells. A series of **presporogonic stages** follows, which may be intra- and/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 plasmotomy, 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, **sporogonic cell**, each of which produces a spore by division and differentiation, or of two types, sporogonic cell and **pericyte**. These two latter cells engage in spore formation, **sporogony**. The pericyte envelops the sporogonic cell which divides into differentiated **capsulogenic**, **valvogenic** and **sporoplasmodic 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 sporogonic 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-spore**. **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 sporoplasms, each with a uninucleate secondary cell. Sporoplasms contain sporoplasmosomes (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, **extrasporogonic 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 tetranucleate stage, two sporogonic cells enveloped by a pair of pericytes, the future **pansporocyst**. During further development of these cells the two (or more) **enveloping cells** harbour inside them eight pairs of **gametic cells** ( $\alpha$  and  $\beta$  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 capsules, except for sphaeractinomyxon, in which the polar capsules are embedded beneath the surface of the spore. There is, as a rule, a **plasmodium-like sporoplasm** with many nuclei and many **infectious cells**. Behind the spore body the shell valves extend in most actinosporean stages into very long, hollow and mutually divergent **caudal projections**, inflatable 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*).

References: life cycle and fine structure – Lom and de Puytorac (1965a, b), Desser and Patterson (1978), Grassé and Lavette (1978), Current (1979), Current et al. (1979), Desportes and Théodorides (1982), Marques (1984), Wolf and Markiw (1984), Lom and Dyková (1988, 1996, 1997), El-Matbouli et al. (1992b, 1995), Kent et al. (1994a, 2001), Lom et al. (1997b), El-Matbouli and Hoffmann (1998).

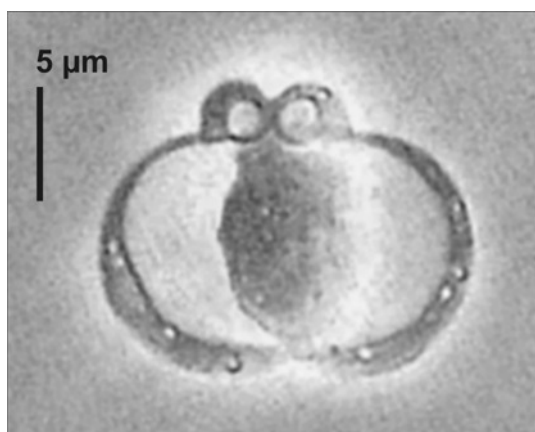
### Hosts

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 Osteichthyes. 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, myxospores 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 (Lowenstine 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 phase in invertebrates: a *Kudoa* sp. was found in the muscles of the arm of the giant octopus *Paroctopus dofleini* (Yokoyama and Masuda 2001). The following are doubtful reports: *Chloromyxum diploxys* (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, *Dactilopius indicus*, described as *Symmetrula cochinealis* 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.** *Cardimyxobolus leshanensis* in frontal (a) and sutural view (b); modified from Chen and Ma (1998). **Fig. 11.** *Triangula yankiangensis* in frontal view. **Fig. 12.** *Triangulamyxa amazonica* in oblique partly dissected view (courtesy of Dr. C. Azevedo 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.** *Sinuolinea dimorpha* (after Kudo 1919). **Fig. 15.** *Davisia diplocrepis*. **Fig. 16.** *Myxoproteus abyssus* (courtesy of Yoshino and Noble 1974 and J. Parasitol.). **Fig. 17.** *Bipteria admiranda*. **Fig. 18.** *Paramyxoproteus reinhardti* in sutural (a) and apical view (b) (after Wierzbicka 1986). **Fig. 19.** *Neobipteria macrouri*. **Fig. 20.** *Schulmania ovale*. **Fig. 21.** *Noblea admiranda*. **Fig. 22.** *Fabespora nana*. **Fig. 23.** *Fabespora vermicola* (courtesy of Dr. R.M. Overstreet and J. Parasitol.). **Fig. 24.** *Ceratomyxa arcuata* (from Meglitsch 1960, courtesy of J. Parasitol.). **Fig. 25.** *Ceratomyxa sparusaurati* (courtesy of Dr. A. Sitja-Bobadilla and J. Eukaryot. Microbiol.). **Fig. 26.** *Leptotheca agilis* (from Kudo 1919). **Fig. 27.** *Meglitschia 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.



**Fig. 2.** Photograph of a fishmalacospore of *Tetracapsuloides bryosalmonae* (Courtesy of Dr. R.P. Hedrick and Parasitol. Res.).

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 *Moron labrosus* in Egypt (Abdel-Aal et al. 2001).

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. – Køie 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 ap-

proach 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 mugilis*. 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. exiguus* 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).

References: Andree et al. (1999), Salim and Desser (2000), Kent et al. (2001), Dyková et al. (2002), Eszterbauer and Székely (2004), Holzer et al. (2004), Cone and Easy (2005).

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).

Important publications on taxonomy and morphology of Myxosporea as a group include Davis (1917), Kudo (1919), Ward (1919), Fujita (1923), Pinto (1928), Poisson (1953), Tripathi (1953), Shulman (1962, 1966, 1984), Chen (1973), Mitchell (1979), Uspenskaya (1984), Marques (1986–1987), Lom and Dyková (1992, 1997), Moser and Kent (1994), Goia and Cordeiro (1996), Fomena and Bouix (1997), Lom et al. (1997b), Shulman et al. (1997), Chen and Ma (1998), and Hoffman (1999).

Selected publications on myxosporean pathogenicity include Hofer (1904), Plehn (1924), Sindermann (1970), Lom (1985), Dyková and Lom (1988), Schäperclaus (1992), Alvarez-Pellitero and Sitjà-Bobadilla (1993), Kent et al. (1994b, 2001), Lom and Dyková (1995a), Noga (1995), and Longshaw et al. (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 circumspiral 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.

#### Sphaeromyxidae Lom et Noble, 1984

Spore elongated, sometimes slightly curved; the two polar capsules lie in its opposite, tapering and truncate ends. Spores open at the level of the suture line, bisecting the spore and connecting its both ends. Shell valves smooth or ridged. One, binucleate sporoplasm. Plasmodia large (sometimes several mm in size), form disporic pansporoblasts and float free in the gall bladder. Pathogenicity has not been proved.

#### *Sphaeromyxa* Thélohan, 1892

Fig. 3

With characters of the family. Number of species: 39.

References: fine structure – Lom (1969), list of species – Lom (2004).

Type species *Sphaeromyxa balbianii* Thélohan, 1892 (Fig. 3); originally recorded hosts (without specification of the type host) are *Gaidropsarus vulgaris* (syn. *Motella triccirrata* and *M. maculata*), *Cepola macrophthalma* (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 sutural 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 terminally or more or less laterally. The longitudinal sutural 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

Spores are generally fusiform, straight or slightly crescent or even sigmoid, with more or less pointed ends. Shell valves smooth or with ridges, sutural line bisects the spore. Two polar capsules, mostly pyriform, lie one at each end of the spore. Capsular foramina are situated in the sutural plane, at or near the end of the spore and open as a rule in opposite directions. The binucleate sporoplasm lies between the capsules. The species are typically coelozoic (rarely histozoic), forming small or large trophozoites, mono-, di- 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 aurantiactinomoxon (Benajiba and Marques 1993). Molecular analysis identified a raabeia 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 salmonids in Eurasia (McGeorge et al. 1996a, b).

**Enteromyxum** Palenzuela, Redondo et Alvarez-Pellitero, 2002

Fig. 5

Spores 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. Histozoic 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 scopthalmi* 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 Dyková, 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).

Fig. 4

**Zschokkella** Auerbach, 1910

Synonym: *Parazschokkella* Kalavati et Narasimhamurti, 1987

Fig. 6

Spores ellipsoidal in sutural view and slightly bent or semi-circular in valvular 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 heterogenous 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* Kashkowsky, 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 histozoic) 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 (Uspenskaya 1995) and in *Zschokkella* sp. an echinactinomoxon (Yokoyama et al. 1991).

Reference: Sitjà-Bobadilla and Alvarez-Pellitero (1993b).

