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REVISED CLASSIFICATION OF THE CLASS MYXOSPOREA BÜTSCHLI, 1881

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Abstract. Reconsideration of characters important in myxosporean classification resulted in a new revision of the arrangement of taxa within the class Myxosporea Bütschli, 1881. This revision follows the main lines of the classification proposed by Levine's committee (1980) which incorporated Shulman's (1966) system for the class Myxosporea. The following suprageneric changes have been introduced: suborders Bipolarina Tripathi, 1948 and Eurysporina Kudo, 1919, and the family Myxosomatidae Poche, 1913 have been suppressed and new categories have been proposed: suborders Sphaeromyxina subord. n. and Variisporina subord. n. and families Sphaeromyxidae fam. n. and Ortholineidae fam. n. The genus *Myxosoma* Thélohan, 1892 is considered a junior synonym of *Myxobolus* Bütschli, 1881, and reasons for this are reviewed. The new revision continues to be based on the morphology of spores. Dangers of arbitrary decisions in assigning species with spores showing characters of two closely resembling genera are discussed. Further research is needed to make full use of trophozoite morphology, life cycle stages and mode of sporogony in myxosporean classification.

A growing interest in myxosporeans as important pathogens of fish, especially in intensive aquaculture, and discoveries of formerly never-dreamed-of stages in their life cycle (e.g., Lom et al. 1983a, Markiw and Wolf 1983, Molnár 1984), along with ultrastructural and histopathological studies greatly advance the existing knowledge of these parasites. The class Myxosporea Bütschli, 1881 along with the class Actinosporea Noble, 1980 have become quite recently (Levine et al. 1980) widely recognized as an independent phylum Myxozoa Grassé, 1960.

All this progress should have an impact on the rather unchanging taxonomic situation within the class Myxosporea. The presently most widely accepted classification is that of Shulman (1966). Its main principles were proposed seven years earlier by Shulman (1959) to whom goes the great credit for designing a classification which has survived a period of 25 years during which most other protistan phyla were subject to sometimes quite drastical taxonomical changes.

In the absence of dependable, taxonomically significant differential characters in trophozoite stages, Shulman (1959), like his predecessors, based his classification almost exclusively on spore morphology. His system is a major revision of Kudo's (1933) and Tripathi's (1948) classifications, leaving completely aside the proposal of Meglitsch (1960). He wanted his classification to be a natural one and to reflect his ideas on myxosporean phylogeny (Shulman 1966). He finds the initial, most primitive genera in his order Bivalvulea, suborder Bipolaria, among coelozoic parasites of marine, especially perciform, fishes (*Sphaeromyxa* and e.g., *Myxidium*). From these, the evolution led to histozoic parasites and to parasitism in freshwater fishes.

As a base for his interesting phylogenetical conclusions he considered mostly if not exclusively the adaptive evolution of spores. Among the factors that control it he attached paramount importance to adaptations enhancing the capacity of spores to resist pressures within infected organs, and to their floating capacity. In the first case, it was the attractive idea that living as a tissue parasite involves mechani-

cal pressures favouring spores of more flattened shapes to prevent premature gaping of the shell valves. This applies to the family Myxobolidae while spores of various tissue-dwelling multivalvulids do not comply with this rule, having spores of quite other shapes.

The evolutionary significance of an increased floating capacity of spores and division of species into groups with fast sinking and slowly sinking spores in relation to further diversification in different host groups was considered by Shulman (1966) to be an even more important factor in adaptive evolution of spores and hence of myxosporean genera. Its significance was widely discussed (Shulman 1966, Shulman et al. 1978, Donets 1979) but has still not been completely understood, leaving some important questions unanswered. To quote just a few: why are the bottom-feeding flatfish among the most common hosts for *Ceratomyxa* species having spores with an apparently great floating capacity; what is the significance of floating capacity in respect to the evidence (Hoffman and Putz 1969, Uspenskaya 1957) that spores of *Myxobolus* (= syn. *Myxosoma*) *cerebralis*, and possibly many other species, require a long period of spore maturation outside the host, or that some fishes may be susceptible only as a young fry with feeding habits different from those taken into consideration, i.e., of the adult fish?

In addition to special sporal mechanisms and structures serving for an improved dispersal of a species in the aquatic environment, such as an increased spore surface, projections and mucous envelopes, the variety of spore shapes and vegetative life cycle stages demonstrates that there may be many other selective forces favouring a particular pattern of growth and differentiation. The discussion of all factors possibly initiating the transition from one type of spores to the other, however, is beyond the scope of this paper.

Although some thoughts underlying Shulman's classification are still open to discussion, his system was the best thus far devised. Nevertheless, with the passing of the time and due to the results obtained by recent studies, many controversial features inherent in Shulman's system have become more obvious. Also, ultrastructural studies contributed many facts, some of which already have their bearing on the system. At the present time, a revision is urgently needed.