Type species *Zschokkella hildae* Auerbach, 1910 (Fig. 6) described originally from the urinary bladder of *Phycis blennoides*, *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 icterica* Diamant et Paperna, 1992 causes cholestasis and bile duct breakdown in *Siganus luridus* from the Red Sea. It may also invade liver parenchyma (Diamant and Paperna 1992).

**Coccomyxa** Léger et Hesse, 1907

Fig. 7

Spores ellipsoidal rounded in transverse section, with a single elongated polar capsule (the second presumably lost), which opens in the sutural plane. Suture 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 histozoic (*C. hoffmani* Cheung et Nigrelli, 1990 in gill cartilage of *Plotosus 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

Spores spherical 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 *Neomixobolus* and *Triangula* to the family is rather tentative.



**Ortholinea** Shulman, 1962

Fig. 8

Spores spherical to subspherical, may be slightly flattened parallel to the sutural plane or may be pointed posteriorly. Polar capsules are subspherical to pyriform. 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. *Blennius pholis*) and *Symphodus melops* (syn. *Crenilabrus melops*) from the northern coast of France, also infects other marine fishes.

**Neomyxobolus** Chen et Hsieh, 1960

Fig. 9

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

Type species *Neomyxobolus ophioccephalus* Chen et Hsieh, 1960 (Fig. 9) in renal tubules of the freshwater fish *Channa argus* (syn. *Ophioccephalus argus*) and *C. maculata* (syn. *O. maculatus*) in China.

**Cardimyxobolus** Ma, Dong et Wang, 1982

Fig. 10

Spores in frontal view oval, with one side very vaulted and with sutural markings along the posterior border; spindle-shaped in sutural view. Subspherical polar capsules. Shell valves are smooth, in the sporoplasm is an iodophilous 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

Fig. 11

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

Type species *Triangula yangkiangensis* Chen et Hsieh, 1984 (Fig. 11) in the skin and gills of *Rhinogobius giurinus* and *Rhodeus lighti* (syn. *Pseudosperilampus 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

Fig. 13

Synonym: *Paraortholinea* Kovaleva in Shulman et al. 1997

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

Spores spherical or inversely pyramidal, may have caudal or lateral projections. Two spherical or subspherical 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.

**Sinuolinea** Davis, 1917

Fig. 14

Spores spherical or subspherical, sutural line sinuous or extremely meandering so that its orientation to the two polar capsules, which are set widely apart, is sometimes difficult to assess. Sporoplasm binucleate, plasmodia mono- to polysporic. Number of species: 21.

Type species *Sinuolinea dimorpha* (Davis, 1916) Davis, 1917 (Fig. 14) described from the urinary system of the marine fish *Cynoscion regalis* along the U.S. Atlantic coast.

**Davisia** Laird, 1953

Fig. 15

Spores spherical or subspherical, sutural line straight or sinuous. Shell valves extend into long hollow lateral appendages, the cavity of which is discontinuous with the spore cavity. Polar capsules lie anteriorly at a certain distance from each other. Trophozoites mono-, di- and polysporic. Number of species: 19.

Reference: list of species – Aseeva (2002).

Type species *Davisia diplocrepis* Laird, 1953 (Fig. 15) common in the urinary bladder of the marine fish *Diplocrepis puniceus* in New Zealand waters.

**Myxoproteus** Doflein, 1898

Fig. 16

Synonym: *Conispora* Sankurathri, 1977

Spores inversely pyramidal or triangular in sutural view, with rounded outlines. Anterior end broad and more or less flattened. Thick spore valves may have various projections. Sutural line straight or sinuous. Polar capsules lie well apart, sporoplasm binucleate. Trophozoites mono- to polysporic. Number of species: 7.

Type species *Myxoproteus ambiguus* (Thélohan, 1895) Doflein, 1898 in the urinary bladder of the marine fish *Lophius piscatorius*. (In the absence of a reliable picture of the type species, Fig. 16 shows *M. abyssus* Yoshino et Moser, 1974 adapted from their original paper).

**Bipteria** Kovaleva, Zubchenko et Krasin, 1983

Fig. 17

Spores inversely pyramidal in sutural view with pointed end extending backwards. In transverse section, the spore is ellipsoid. Suture sinuous. Anterior end of each shell valve extends into a wing-like projection containing parts of valvogenic nucleus. Polar capsules spherical, a single sporoplasm. Plasmodia di- and polysporic. Number of species: 8.

Type species *Bipteria admiranda* Kovaleva, Zubchenko et Krasin, 1983 (Fig. 17) described from the urinary bladder of the marine fish *Pagellus acarne* from the East-Central Atlantic.

**Paramyxoproteus** Wierzbicka, 1986

Fig. 18

Like *Bipteria*, but valvular 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. Kovaleva (1989) takes it for a junior synonym of *Myxoproteus*. Number of species: 2.

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

**Neobipteria** Kovaleva, Gaevskaya et Krasin, 1986 Fig. 19

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 Fig. 20

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 Fig. 21

Spores inversely pyramidal and rounded. Two keel-like membranes extend along the slightly wavy sutural line; two thickenings adhere 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 *Urophycis chuss* 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 and in the parenchyma of a platyhelminth.

**Fabespora** Naidenova et Zaika, 1969 Figs. 22, 23

With characters of the family; disporous trophozoites. In capsulogenesis the external tube is missing. Sporoplasm binucleate. Number of species: 2.

Type species *Fabespora nana* Naidenova et Zaika, 1969 (Fig. 22) originally described from the gall bladder of three marine fishes *Mesogobius batrachocephalus*, *Scorpaena porcus* and *Proterorhinus marmoratus* in the Black Sea.

*Fabespora vermicola* Overstreet, 1976 (Fig. 23) was described from the digenean parasite *Crassicutis archosargi* of the estuarine sparid fish *Archosargus probatocephalus* from Mississippi state, USA. The assignment to the genus may rise doubts. Spores can exhibit a weak movement due to contractile fibres fastened up to the shell valves. This is the only case of spore movement among Myxosporea (Weidner and Overstreet 1979).

**Ceratomyxidae** Doflein, 1899

The two valves of the spores are elongated or drawn out to an enormous length in the direction perpendicular to the straight central transverse suture. Sometimes the two valves are asymmetrical. Polar capsules close to the suture line, in a plane perpendicular to it, are spherical or subspherical and have foramina near the sutural line at the anterior pole of the

spore. Plasmodia mostly disporic, sometimes mono- to polysporic. Coelozoic in marine fishes, rarely histozoic in freshwater fishes.

Reference: Meglitsch (1960).

**Ceratomyxa** Thélohan, 1892 Figs. 24, 25

Spores elongated, as a rule crescent-shaped or arcuate, thin shell valve exceeds in length the axial diameter of the spore. Shell valves often pliable rather than being rigid as in other genera. Subspherical polar capsules are located and open as is typical of the family, exceptionally they open laterally from the central suture line. Binucleate sporoplasm does not fill the spore cavity completely; in some species, two uninucleate sporoplasms were reported. Trophozoites usually disporic, sometimes mono- to polysporic. Coelozoic parasites of marine fishes. There are at least five species from freshwater hosts, obviously derived from marine ancestors: *Ceratomyxa anguillae* 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 *Tenualosa ilisha* (syn. *Hilsa ilisha*), *C. hongzhensis* Hsieh et Chen, 1984 from the gall bladder of *Pelteobagrus eupogon* (syn. *Pseudobagrus eupogon*) from China, *C. hungarica* Molnár, 1992 from Bowman's capsules and renal tubules of freshwater goby *Proterorhinus marmoratus* from the Danube river basin, and *C. shasta* 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 myxosporeans (Kent et al. 2001). Its actinospore 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. (2004).

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. centrodonatus*), *Scorpaena porcus* and *S. scrofa* in the Mediterranean.

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

**Leptotheca** Thélohan, 1895 Fig. 26

Spores oval, ellipsoidal, 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., 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 sporoplasms. 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 *Dasyatis pastinaca* (syn. *Trygon pastinaca*) and of a species of the genus *Scorpaena* along the French coast.

**Meglitschia** Kovaleva, 1988

Fig. 27

Differs from *Ceratomyxa* by an almost V-shaped spore; elongate polar capsules lie almost axially in each valve. Coelozoic, polysporic trophozoites.

Type and only species *Meglitschia insolita* (Meglitsch, 1960) Kovaleva, 1988 (Fig. 27) in the gall bladder of the marine fish *Dactylopagrus macropterus* from off New Zealand.

**Ellipsomyxa** Køie, 2003

Fig. 28

Spores elongated in direction perpendicular to the straight central transverse suture. Thin-walled valves hemispherical to elongate. Two equal spherical polar capsules at some distance from sutural plane on opposite sides of the spore close to the surface, discharging in opposite directions. Disporic plasmodia coelozoic in the gall bladder of marine fish.

Type and only species *Ellipsomyxa gobii* Køie, 2003 (Fig. 28) in the marine fish *Pomatoschistus microps* in the sea near Helsingør, Denmark. Forms tetractinomyxon actinospore stages in definitive hosts, polychaetes of the genus *Nereis* (Køie 2003a, Køie et al. 2004).

**Sphaerosporidae** Davis, 1917

Spores generally spherical or subspherical, 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 polysporic. Mostly coelozoic in marine and freshwater fishes, sometimes histozoic.

Reference: Meglitsch (1970).

**Sphaerospora** Thélohan, 1892

Figs. 29, 30

Synonym: *Podospora* Chen et Hsieh, 1984

Spherical or subspherical spores, valvular 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 subspherical 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 extrasporogonic stages in blood and various other tissues. Many species are pathogenic. Number of species: 78, one of which in anuran amphibians.

Complete life cycle has been revealed in two species: *Sphaerospora renicola* (see below); in *S. truttae* occurs the echinactinomyxon stage (Özer and Wootten 2000).

References: key to species – Sitjà-Bobadilla and Alvarez-Pellitero (1994); fine structure – Sitjà-Bobadilla and Alvarez-Pellitero (1992), McGeorge et al. (1994), Dyková and Lom (1997).

Type species *Sphaerospora elegans* Thélohan, 1892 (Fig. 29) occurs in renal tubules and connective tissue of the ovary of *Gasterosteus aculeatus* and *Pungitius pungitius* in France and UK (Feist et al. 1991).

Pathogenic species: *Sphaerospora ictaluri* Hedrick, McDowell et Groff, 1990 commonly infects renal tubules of farmed alevis of *Ictalurus punctatus* in California. Its developmental stages are the possible cause of the “hamburger disease” of this host (Hedrick et al. 1990). *S. molnari* Lom, Dyková, Pavlásková et Grupcheva, 1983, a histozoic species largely distributed in the gills of common carp, *Cyprinus car-*

*pio*, in Europe (Molnár 1979a, Lom et al. 1983b, Svobodová and Groch 1986). *S. renicola* Dyková et Lom, 1982 (Fig. 30) is a widely distributed and serious pathogen in renal tubules of cultured common carp, *Cyprinus carpio*, throughout Eurasia, Israel and Australia. The definitive host is the oligochaete *Branchiura sowerbyi*, in which neoactinomyxon stage develops (Grossheider and Körting 1993, Molnár et al. 1999b). Odening et al. (1989) claimed a direct transmission by means of spores or infected kidney tissue. This finding warrants re-examination. Curiously, this species and *S. molnari* are sister species (Eszterbauer and Székely 2004). *S. testicularis* Sitjà-Bobadilla et Alvarez-Pellitero, 1990 in seminiferous tubules in the testes of cultured *Dicentrarchus labrax* in the Mediterranean (Sitjà-Bobadilla and Alvarez-Pellitero 1993a). *S. tincae* Plehn, 1925 in pronephros of *Tinca tinca* in Europe (Hermanns and Körting 1985). *S. truttae* Fischer-Scherl, El-Matbouli et Hoffmann, 1986 in the renal tubules of *Salmo trutta* in Europe (McGeorge et al. 1996a, Holzer et al. 2003).

References: *Sphaerospora renicola*, blood phase – Lom et al. (1983a), Grupcheva et al. (1985); swimbladder phase – Csaba et al. (1984), Körting et al. (1984), Molnár and Kovacs-Gayer (1986b), Odening et al. (1988), Dyková et al. (1990).

**Polysporoplasma** Sitjà-Bobadilla et Alvarez-Pellitero, 1995

Fig. 31

Differs 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 sparisi* Sitjà-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).

**Hoferellus** Berg, 1898

Fig. 32

Synonyms: *Hoferia* Doflein, 1898; *Mitraspora* Fujita, 1912

Spores in valvular view pointed, mitre-like or completely rounded, with many stiff filaments at the posterior end. Polar capsules pyriform, sporoplasm 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 *Hoferellus*, 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 as a *nomen conservandum*.

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

Type species *Hoferellus cyprini* (Doflein, 1898) Mercier, 1908 (Fig. 32) is a common pathogen in the urinary system of common carp, *Cyprinus carpio* in Eurasia. Actinospore phase represented by aurantiactinomyxon stage (Grossheider and Körting 1992).

*Hoferellus carassii* Akhmerov, 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). Actinospore phase found to be an aurantiactinomyxon (according to El-Matbouli et al. 1992a) or neoactinomyxon stage (Yokoyama et al. 1993); this indicates the uncertain identification of this species.

**Wardia** Kudo, 1919

Fig. 33

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, histozoic 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 ovinocua* Kudo, 1919 (Fig. 33) described from oocytes and connective tissue in ovaries of *Lepomis humilis* in Illinois, USA.

**Palliatius** Shulman, Kovaleva et Dubina, 1979

Fig. 35

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 binucleate. 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 *Palliatius mirabilis* Shulman, Kovaleva et Dubina, 1979 (Fig. 35) in the gall bladder of the marine fish *Xenodermichthys copei* (syn. *X. socialis*) off Guinea-Bissau.

**Myxobilatus** Davis, 1944

Fig. 34

Elongated spores are anteriorly pointed. Shell valves often with fine ridges extend posteriorly into two caudal appendages. Polar capsules pyriform in the level perpendicular to the sutural plane, binucleate sporoplasm may contain an iodophilous vacuole. Coelozoic trophozoites, small or large, disporic or polysporic with pansporoblast formation, occur all the length through the urinary system. They are rarely histozoic. Number of species: 33 in freshwater and marine fishes.

References: discussion on taxonomy – Lom (1986); fine structure – Booker and Current (1981).

Type species *Myxobilatus gasterostei* (Parisi, 1912) Davis, 1944 (Fig. 34) described from renal tubules of the freshwater and estuarine fish *Gasterosteus aculeatus* in Eurasia.

## Chloromyxidae Thélohan, 1892

Spores spherical, subspherical or slightly elongated are bisected by a straight meridional suture. They may bear fine caudal appendages. Four polar capsules are located at the spore apex: either one pair in the level of the sutural line and the second pair perpendicularly to the suture, or both pairs diagonally beyond the plane of the suture. Plasmodia either small (monosporic) to medium-sized, polysporic, in which formation of pansporoblasts occurs. Coelozoic, rarely histozoic, in freshwater and marine fishes, some in amphibians.

**Chloromyxum** Mingazzini, 1890

Figs. 36, 37

Spore valves smooth or ridged, rarely with caudal filamentous projections. Polar capsules often in two pairs of unequal size. Sporoplasm binucleate, rarely uninucleate. For exact determination of species, one has often to resort to scanning electron microscope. Species composition of the genus is heterogeneous. *Chloromyxum* species differ in phylogeny as well as in actinospore stages. Neoactinomyxon was found in a freshwater *Chloromyxum* sp., antonactinomyxon in *C. auratum*

(Hallett et al. 2006) and aurantiactinomyxon in *C. truttae* (Holzer et al. 2004). Number of species: 115, including 3 in amphibians.

References: Listerbarger and Mitchell (1980), Lom and Dyková (1993); phylogeny – Fiala and Dyková (2004).

Type species *Chloromyxum leydigii* Mingazzini, 1890 (Fig. 36) described originally —without specifying the host— from the gall bladder of various species of a number of sharks and skates of the genera *Mustellus*, *Galeus* (syn. *Pristiurus*), *Raja*, *Scyllium*, *Squatina*, *Torpedo* and *Trygon*. A thorough revision will probably show the present *C. leydigii* described from many hosts to be an assemblage of several species, as suggested by Jameson (1929) and Kuznetsova (1977).