Necessarily, we have to continue the exclusively spore-based and therefore rather artificial taxonomy but we try to make the system less arbitrary. Presently, we do not know to what extent some features of the vegetative stages and the existence or absence of the presporogonic life cycle stages or possible existence of intermediate hosts will affect the taxonomic criteria at the generic or suprageneric levels. Hence the object of our revision is to establish a more logical, improved version of the existing classification rather than to design a really natural, phylogenetically founded classification, which is a task for the future. Génermont (1980) clearly outlined what a desirable goal for protistan taxonomy should be: to define suprageneric taxons in an essentially practical way, which does not exclude phylogenetical hypothesis, but is aware of their extreme frailty, and to establish safe criteria for species identification. We fully endorse his ideas, especially in conditions when the chaotic situation within some genera (e.g., *Myxobolus*, *Myxidium*) makes a safe determination of species extremely difficult.

Major justifications for a revision of the classification in the class Myxosporea Bütschli, 1881

1. The two guidelines defining the major taxa in Shulman's (1966) classification — number of shell valves at ordinal level and arrangement of polar capsules in relation to the sutural plane at subordinal level — have been retained in the revised system proposed here. Another subordinal criterion has been added — the structure of the polar filament characterising the Sphaeromyxina n. subord.

Character of the polar filament is one of the major factors defining Myxozoa and its structure is therefore of a great importance. In *Sphaeromyxa*, the filament is very broad at the base, tapers sharply to the end and is relatively short; thus it is at variance with all other myxosporeans. While still within the capsule, it is arranged in irregular, elongate loops or in close zig-zag bends (Plate IA, C) contrasting with the regular spirally wound threads (Plate IIA) of other genera. This peculiar arrangement is observed in all species studied in this respect including type species *S. balbiani* (ultrastructural interpretation of Grassé and Lavette (1978) does not adequately reflect its structure) and has to be considered as a character of at least the same level as the spatial relation between the capsules and shell valves.

The spatial relation between the capsules and shell valves seems to be a rather arbitrary feature, but it is to be retained for its practical value in separation of the two biologically rather distinct groups of species — the proposed suborder Variisporina (mostly coelozoic, with enormous range of spore shapes) and the suborder Platysporina (mostly histozoic, mostly in freshwater fishes and with spores of rather similar shapes).

While in Actinosporea there are always 3 polar capsules and 3 shell valves, their number is rather variable in Myxosporea; however, the initial original number seems to have been two capsules and two valves. The number of shell valves in Myxosporea seems to be more constant and less subject to deviations — teratological or genetically fixed — than the number of polar capsules and therefore it was rightly chosen by Shulman (1959, 1966) as the main ordinal criterion. Polar capsules may be reduced in size in some species (one of the pair in *Myxobolus*) or stay rudimentary (two of the three capsules in *Unicapsula*) or may disappear completely in *Thelohanellus*, although in sporogenesis there are two capsulogenic cells (Desser et al. 1983). In the latter case we can easily trace the lineage from *Myxobolus* while in other unicapsulate spores (e.g., *Auerbachia*, *Coccomyxa*) it may be difficult or even impossible to determine safely their kinship. For these reasons, and to prevent an arbitrary solution we retain the family Auerbachiidae.

The constancy of shell valve number, however, is not absolute. A variation, although less frequent, can also be observed, as evidenced by our findings of a third, supernumerary shell valve in spores of *Sphaerospora* or *Thelohanellus*. Possibly, in this way proceeded the evolution from *Ceratomyxa*, via *Trilospora*, to the multivalvulids.

The importance of shell valve number does not mean, however, that the number of such phylogenetically and taxonomically important constituents as polar capsules should not serve as family criterion. It is true, that some families include genera with a different number of capsules: the assignment of unicapsulate *Coccomyxa* and *Thelohanellus* in "bicapsulate" families is due to their obvious kinship with other genera included. The family Parvicapsulidae includes both bi- and tetracapsulate species, since here the definition is given by a complex of features including tiny polar capsules. At variance with these two cases, the family Chloromyxidae consitutes a well formed, probably phylogenetically coherent family. The assignement of its genera elsewhere would be an unnatural relationship. In any case, the legitimacy of Chloromyxidae is far superior to that of Myxoproteidae separated by Kovaleva et al. (1983) from Sinuolineidae on the basis of a mere spore shape difference (subspherical vs. elongated ellipsoid or pyramidal). Such differences can also be found in other families (e.g., Sphaerosporidae). Myxoproteidae is a family not included in the present proposal.

2. We propose to abolish the suborder Bipolarina Tripathi, 1948 emend. Schulman, 1959 as well as the suborder Eurysporea Kudo, 1919 emend. Schulman, 1962 and to replace both taxons by a single suborder Variisporina subord. n. Bipolarina and Eurysporea together were a rather strange combination consisting of parts of two quite different if not opposing classifications of Kudo (1933) and Tripathi (1948). In Shulman's conception (1966) they contain each a mix of quite different genera from that originally included in these taxons. What is more important, Shulman's Bipolarina is a very heterogeneous group as difficult to define as were Tripathi's (1948) Unipolarina. Also, there are indications of transitions between Bipolarina and Eurysporea suggesting that, from the view of possible phylogenetic speculations, both groups should be merged into one which would be a good counterpart to the relatively homogeneous suborder Platysporina Kudo, 1919 emend.