Pathogenic species: *Chloromyxum cristatum* Léger, 1906 (Fig. 37) in the gall bladder of *Tinca tinca* and other cyprinids; may cause necrosis of the liver parenchyma of *Cyprinus carpio* (Lom and Dyková 1984). Complete life cycle of this species has been solved by Hallett et al. (2006): myxospores alternate with antonactinomyxon actinospores. *C. truttae* Léger, 1906 in the gall bladder of *Salmo trutta fario*, *S. salar*, *Onchorynchus mykiss* and other salmonids (Bauer et al. 1981).

**Caudomyxum** Bauer, 1948

Fig. 38

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 *Molge 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

Fig. 39

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. Histozoic 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.

## Auerbachiiidae Evdokimova, 1973

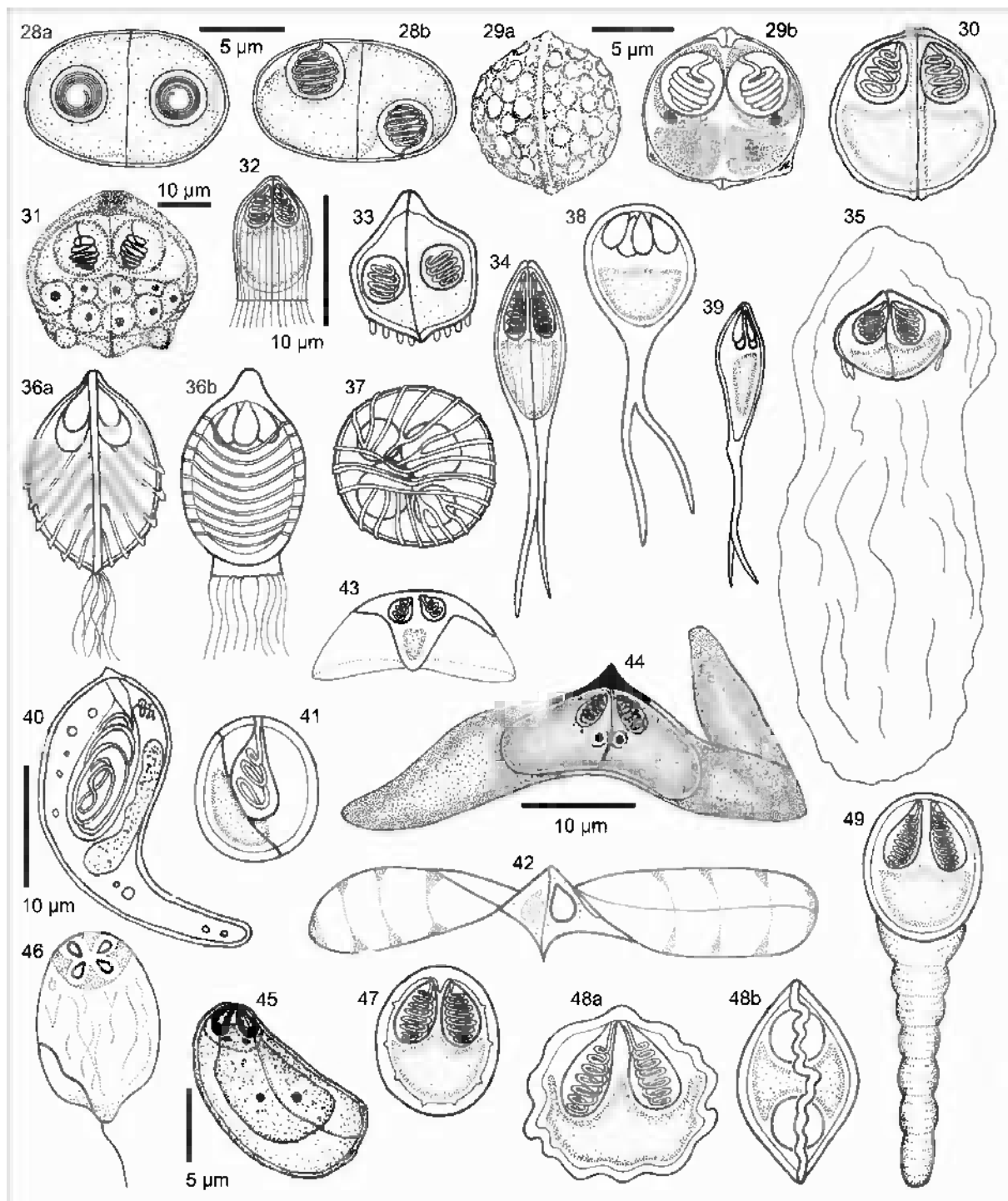
Spores have asymmetrical unequal smooth shell valves and a single elongated polar capsule with a filament making a few longitudinal turns. Coelozoic, polysporic plasmodia in the gall bladder of marine fishes.

**Auerbachia** Meglitsch, 1968

Fig. 40

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 plasmodia. Number of species: 3.

Type species *Auerbachia anomala* Meglitsch, 1968 (Fig. 40) in the gall bladder of the deep-sea fish *Genypterus blacodes* 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 ovinocua*. **Fig. 34.** *Myxobilatus gasterostei* in sutural view. **Fig. 35.** *Palliatius mirabilis* in sutural view. **Fig. 36.** *Chloromyxum leydigi* 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.** *Pseudoalatospora 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 clavicauda*.

**Globospora** Lom, Noble et Laird, 1975 Fig. 41

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. Sporogonic 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 samaroidea* 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 scomberi* 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 spore 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 Køie (2003b).

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

Pathogenic species: *Parvicapsula minibicornis* Kent, Whitaker et Dawe, 1997 may cause severe infections in kid-

ney of feral and cultured salmonids of the genus *Oncorhynchus* at the northern U.S. Pacific coasts (St-Hilaire et al. 2002, Jones et al. 2003). Its morphology differs somehow from that of other species of this genus. It has an actinospore stage, probably a tetractinomyxon, in the coelom of the polychaete *Manayunkia speciosa* (Bartholomew et al. 2005). *P. pseudo-branchicola* Karlsbakk, Saether, Hostlund, Fjellsoy et Nylund, 2002 infects pseudobranchs of cultured *Salmo salar* in Norway, causing mortalities (Karlsbakk et al. 2002, Nylund et al. 2005). Probably identical is *Parvicapsula* sp. infecting pseudobranchs and kidney of *Oncorhynchus kisutch* in maricultures at the U.S. Pacific coast (Yasutake and Elliot 2003).

**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 spore 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 gibberifrons* (syn. *Notothenia gibberifrons*) from the South Atlantic.

**SUBORDER PLATYSPORINA** Kudo, 1919

Spores as a rule flattened parallel to the sutural plane, bilaterally symmetrical. Generally two, sometimes one polar capsule lies solely in the sutural plane. As a rule, histozoic parasites of freshwater fishes, which produce large polysporic plasmodia; spores—as a rule with hard shells—arise in pansporoblasts. Plasmodia up to several mm in size are enveloped by the connective tissue of the host and appear like small cysts.

**Myxobolidae** 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; *Facieplatyscauda* Wyatt, 1979; *Rudicapsula* Kalavati et Narasimhamurti, 1984

Spores in valvular view ellipsoidal, 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 iodophilous 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. cone* 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 cerebalis* (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. portucalensis* (El-Mansy et al. 1998), *M. hungaricus* (El-Mansy and Molnár 1997b), *M. pseudodispar* (Székely et al. 2001), *M. bramae* (Eszterbauer et al. 2000), *M. macrocapsularis* (Székely et al. 2002) and *M. parviformis* (Kallert et al. 2005b) the actinospore stage is a triactinomyxon. In *M. pavlovskii* it is hexactinomyxon (Ruidisch et al. 1991), in *M. cultus* (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 – Eszterbauer (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.

Pathogenic species: *Myxobolus acanthogobii* Hoshina, 1952 (syn. *M. buri* Egusa, 1985), parasite of the brain, causes scoliosis of cultured marine fish *Seriola quinqueradiata* in Japan (Sakaguchi et al. 1987, Yokoyama et al. 2004). *M. buckei* Longshaw, Frear et Feist, 2003 is highly pathogenic to juvenile cyprinids of the genera *Leuciscus*, *Rutilus* and *Abramis*, in which it destroys the spinal column (Longshaw et al. 2003). *M. cerebalis* Hofer, 1903, agent of the “whirling disease” of salmonid fry of the genera *Hucho*, *Oncorhynchus*, *Salmo* and *Salvelinus*, infecting mainly head and gill cartilage, originally probably a mild pathogen of *Salmo trutta* in Central Europe, it is now globally distributed (Hoffman 1990, El-Matbouli et al. 1995, 1998, 1999, Andree et al. 1997, 2002, Hedrick et al. 1998, Bartholomew and Wilson 2002, Hedrick and El-Matbouli 2002, Gilbert and Granath 2003). *M. drjagini* (Akhmerov, 1954) in subcutaneous tissue, central nervous system and organs of balance of *Hypophthalmichthys molitrix* in Asia; it is the agent of epizootics of “twist disease” and mass mortalities in China (Wu et al. 1979). *M. encephalicus* (Mulsow, 1911) in brain blood vessels of *Cyprinus carpio* in Europe (Dyková et al. 1986). *M. insidiosus* Wyatt et Pratt, 1963 in the muscle of North American salmonids of the genera *Oncorhynchus* and *Salmo* (Wyatt 1979, Amandi et al. 1985). *M. pavlovskii* Akhmerov, 1954, common in the gills of *Hypophthalmichthys molitrix* and *Aristichthys nobilis* in the Far East Amur region, was imported along with these hosts to Europe (Molnár 1979b). *M. sandrae* Reuss, 1906 in subcutaneous connective tissue of the head, in branchial cavity, sometimes in the gills of *Sander lucioperca* (syn. *Stizostedion lucioperca*) in Europe. In the spinal cord of *Perca fluviatilis* in Scotland, infections result in severe deformations of the vertebral column (Lom et al. 1991a).

#### *Spirosuturia* Chen et Hsieh, 1984

Fig. 48

Differs 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. Histo-zoic 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

Spores similar to those of *Myxobolus* have a single caudal appendage. This, unlike in *Henneguya*, 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 histo-zoic 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.

Reference: synopsis of the genus – Cone and Melendy (2000).

Type species *Unicauda clavicauda* (Kudo, 1934) Davis, 1944 (Fig. 49) in subcutaneous tissue of *Notropis bleinnius* 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 atherinoidi* Hoffman et Walker, 1978 (Fig. 50) in subcutaneous tissue of freshwater fish *Notropis atherinoides* 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 histo-zoic parasite of the gills of freshwater fish *Mystus bleekeri* from India (Qadri 1962a).

#### *Laterocaudata* Chen et Hsieh, 1984

Fig. 52

Spores similar to those of *Myxobolus* are ellipsoidal in valvular view and have a long, thin and curved process split at the end. The process originates posteriolaterally 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 *Macrognathus aculeatus* (syn. *Mastacembelus aculeatus*) from China.

#### *Henneguya* Thélohan, 1892

Fig. 53

Spores ellipsoid, spindle-shaped or rounded in valvular 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 pansporoblast 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 *Henneguya* is an invalid taxon is probably legitimate, since the distinguishing character, the two caudal projections, 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).

References: Minchew (1977), Kent et al. (2001), Eiras (2002 – list of species); fine structure – Lom and de Puytorac (1965b), Schubert (1968).

Complete life cycle is known in three species: in *Henneguya exilis* the actinospore is an aurantiactinomyxon earlier described as *A. janszewskaei* (Lin et al. 1999), in *H. ictaluri* the aurantiactinomyxon was earlier named as *A. ictaluri* (Pote et al. 2000), in *H. nuesslini* Schubert 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 *Esox lucius* and *Perca fluviatilis*, perhaps also *Sander lucioperca* (syn. *Stizostedion lucioperca*) in Eurasia (Dyková and Lom 1978).

Pathogenic species: *Henneguya exilis* Kudo, 1929 in the gills of *Ictalurus punctatus* in North America. (Current and Janovy 1978, Bowser and Conroy 1985, Duhamel et al. 1986). *H. ictaluri* Pote, Hanson et Shivaji, 2000, one of the agents of the proliferative gill disease (PGD, also hamburger disease) of *Ictalurus punctatus* in North America (Pote et al. 2000, Bolein and Pote 2001). *H. lateolabracis* Yokoyama, Kawakami, Yasuda et Tanaka, 2003 causes cardiac henneguyosis with chronic mortalities in cultured *Lateolabrax* sp. in Japan (Yokoyama et al. 2003). *H. pagri* Yokoyama, Itoh et Tanaka, 2005 infects bulbus arteriosus of the heart of cultured *Pagrus major* in Japan, causing degenerative cardiomyopathy and chronic mortalities (Yokoyama et al. 2005). *H. zschokkei* Gurley, 1894 [probable synonyms are *H. salminicola* Ward, 1919 and *H. tegidiensis* Nicholas et Jones, 1959; possibly also *H. kolesnikovii* (Gurley, 1894) Labbé, 1899] in muscles of several species of the genus *Coregonus* in Europe and five species of the Pacific salmon common to North American and Asian coasts – *Oncorhynchus gorbuscha*, *O. keta*, *O. kisutch*, *O. nerka*, *O. tshawytscha* and *O. mykiss* (Awakura and Kimura 1977, Boyce et al. 1985).

#### ***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 pansporoblast 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**

Spores 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. Histo-zoic in freshwater fishes. Number of species: 2.

Reference: Azevedo and Matos (1996).

Type species *Tetrauronema macropodus* Wu, Wang et Jiang, 1988 (Fig. 55) in gill filaments of *Macropodus opercularis* (syn. *M. chinensis*) in Fujian province, China.

#### ***Thelohanellus* Kudo, 1933 Figs. 56, 57**

Spores 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 subspherical 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 pansporoblast formation are mostly large. Histo-zoic 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 (Sołtynska 1967, Dyková and Lom 1987).

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

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 thelohanellosis (Molnár and Kovacs-Gayer 1986a, Yokoyama et al. 1998 Liyanage et al. 2003). *T. kitauei* Egusa et Nakajima, 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.

References: Molnár (1982), Desser et al. (1983), Székely et al. (1998).