"Bipolarina" implies that there are "Unipolarina" a taxon presently not valid; also, previous attempts to sort out bi- and unipolar species were not convincing (Meglitsch 1960). The definition

of Bipolarina (Shulman 1966, p. 120) does not really apply to the genera included. It begins with the statement that the spores are — irrespective of minor deviations from this plan — radially symmetrical. This is certainly not the case if one looks at the spores of genera *Davisia*, *Myxoproteus*, *Neomyxobolus*, *Ortholinea*, *Sinuolinea*, *Zschokkella*, included in Bipolarina. Further, according the definition, the "polar capsules are situated in opposite poles of the spore". Again, if one looks at the spores of many species of all above mentioned genera, this is not the impression one gets, as exemplified by *Davisia ophidii* Zaika, 1965, *Sinuolinea sinuosa* Shulman, 1953, and many others. They rather exhibit a unipolar, bilaterally symmetric appearance. A "true" bipolarity can be seen, sometimes with some restrictions, in the genera originally listed by Tripathi (1948) — *Sphaeromyxa*, *Zschokkella* and especially *Myxidium*. Even in the latter genus, some species are hardly bipolar, with polar capsules shifted to one side and the sporoplasm to the other. This may be restricted to some specimens only as manifestation of variability (Plate III H); however, there were some myxidia described which comply with the definition of *Ortholinea* in that their ellipsoid or rounded traingular spores have capsules side by side along the (anterior?) side of the spore and sporoplasm facing them at the bottom of the spore (e.g., *Myxidium triangulum* Schulman, 1962, *M. monstruosum* Shulman, 1962).

Shulman's (1966) diagnosis ends by stating that the polar capsules "lie at the same time in the sutural level and also in the level perpendicular to it". This is rather confusing. Once the uniting character of "bipolarity" is in fact absent in most forms included, the result is a quite heterogeneous assemblage. Such a heterogeneity is clearly evident if one compares the spore polarity and the orientation of polar capsules in relation to the sutural plane in e.g., *Myxidium*, *Myxoproteus* and *Neomyxobolus*.

In addition, it is not nomenclatorily quite proper to include *Coccomyxa*, having a single capsule at eno pole, with Bipolarina, although it is presumably related to *Myxidium*. For all these reasons, the category "Bipolarina" is no more suitable, is outdated and should be suppressed. We propose a new taxon, Variisporina n. subord. rather than to allot the "bipolarine" genera into the suborder Eurysporea which would thus have a completely changed contents and whose original definition would be entirely upset.

Davisia newfoundlandia, described by Yoshino and Noble (1973) in which the space in the lateral projections is according to Meglitsch (unpublished), continuous with the central sporoplasmic cavity as is the case in *Ceratomyxa*, may constitute one of the possible links between the former Bipolarina and Eurysporea. Such links are in favour of a common category, Variisporina.

3. We reduce the genus *Myxosoma* Thélohan, 1892 to synonymy with *Myxobolus* and, accordingly, suppress the family Myxosomatidae Poche, 1913 as already proposed by Akhmerov (1960) and Walliker (1968). The existence of these taxons is not logical and yet they continue to survive in the literature. That is why we once again review the major points of the problem. The history of these taxa is told in full by Walliker (1968) and Shulman et al. (1978).

Polysaccharide reserves (glycogen) are stored in practically all stages of myxosporean life cycle. In the sporoplasm, the β-glycogen particles may be grouped together to form aggregations and in some genera, there may be a single large agglomeration, appearing as a large spherical inclusion, a "vacuole" in fresh spores and stainable by iodine compounds such as Lugol's solution, and called "glycogen" or "iodinophile vacuole". Thélohan (1892) in the early days of discovering myxosporea considered the mere presence or absence of this "vacuole" a reason sufficient to distinguish two separate, but otherwise identical genera *Myxobolus* and *Myxosoma*, and Poche in 1913 used this character to establish a separate family Myxosomatidae. Since then, Myxosomatidae and *Myxosoma* have been part of all myxosporean classifications. Until the work of the distinguished Soviet parasitologist Akhmerov (1960) no one questioned the validity of the genus *Myxosoma* although it became obvious that the use of the "glycogen vacuole" as the only differentiating character allotting the species to genera *Myxosoma* or *Myxobolus* is rather tricky. The "vacuole" may or may not be present in spores of a given species, and it may stain with varying intensity so that, as aptly summarized by Walliker (1968), *Myxobolus* was confused with *Myxosoma* many times in the past.

In species of the genera *Myxobolus* and *Henneguya* in which the presence of the "vacuole" was studied (Walliker 1968, Lom 1969, Podlipaev and Shulman 1978) polysaccharide reserves occurred either diffused throughout the sporoplasm, or concentrated into several aggregates or into a single "vacuole". A well defined "vacuole" was present only from 0 % to 33 % (Walliker 1968) or 80—90 % spores (Podlipaev and Shulman 1978); the moiety of spores with a "vacuole" in a given *Myxobolus* species differed greatly in various host species, in different localities, in individual host specimens and organs. Further, Podlipaev and Shulman (1978) found that in order to assess correctly the number of spores with a "vacuole" spores have to be examined immediately after their

release from the cyst. In 5 to 6 days the percentage of spores with a vacuole may decrease from 82 % to about 2 %.

Such an inconstant and unstable character is by no means sufficient to be used as the sole criterion for generic differentiation. The presence of the "vacuole", if properly and statistically documented, can serve as an additional feature for species characterisation along with the presence of mucous envelope, site of infection in the host and the like. We would hardly find any other example of a taxonomic character which may even be absent in some parasite populations and which disappears from the living organism after a few days and yet is considered by itself sufficient to separate otherwise congeneric organisms or even families.

The recognition of the family Myxosomatidae was still more far fetched, the more so that the "vacuole", the sole difference between Myxobolidae and Myxosomatidae can also be found in the genera *Neomyxobolus* and *Myxobilatus* assigned in Shulman's and the present classification to other suborders.

The most common argument used to uphold the taxonomic significance of the "vacuole", that reduction of *Myxosoma* to junior synonym of *Myxobolus* would result in too many myxoboli, is rather naive. There would be really about 395 *Myxobolus* species but to divide them formally in two genera (308 *Myxobolus* and 87 *Myxosoma*) would be of no help to practical determination. A meticulous description taking into account the natural variability and such important features as e.g., the arrangement of the polar filament, presence of mucous envelopes and surface details revealed by the scanning electron microscopy can only put in order the chaotic, synonymy-ridden classification within the genus.

Shulman et al. (1978) claimed that the "vacuole" having a higher specific weight than the rest of the spore, plays an important role in the ecology of the species since it determines the rate of sinking of the spore. Thus the species with fast sinking spores which have developed the "vacuole" got into a variety of benthophagic fish — mostly cyprinids — in which they enjoyed a new evolution. Hence they consider the "vacuole" to be phylogenetically, and it follows also taxonomically, important. This may be an interesting conjecture. Unfortunately, it does not take into account other factors affecting the rate of sinking of the spore in water such as the important presence or absence of a mucous envelope, the massiveness of the spore shell and many other biotic and abiotic factors that may be far more important than the weight difference due solely to the "vacuole".

4. At the present state of knowledge, it is impossible to remove from the system the many still persisting confusing points, especially concerning intergeneric relations. What is most urgently needed is a meticulous time-taking morphological analysis of species — of their spores and vegetative stages, taking into account their variability. Only such approach can solve the chaotic situation e.g., within the genus *Myxobolus* where, according to present descriptions, it is sometimes impossible to tell the species apart. Equally important is the study of life cycles in view of the possible existence of presporogonic stages in many (or all?) genera.

Elements of arbitrariness in distinction between genera still persist:

a) Some species are difficult to assign to *Myxidium* and to *Zschokkella* — the polar capsules are neither exactly pyriform nor spherical and do not open in the directions required (see generic diagnosis).

b) Some species of *Leptotheca* are difficult to separate from *Ceratomyxa* — there is a gradual transition of forms (see diagnosis of *Leptotheca*). In their turn, some *Sphaerospora* species were in fact described as *Leptotheca* (e.g., *Leptotheca* (= *Sphaerospora*!) *krogiusi* Konovalov et Shulman, 1965).

c) The affinities of *Wardia* to *Sphaerospora* and *Mitraspora* are not quite distinct. This genus, like several others (*Agarella*, *Trigonosporus*) needs redescription.

d) A revision is needed in the genus *Hoferellus*, too. The original type species *H. cyprini* (Doflein, 1898) is most probably non existent (see Dyková and Lom 1983, Lom et al. 1983b). We replace it by *H. carassii* Achmerov, 1960. This is a tentative solution, since vegetative stages of the latter species are unknown; a redescription is much required.

e) Differences between *Ortholinea* and *Neomyxobolus* are very delicate and consist mainly of details of spore shape, since their distinction by means of the "iodinophile vacuole" cannot be recognized.

f) Some of the present genera may easily be split in two, once a well-founded morphological basis is available; e.g., some species of *Chloromyxum* are quite different from the type species, *C. leydigi*.

5. On the whole, there are only a few clusters of wholly histozoic or coelozoic genera with similar spores, constituting reasonably natural families (e.g., Myxobolidae).

There appear only a few true evolutionary lines such as the origin of *Thelohanellus* from *Myxobolus* through the suppression of one capsulogenic cell, or the *Ceratomyxa* — *Trilospora* — *Kudoa* — *Pentacapsula* — *Hexacapsula* lineage. The latter lineage evidently reflects a genetically fixed change or disorder in cell division producing supernumerary polar capsules and cell valves and stabilized by some (?) selective environmental pressures.

REVISED CLASSIFICATION AND DEFINITIONS OF TAXA

PHYLUM MYXOZOA GRASSÉ, 1960

Microscopic parasitic organisms which exceed the protistan level in being pluricellular, having a distinct vegetative (soma) and generative (germ) constituent and, accordingly, morphologically different and functionally specialized cells. They are characterized by the "enveloped state" of generative cells encased within the somatic ones, and by multicellular spores developing from generative cells and containing nematocyst-like polar capsules with an extrudible filament and one to many amoeboid infective germs, sporoplasms. The spore wall is formed by two to seven valves produced by cells adhering together by cell junctions. The sexual process is autogamy or copulation of gametes.