#### ***Neothelohanellus* Das et Haldar, 1986 Fig. 58** Synonym: *Lomosporus* Gupta et Khera, 1988

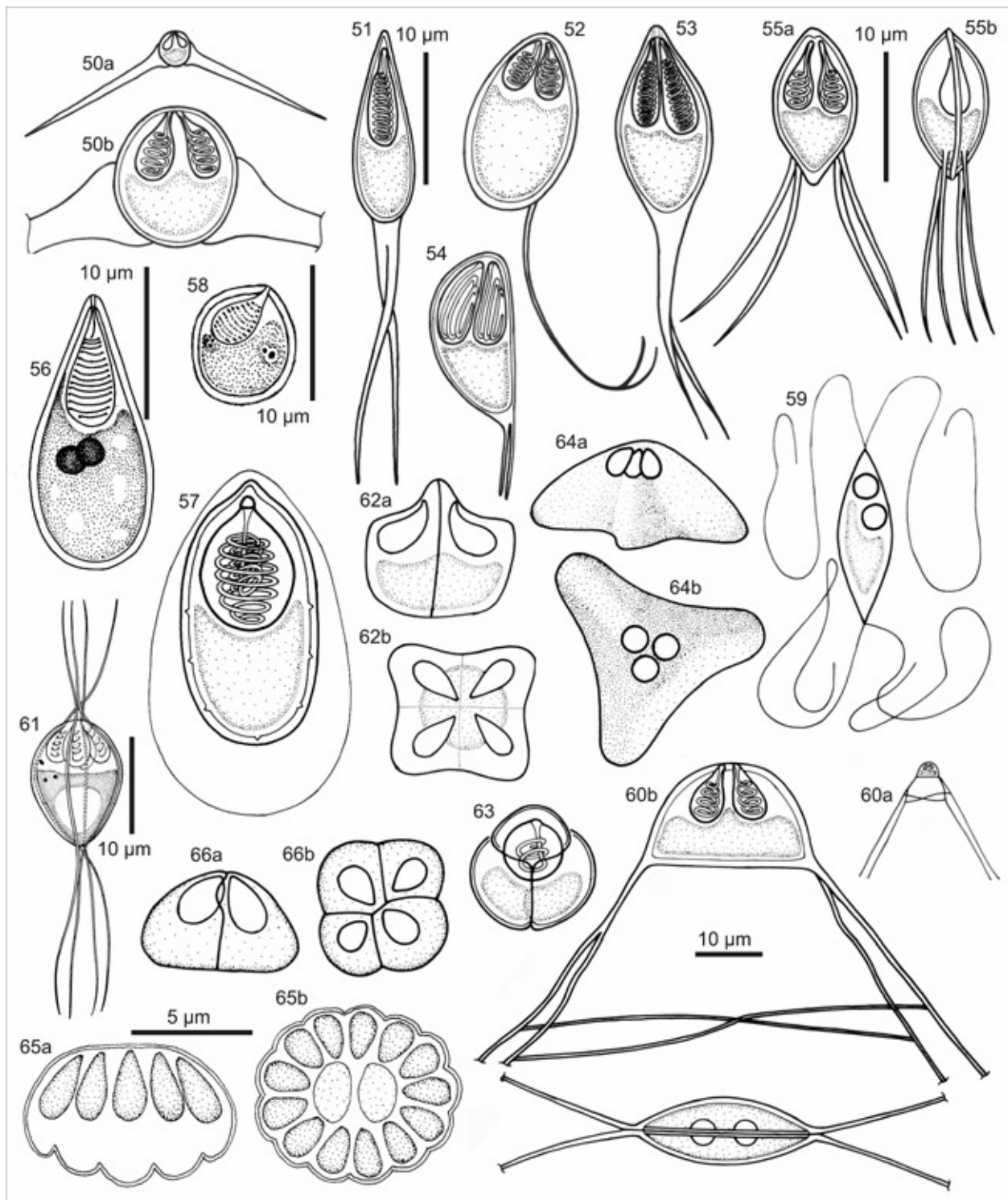
Spores in frontal view oval or egg-shaped with a wider anterior end; longitudinal suture line. A single elliptical polar capsule at the anterior end opens laterally or subapically. Large polysporous plasmodia. Histo-zoic in freshwater fish. The genus does not differ essentially from *Thelohanellus* and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

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

#### ***Neohenneguya* Tripathi, 1953 Fig. 59**

Spores spindle-shaped in valvular view and flattened spindle-shaped 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 polysporic plasmodia histo-zoic in freshwater fishes.

Type and only species *Neohenneguya tetradia* Tripathi, 1953 (Fig. 59) is histo-zoic 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.** *Trigonosporus acanthogobii*. **Fig. 61.** *Octospina tongrensis* (modified from Hsieh and Xiao 1993). **Fig. 62.** *Trilospora californica* in side (a) and apical view (b). **Fig. 63.** *Uncapsula seriola*. **Fig. 64.** *Kudoa chupeiidae* 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

Fig. 60

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 suture 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.

References: Kovaleva and Shulman (1978), Egusa (1986).

Whipps et al. (2003) described a multivalvulid species with 13 polar capsules as *Kudoa permulticapsula*, 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 Whipps 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 outlier 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<sup>1</sup>. However, the results of Whipps 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 Whipps 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

Fig. 62

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.

Pathogenic species: *Trilospora muscularis* Priebe, 1987 in the muscle of *Molva dypterygia* in the North Atlantic (Priebe 1987).

**Unicapsula** Davis, 1924

Fig. 63

Synonyms: *Pileispora* Naidenova et Zaika, 1970; *Parapileispora* Naidenova et Zaika, 1970, pro parte

Spores subspherical, with three unequal shell valves. The small one covers a single spherical polar capsule, while two larger valves, arranged symmetrically contain each a capsular rudiment only discernible by electron microscopy, and two uninucleate sporoplasms, one enveloping the other. In marine fishes. Large polysporic plasmodia in muscles or, in one species, gill filaments. Number of species: 8.

References: fine structure – Schubert et al. (1975), Lester (1982).

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.

**Kudoidae** Meglitsch, 1960

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

**Kudoa** Meglitsch, 1947

Figs. 64–66

Synonyms: *Neochloromyxum* Matsumoto, 1954; *Tetraspina* Xie et Chen, 1988

Spores in apical view stellate, quadrate or rounded quadrate; sometimes they are asymmetrical with one valve bigger than the others. Polar capsules pyriform. Two uninucleate sporoplasms, one enveloping the other. Trophozoites small, producing one to seven spores, or large, producing many spores. Parasites of marine fishes; most species are intracellular in muscle cells, exceptionally they infect tissues other than muscles or are coelozoic. Typical parasites of cultured marine fishes (e.g., Egusa and Shiomitsu 1983). Number of species: 63.

References: Kovaleva et al. (1979), Moran et al. (1999a); recent list of species – Swearer and Robertson (1999).

Type species *Kudoa clupeiidae* (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).

<sup>1</sup>Whipps et al. (2004) discussed thoroughly their results and options they offered: either leave the classification as it was – but they thought the revision was appropriate; or introduce subgenera which they did not want since by far not all *Kudoa* species have been sequenced and thus could not be assigned. So they chose the third, more radical option to reclassify multivalvulids with four or more shell valves as *Kudoa* species. As one of their supporting arguments they took comparison of genetic distances: maximum distance between any pair of multivalvulid species was 15.9%, while e.g., maximum distance observed within *Myxobolus* spp. was 31.1%. However, it is quite feasible (see above) that the latter genus will be split into separate genera. Also, according to Fiala (pers. comm.), “the monophyly” of multivalvulids has been disturbed by two *Sphaerospora* species, clustered within the *Kudoa* clade.

*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* (Pérard, 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 *Sphyrna 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, Moran et al. 1999b).

Species damaging the muscle tissue by proliferation of a mass of trophozoites: *Kudoa amamiensis* Egusa et Nakajima, 1978 in cultured *Seriola quinqueradiata* 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** Fig. 67

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

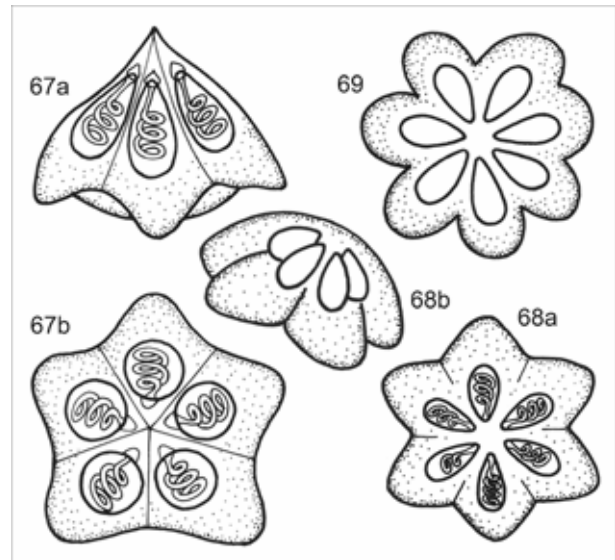
Type species *Pentacapsula shulmani* Naidenova et Zaika, 1970 (Fig. 67) in skeletal muscles of *Nemipterus japonicus* from the Pacific.

Pathogenic species: *Pentacapsula neurophila* Grossel, Dyková, Handlinger et Munday, 2003 causes severe granulomatous encephalomyelitis in cultured *Latris lineata* in Tasmanian waters (Grossel et al. 2003).

#### ***Hexacapsula* Arai et Matsumoto, 1953** Fig. 68

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 sporogonic plasmodia were given. The parasite induces "jellied condition" of the flesh (Arai et Matsumoto 1953). Such fish are unmarketable.



**Fig. 67–69.** Line drawings of myxosporean spores. **Fig. 67.** *Pentacapsula shulmani* in side (a) and apical view (b). **Fig. 68.** *Hexacapsula neothunni* in side (a) and apical view (b). **Fig. 69.** *Septemcapsula yasunagai* in apical view. Figs. 68–70, 72–80 and 82 are reproduced through courtesy of Dr. A. Marques from his thesis (Marques 1984).