CLASS MYXOSPOREA BÜTSCHLI, 1881

A pluricellular trophozoite stage is the main site of proliferation. Trophozoites, often amoeboid in shape, contain their own vegetative nuclei and generative cells producing multicellular spores. Trophozoites range from uninucleate pseudoplasmodia producing one spore to macroscopic plasmodia containing numerous spores. Spore with one or two sporoplasms, 1 or 7 (mostly 2) polar capsules and two to seven (mostly two) shell valves which meet in sutural line(s).

Sexual process is autogamy and takes place in the sporoplasm before or just after hatching.

Includes parasites histozoic in tissues (intercellular, sometimes intracellular) or coelozoic in body organs, primarily of fishes, occasionally of amphibians and reptiles, exceptionally in invertebrates. Mostly rather inocuous, some — especially histozoic species — are serious pathogens of fishes.

Order Bivalvulida Schulman, 1959

Spore shell composed of two valves meeting in one circumsporal suture and containing two, sometimes four or rarely one polar capsule.

Suborder Sphaeromyxina subord. n.

A short polar filament, unlike all other myxosporea, is not tube-like, being very broad and flat at the base and gradually tapering to the end; in each of the two polar capsules, it is not spirally wound but folded several times. Coelozoic in marine fishes.

1. Family **Sphaeromyxidae fam. n.** — Two polar capsules lie in the opposite, tapering and truncate ends of the elongated, sometimes slightly curved spore; they open in the level of the suture line, connecting both ends and bisecting the spore. Valves smooth or ridged. One binucleate sporoplasm. Large polysporous plasmodia live in the gall bladder. Pansporoblast formation observed.

Genus *Sphaeromyxa* Thélohan, 1892. — With characters of the family.*) — Type species *S. balbianii* Thélohan, 1892.

*) As far as possible, characters defining families are not repeated in generic diagnosis.

Suborder Variisporina subord. n.

The polar capsules (as a rule two, sometimes four, rarely one) may occupy various positions in the spore. If they are located together at one pole of the spore, they do not lie solely in the sutural plane, or they lie in a plane perpendicular to it. Mostly coelozoic parasites, most genera live in marine fishes.

2. Family **Myxidiidae** Thélohan, 1892. — Spores spindle shaped, sigmoid or crescentic, sometimes almost semicircular in valvular view, ellipsoidal, have two (in *Coccomyxa* one is eliminated) polar capsules located in the opposite ends with terminal or slightly lateral capsular foramina; the longitudinal sutural line is straight, curved or sigmoid. Mostly coelozoic, rarely histozoic parasites in marine and freshwater fishes.

Genus *Myxidium* Bütschli, 1882. — Spores as a rule fusiform, straight or slightly crescentic or sigmoid, with more of less pointed ends; shell valves smooth or with ridges; sutural line bisecting the spore. Two mostly pyriform capsules are situated one at each end of the spore, capsular foramina lie in the sutural plane, at or near the end of the spore and open mostly in opposite directions. One binucleate sporoplasm is located as a rule between the capsules. Typically coelozoic, small or large trophozoites, monosporous, disporous and polysporous, the latter with pansporoblast formation, also histozoic; intracellular stages are known. In marine and freshwater fishes, rarely in amphibians or reptiles. — Type species *M. lieberkuehni* Bütschli, 1882.

Genus *Zschokkella* Auerbach, 1910. — Spores ellipsoidal in sutural view and slightly bent or semicircular in valvular view, with rounded or bluntly pointed ends. Almost spherical capsules open mostly slightly subterminally and both to one side. One binucleate sporoplasm. Trophozoites disporous to polysporous with pansporoblast formation. Coelozoic in marine and freshwater fishes; a few species in amphibians and reptiles. — Type species *Z. hildae* Auerbach, 1910.

Genus *Coccomyxa* Léger et Hesse, 1907. — Ellipsoidal spores, rounded in transverse section with a single elongated pyriform polar capsule with foramen in the sutural plane. Sigmoid sutural line. One binucleate sporoplasm. Trophozoite monosporous or polysporous. Coelozoic in gall bladder of marine fishes. — Type species *C. morovi* Léger et Hesse, 1907.

3. Family **Ortholineidae fam. n.** — Spherical to irregularly ellipsoidal spores are bilaterally symmetrical along the straight sutural line. The two polar capsules are set wide apart in sutural plane, with capsular foramina directed away from each other at an angle. Binucleate sporoplasm lies in the spore cavity opposite to the part in which polar capsules lie. Coelozoic trophozoites, monosporous to polysporous in marine and freshwater fishes.

Genus *Ortholinea* Shulman, 1962. — Spherical or subspherical spores may be slightly flattened parallel to the sutural plane or pointed posteriorly; polar capsules subspherical to pyriform. Sporoplasm binucleate. Trophozoites monosporous to polysporous, coelozoic in the urinary tract of marine fishes. — Type species *O. divergens* (Thélohan, 1895) Shulman, 1962.

Genus *Neomyxobolus* Chen et Hsieh, 1960. — Spores ovoid in valvular view, anterior end slightly convex, posterior semicircular, flattened parallel to the sutural plane. Sporoplasm binucleate, may contain an "iodinophile vacuole". Trophozoites disporous to polysporous, coelozoic in the urinary tract of freshwater fishes. — Type species *N. ophiocephalus* Chen et Hsieh, 1960.