#### ***Septemcapsula* Hsieh et Chen, 1984**

Fig. 69

Multivalvulids with seven shell valves, each containing one polar capsule, parasitic in muscles of marine fishes.

Type and only species *Septemcapsula yasunagai* Hsieh et Chen, 1984 (Fig. 69) is a pathogen in brain cavity of cultured marine fishes *Lateolabrax japonicus* and *Oplegnathus fasciatus* in China. No data on sporogonic plasmodia were given.

As an appendix to multivalvulids, two organisms are added which, in spite of having three and four shell valves and reminding in this respect of this order, do not comply with its definition.

#### ***Trilosporoides* Køie, 2005**

Fig. 85

Køie (2005b) described a myxosporean, which she placed temporarily in the vicinity of the family Trilosporidae Shulman, 1959 because of spores equipped with three polar capsules. However, the polar capsules are situated peripherally and discharge laterally, the spore has a long conical posterior end and tips of polar capsules protruding through the shell valve unlike most myxosporeans and much alike actinospore stages. This is strongly at variance with Trilosporidae and therefore one has to consider *Trilosporoides* to be of *incertae sedis* in Multivalvulida.

Type and only species *Trilosporoides platessae* Køie, 2005 (Fig. 85) infects the gall bladder of *Pleuronectes platessa* from the sea off Helsingør, Denmark. The spores were 24 µm long and only 9 µm in diameter. Plasmodia were not described.

#### ***Spinavaculida* Hsieh et Xiao, 1993**

Spores stout, spindle-shaped, with four identical valves; the sutural ridge of each of them extends anteriorad and posteriorad as a spine for a distance equalling spore length. Four polar capsules at the anterior pole. In body cavities of freshwater fishes. The position within multivalvulids is preliminary and may be artificial since spores of the only genus are built according to a

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 Tetravalvulida 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

Fig. 61

With characters of the family, sporoplasm with an iodophilous vacuole.

Type and only species *Octospina tongrensis* 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 Actinosporea. 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 cycles (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 (Køie et al. 2004). Consequently, also former actinospore genera of which no myxospore counterpart has yet been found can be taken as developmental stages (e.g., Guyenotia, Ormieractinomyxon). Moreover, even the recently erected actinospore genera (Endocapsa, Tetrasporea) should be taken for such collective groups and treated as vernacular names. It is possible that they belong to an already described myxosporean 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 tetrasporea, 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 Actinosporea, 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

Fig. 70

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 antonii 1957 (syn. Siedleckiella antonii Janiszewska, 1954) described from freshwater oligochaete *Limnodrilus claparedaeus*, from the Oder River at Wrocław, Poland.

RZS: 1, DS: 2.

#### **Aurantiactinomyxon** Janiszewska, 1952

Fig. 71

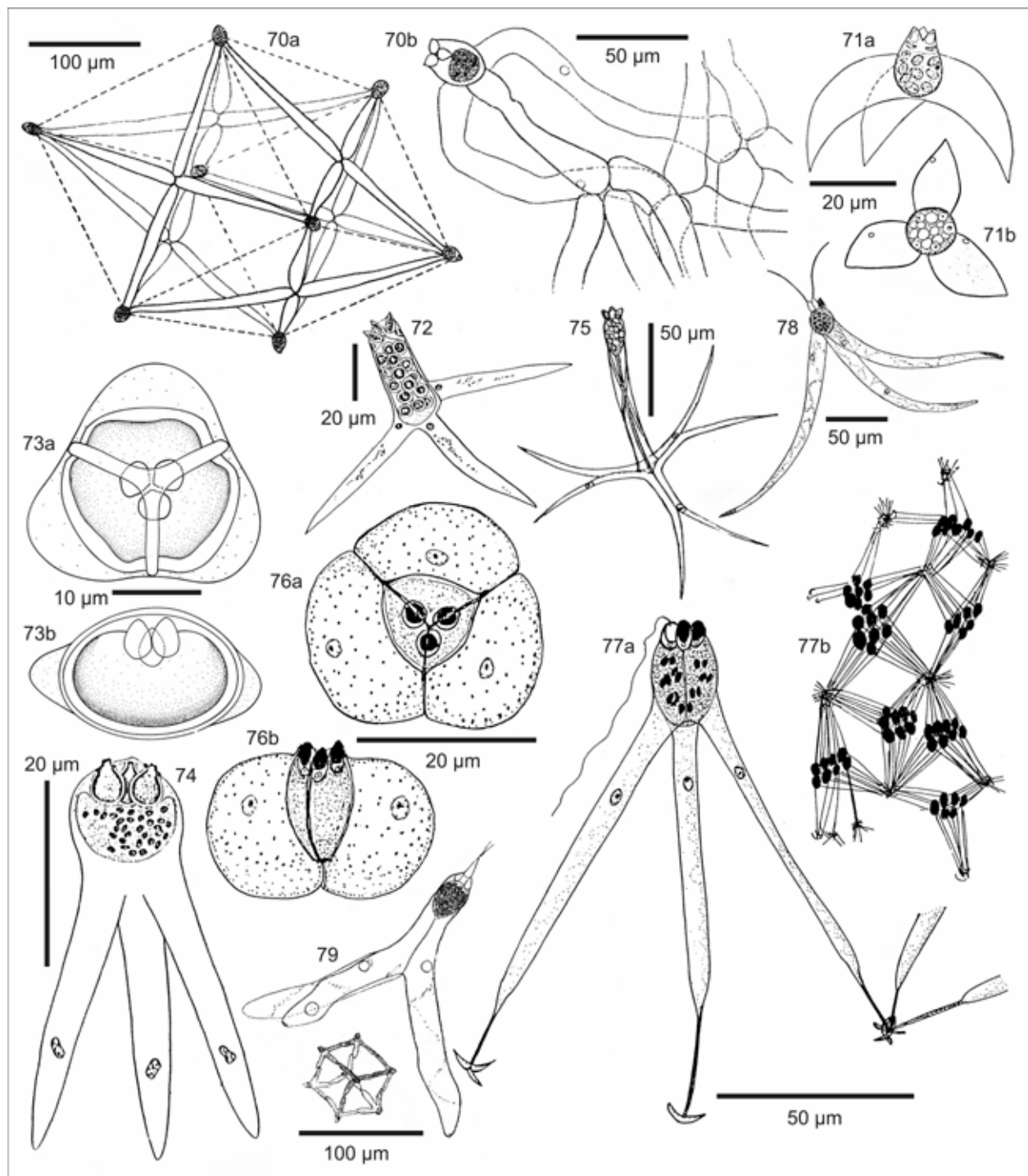
Three stout, semicircularly curved, leaf-like caudal projections are attached to an ellipsoidal spore body with protruding tips of polar capsules and a plasmodial sporoplasm with many infectious cells. In freshwater oligochaetes. Known as developmental stage in the life cycle of species of the genera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

RZS: 6, DS: 28.

#### **Echinactinomyxon** Janiszewska, 1957

Fig. 72

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 *raabeiunioris* 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 *psammoryctis* Štolc, 1899). **Fig. 76.** *Neoactinomyxum* (type *globosum* 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).

tal stage of *Sphaerospora truttae* and *Zschokkella* sp. Original type Echinactinomyxon radiatum Janiszewska, 1957 described from freshwater oligochaete *Tubifex tubifex* from the Oder River, Poland.

RZS: 4, DS: 15.

**Endocapsa** Hallett, Erséus et Lester, 1999

Fig. 73

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 rosulata* Hallett, Erséus et Lester, 1999 described from marine oligochaete *Heterodrilus* cf. *keenani* from Great Barrier Reef off Australia.

RZS: 2, DS: 0

**Guyenotia** Naville, 1930

Fig. 74

The subspherical spore body 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 Calvados region in France.

RZS: 1, DS: 0.

**Hexactinomyxon** Štolc, 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. In freshwater oligochaetes. Known as developmental stage in the life cycle of *Myxobolus pavlovskii*. Original type *Hexactinomyxon psammoryctis* Štolc, 1899 described from freshwater oligochaete *Psammoryctis barbatus* from the Vltava River in Prague, Czech Republic.

RZS: 2, DS: 6.

**Hungactinomyxon** Rácz, Eszterbauer et Molnár, 2005

Fig. 86

Subspherical spore body similar to echinactinomyxon, with three finger-like, lateroposterior 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 Száshalombatta, Hungary.

RZS: 0, DS: 1.

**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 oligochaetes. Known as developmental stage in the life cycle of *Hoferellus carassii* and *Chloromyxum* sp. Original type *Neoactinomyxum globosum* Granata, 1922 described from freshwater oligochaete *Limnodrilus udekemianus* from the Mugove River, Florence, Italy.

RZS: 4, DS: 14.

**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 oligochaete *Tubifex* sp. from the Plaine de Rousillon, 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 oligochaetes. 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 oligochaetes. Known as developmental phase in the life cycle of *Myxobolus dispar* and *Myxidium truttae*. Original type *Raabeia gorlicensis* Janiszewska, 1955 described from freshwater oligochaete *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 (of 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 oligochaetes. Original type *Siedleckiella silesica* Janiszewska, 1952 described from freshwater oligochaete *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 oligochaetes. Not known as developmental stage in the life cycle of any myxosporean. Original type *Sphaeractinomyxon stolci* Caullery et Mesnil, 1904 described from marine oligochaete species of genera *Clitellio*, *Pelosclex* and *Tubifex* at the Atlantic coast of France.

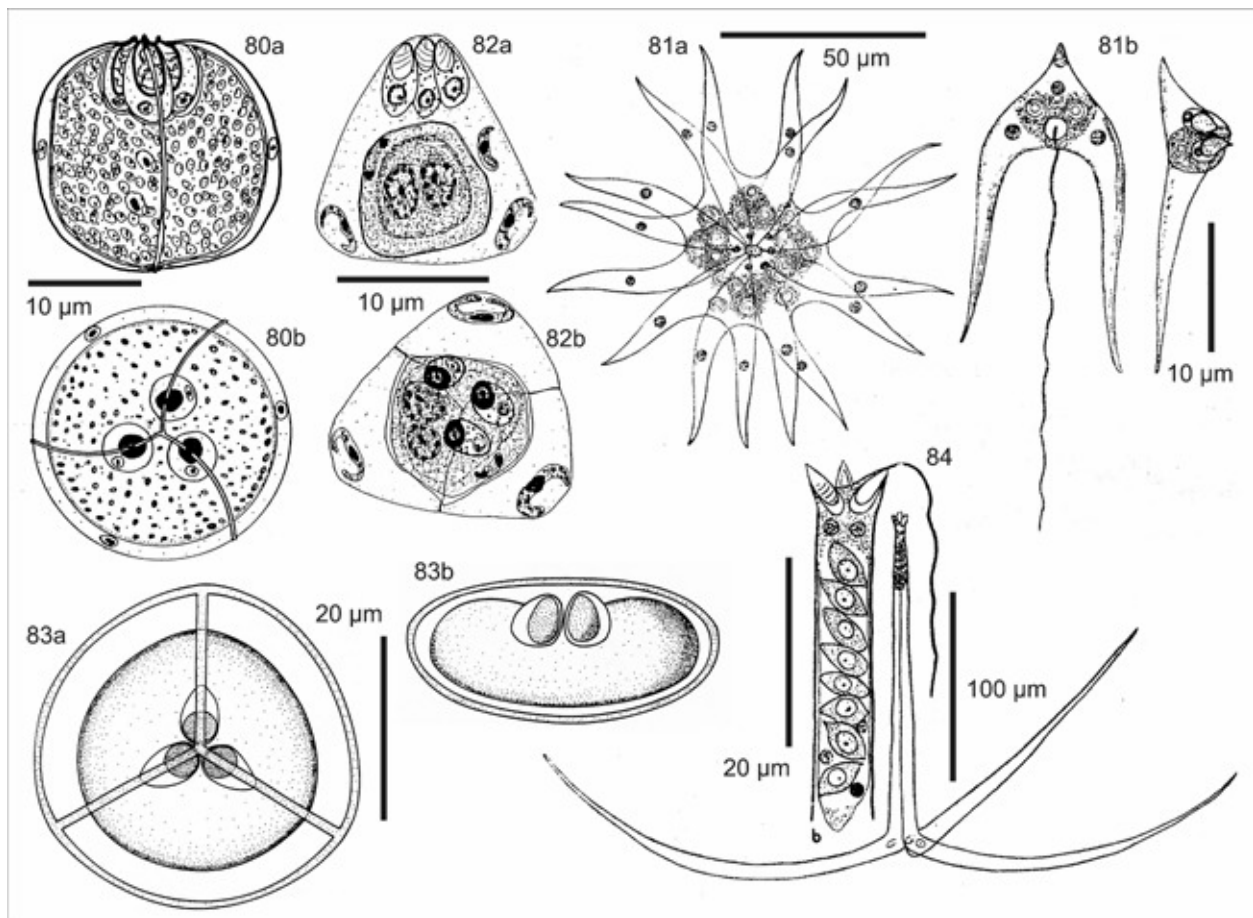
RZS: 8, DS: 0

**Synactinomyxon** Štolc, 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. Sporop-





**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

Fig. 82

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: 4.

#### **Tetraspora** Hallett et Lester, 1999

Fig. 83

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. Original type *Tetraspora discoidea* Hallett et Lester, 1999 described from marine oligochaete *Doliodrilus divicularis* from Moreton Bay, Queensland, Australia.

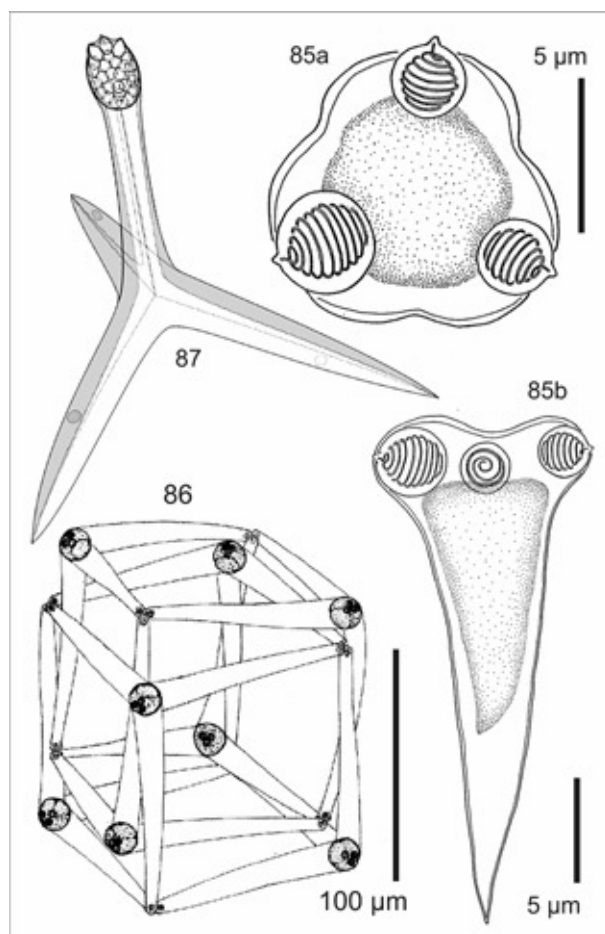
RZS: 2, DS: 0

#### **Triactinomyxon** Štolc, 1899

Fig. 84

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 nuesslini*. Original type *Triactinomyxon ignotum* Štolc, 1899 described from freshwater oligochaete *Tubifex* sp. from the Vltava River in Prague, Czech Republic.

RZS: 11, DS: 42.



**Fig. 85.** *Trilosporoides platessae*, myxospore in apical (a) and side view (b) (courtesy of Dr. M. Køie and Folia Parasitol.). **Fig. 86.** Hungactinomyxon, eight spores from a pansporocyst in a cube-like formation (courtesy of Dr. K. Molnár and Syst. Parasitol.). **Fig. 87.** Schematic representation of the valve cells and associated sutures in Pseudotriactinomyxon (courtesy of Dr. S. Hallett and Dis. Aquat. Org.).

#### **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., *Alato-sporea* vs. *Pseudoalato-sporea* 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 properly 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 situation of e.g., *Myxobolus cultus* 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.

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