4. Family **Sinuolineidae** Schulman, 1959. — Spherical or inversely pyramidal spores may have caudal or lateral projections; the two anteriorly located, spherical or subspherical polar capsules are set apart sometimes even at opposing sides of the spore; the plane connecting them is perpendicular to the mostly sinuous sutural line, often appearing as a figure of "8". Trophozoites monosporous to polysporous, coelozoic in marine fishes.

Genus *Sinuolinea* Davis, 1917. — Spherical or subspherical spores, sutural line sinuous or extremely sinuous so that its orientation to the two polar capsules set widely apart may be difficult to determine. Binucleate sporoplasm. Trophozoites monosporous to polysporous, coelozoic in the urinary tract of marine fishes. — Type species *S. dimorpha* (Davis, 1916) Davis 1917.

Genus *Davisia* Laird, 1953. — Spherical or subspherical spores, sutural line straight or sinuous,

shell valves bear long hollow lateral appendages the cavity of which is discontinuous with the spore cavity. Polar capsules anteriorly at a certain distance from each other. Trophozoites mono-, di- and polysporous, coelozoic in the urinary system of marine fishes. — Type species *D. diplocrepis* Laird, 1953.

Genus *Myxoproteus* Doflein, 1898. — Spores inversely pyramidal or triangular in sutural view with rounded outlines; anterior end broad and more or less flattened; thick spore valves sometimes with various projections. Sutural line straight or sinuous; polar capsules are set well apart. Binucleate sporoplasm. Trophozoites monosporous and disporous. Coelozoic in the urinary system of marine fishes. — Type species *M. ambiguus* (Thélohan, 1895) Doflein, 1898.

Genus *Bipteria* Kovaljova, Zubtchenko et Krasin, 1983. — Spores inversely pyramidal in sutural view with pointed end extending backwards; sinuous sutural line. Anterior end of each shell-valve extends into wing-like projection, containing parts of the valvogenic nucleus. Spore ellipsoid in transverse section. Spherical polar capsules. A single sporoplasm. Trophozoites disporous and polysporous, coelozoic in the urinary system of marine fishes. — Type species *B. admiranda* Kovaljova, Zubtchenko et Krasin, 1983.

Genus *Shulmania* Kovaljova, Zubtchenko et Krasin, 1983. — Differs from *Bipteria* in having sometimes straight sutural line, in having monosporous or disporous trophozoites, and chiefly by four longitudinal valvular projections; two run along each side of the sutural line, two others extend along the middle line of each shell valve. — Type species is *S. ovalis* Kovaljova, Zubtchenko et Krasin, 1983.

5. Family **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 near opposite ends discharge laterally. Spores capable to move by means of contractile fibers attached to the valves. Coelozoic in marine fishes and in the parenchyme of a platyhelminth.

Genus *Fabespora* Naidenova et Zaika, 1969. — Which characters of the family. Binucleate sporoplasm. — Type species *F. nana* Naidenova et Zaika, 1969.

6. Family **Ceratomyxidae** Doflein, 1899. — Spores have valves elongated or drawn out to an enormous length in the direction perpendicular to the straight central transverse suture; sometimes the two shell valves are asymmetrical. Polar capsules — spherical or subspherical — close to the sutural line in a plane perpendicular to it. Trophozoites monosporous to polysporous, mostly disporous. Coelozoic in marine fishes; rarely histozoic or in amphibians.

Genus *Leptotheca* Thélohan, 1895. — Spores oval, ellipsoidal (sometimes arcuate); the length of the individual laterally prolonged shell-valve (measured from the midpoint of the suture to the most distant point of the valve) does not exceed the axial diameter of the spore (the difference from *Ceratomyxa*) but significantly exceeds one half of this diameter (at variance with *Sphaerospora*). Capsular foramina near the sutural plane. Sporoplasm often fills the spore cavity completely; mostly one binucleate, sometimes two uninucleate sporoplasms. Trophozoites as a rule disporous; coelozoic in the urinary system, rarely histozoic in marine fishes, sometimes in urinary system of amphibians. — Type species *L. agilis* Thélohan, 1895.

Genus *Ceratomyxa* Thélohan, 1892. — Elongated, crescent-shaped or arcuate spores with shell-valves often conical, exceeding in length the axial diameter of the spore. Subspherical polar capsules, sometimes unequal in size, have capsular foramina near the sutural line at the anterior pole of the spore. Exceptionally the capsules open at opposing sides of the central sutural line. Binucleate sporoplasm does not completely fill the spore cavity; two uninucleate sporoplasms were also reported. Trophozoites monosporous to polysporous, mostly disporous; coelozoic in marine fishes, rarely histozoic. — Type species *C. arcuata* Thélohan, 1893.

7. Family **Sphaerosporidae** Davis, 1917. — The two polar capsules opening at the anterior tip are situated in a plane perpendicular to the straight sutural line. The spores are spherical, rounded pyramidal with tapering anterior end, or elongated, often with appendages. Trophozoites monosporous to polysporous, mostly coelozoic in marine and freshwater fishes; sometimes histozoic.

Genus *Sphaerospora* Thélohan, 1892. — Spherical or subspherical spores, with valvular diameter not significantly exceeding sutural diameter. Valves smooth or with ridges, often with lateral protuberances or bumps. The sutural ridge often prominent. Polar capsules subspherical or pyriform. Two uninucleate sporoplasms. Mono- or disporous trophozoites coelozoic in the urinary system of freshwater and marine fishes, some are histozoic. Often with intracellular stages and with presporogonic developmental cycle in various body systems. — Type species *S. elegans* Thélohan, 1892.

Genus *Mitraspora* Fujita, 1912. — Spores anteriorly pointed, miter-like or rounded in valvular view, with many filaments at the posterior end; polar capsules pyriform. Binucleate sporoplasm. Trophozoites polysporous. Coelozoic in the urinary system of freshwater fishes with intracellular stages. — Type species *M. cyprini* Fujita, 1912.

Genus *Wardia* Kudo, 1919. — Spores resemble an isocele triangle with two convex sides in sutural view, but oval in valvular view and flattened perpendicular by to the sutural plane. Valves with fine ridges, running into fringe-like processes at the posterior end. Large spherical polar capsules in the central portion of the spore open at the anterior tip of the spore. Large polysporous trophozoites, histozoic of cyst-like appearance, in freshwater fishes, one species possibly in amphibians. — Type species *W. ovinocua* Kudo, 1919.

Genus *Palliatus* Shulman, Kovaleva et Dubina, 1979. — Subspherical spores, with anteriorly prominent sutural ridge, are enveloped in a membranaceous veil which in non-mature spores is twisted in two cords around the spore. Polar capsules pyriform. Binucleate sporoplasm. Trophozoites disporous to polysporous, coelozoic in the gall bladder of marine fishes. — Type species *P. mirabilis* Shulman, Kovaleva et Dubina, 1979.

Genus *Myxobilatus* Davis, 1944. — Spores elongated, anteriorly pointed; shell-valves, often with fine ridges, extend posteriorly in two caudal appendages. Polar capsules pyriform. Binucleate sporoplasm may contain an "iodinophile vacuole". Trophozoites small to large, disporous to polysporous, in the urinary system, rarely histozoic. In freshwater and also marine fishes. — Type species *M. gasterostei* (Parisi, 1921) Davis, 1944.

8. Family **Chloromyxidae** Thélohan, 1892. — Spores spherical, subspherical or elongated, bisected by a straight meridional suture, may bear caudal appendages. Four polar capsules at the apex of the spore; either one pair in the level of the sutural line and the second pair perpendicular to the suture, or both pairs diagonally beyond the level of the suture. Trophozoite small (monosporous) to medium-sized (polysporous) in which pansporoblast formation is known. Coelozoic in freshwater and marine fishes, exceptionally in amphibians; rarely histozoic.

Genus *Chloromyxum* Mingazzini, 1890. — Spore valves smooth or with ridges, rarely with caudal filamentous projections. The two pairs of polar capsules may be of unequal size. Binucleate sporoplasm; two uninucleate sporoplasms were observed, too. Other characters those of the family. — Type species *Ch. leydigi* Mingazzini, 1890.

Genus *Caudomyxum* Bauer, 1948. — Subspherical spores with smooth valves, each equipped with stout tapering caudal projection. Trophozoites polysporous, pansporoblast formation observed; coelozoic in the urinary system of amphibians and histozoic in the kidneys of freshwater fishes. — Type species *C. nanum* Bauer, 1948.

Genus *Agarella* Dunkerley, 1915 — Spores elongate ovoid, very slightly flattened parallel to the sutural line; each valve extending into a caudal projection. Four pyriform polar capsules, two larger and two smaller; with one of each in each shell valve. Trophozoites polysporous, histozoic in freshwater fishes. — The only and type species *A. gracilis* Dunkerly, 1915.

9. Family **Auerbachiidae** Evdokimova, 1973. — Spores with asymmetric unequal smooth shell valves and a single elongated polar capsule with a few longitudinal coils of the filament. Trophozoites polysporous, ceolozoic in the gall bladder of marine fishes.

Genus *Auerbachia* Meglitsch, 1960. — Club-like spores with a broad anterior part and narrow caudal part. The two shell valves are asymmetrical and dissimilar in form and meet in a curved, very indistinct suture. Polar capsule opens at the anterior end of the spore. Binucleate sporoplasm. Trophozoites large, polysporous; coelozoic in the gall bladder in marine fishes. — Type species *A. monstrosa* Meglitsch, 1960.

Genus *Globospora* Lom, Noble et Laird, 1975. — Spore of spherical shape, smooth shell valves are unequal and meet in a curved, delicate suture. Capsular foramen at some distance from the sutural line. Coelozoic in gall bladder of marine fishes. — Type species *G. spherica* (Evdokimova, 1973) Lom, Noble et Laird, 1975.

10. Family **Alatosporidae** Schulman, Kovaljova et Dubina, 1979. — Spores resemble in sutural view an isosceles flat triangle with long tips set perpendicularly to the central suture line, the short being oriented posteriorly. The two polar capsules are set in a plane perpendicular to the suture. Shell valves bear conspicuous wing-like projections. Coelozoic in the gall bladder of marine fishes.

Genus *Alatospora* Shulman, Kovaljova et Dubina, 1979. — Spores extremely elongated in the level perpendicular to the central straight sutural line. Shell valves bear wing-like membranaceous projections adhering along their posterior half. Small pyriform polar capsules. Trophozoites disporous. Coelozoic in the gall bladder in marine fishes. — Type species *A. samaroidea* Shulman, Kovaljova et Dubina, 1979.

Genus *Pseudoalatospora* Kovaljova et Gayevskaya, 1983. — Spores differ from those in *Alatospora* in that their valve projections are doubled to form parachute-like pocket. Trophozoites mono- and disporous, coelozoic in the gall bladder in marine fishes. — Type species *P. scombri* Kovaljova et Gayevskaya, 1983.

11. Family **Parvicapsulidae** Schulman, 1953. — Asymmetrical thin-walled spores elongated roughly in the sutural plane, with unequal valves meeting in a curved suture and two to four conspicuously small polar capsules in the apex. Trophozoites disporous to tetrasporous. Coelozoic in the urinary system and histozoic in marine and anadromous fishes.

Genus *Parvicapsula* Shulman, 1953. — Asymmetrical, somewhat curved spores. Two small pyriform polar capsules are located anteriorly but open sidewise. One relatively large binucleate sporoplasm. Trophozoites disporous, coelozoic in the urinary system or histozoic in kidneys. — Type species *P. asymmetrica* Shulman, 1953.

Genus *Neoparvicapsula* Gayevskaya, Kovaljova et Shulman, 1982. — Asymmetrical, elongated spores; sutural line curved or sinuous. Four small pyriform polar capsules in a cross-like arrangement in the apex of the spore. One relatively large sporoplasm. Trophozoites di- to tetrasporous, coelozoic in the urinary system. — Type species *N. ovalis* Kovaljova, Gayevskaya et Shulman, 1982.

Suborder Platysporina Kudo, 1919 emend.

Polar capsules (generally two, sometimes one) at the apex of the spore lie solely in the sutural plane of a bilaterally symmetrical spore. As a rule, histozoic parasites of freshwater fishes, producing large polysporous trophozoites.

12. Family **Myxobolidae** Thélohan, 1892. — Spores flattened parallel to the straight sutural line; the suture forms an elevated ridge and may be drawn out into long projections. One of the two polar capsules may be smaller; in two genera, it has disappeared completely. Most species have an "iodinophile vacuole". Form as a rule large histozoic trophozoites ("cysts") with numerous spores, mostly in freshwater fishes.

Genus *Myxobolus* Bütschli, 1882. — Spores ellipsoid ovoid or rounded in valvular view, and biconvex in sutural view. Shell valves smooth. Two, mostly pyriform polar capsules; exceptionally, one is ostensively missing, in which case the remaining one is not situated axially. Posteriorly, the sutural ridge may extend into a crescentic ledge. Binucleate sporoplasm, often with an "iodinophile vacuole". Trophozoites as a rule large, polysporous with pansporoblast formation; histozoic in freshwater fishes, some in marine fishes, rarely in amphibians. — Type species *M. muelleri* Bütschli, 1882.

Genus *Henneguya* Thélohan, 1892. — Spores rounded, ellipsoid or spindle-shaped in valvular view, biconvex in sutural view; each valve continues as a caudal projection, both of which can be sometimes apposed. Shell valves smooth. Two polar capsules, sometimes very elongated. Binucleate sporoplasm mostly with spherical polysaccharide inclusion. Trophozoites mostly large, polysporous with pansporoblast formation, histozoic in freshwater, sometimes in marine fishes. Type species *H. psorospermica* Thélohan, 1895.

Genus *Thelohanellus* Kudo, 1933. — Spores pyriform, tear-shaped or ellipsoid in valvular view, tear-shaped or pyriform in sutural view; valves smooth, rarely with a membranaceous crescent at the posterior end. A single pyriform, tear-shaped or subspherical polar capsule. Binucleate sporoplasm mostly with spherical polysaccharide inclusion. Trophozoites large, polysporous, with pansporoblast formation, strictly histozoic in freshwater fishes. — Type species *T. pyriformis* (Thélohan, 1892) Kudo, 1933.

Genus *Unicauda* Davis, 1944. — Differs from *Henneguya* in that the single caudal appendage is not a continuation of the smooth shell valves, but a structure made up from a different material and adhering to the shell valves along a distinct boundary. Strictly histozoic in freshwater fishes. — Type species *U. clavicauda* (Kudo, 1934) Davis, 1944.

Genus *Dicauda* Hoffman et Walker, 1978. — Differs from *Myxobolus* in having two caudal appendages, extending in opposing directions. They are not extensions of the smooth shell valves, being composed of a different material and adhering to the shell valves along a distinct boundary. — Type species *D. atherinoidi* Hoffman et Walker, 1978.

Genus *Phlogospora* Qadri, 1962. — Spores flattened, more or less pyriform, with an independent bifurcated caudal process fitted to the posterior end of the spore along a distinct boundary. A single elongated polar capsule. Binucleate sporoplasm with polysaccharide reserves in form of a spherical inclusion. Large polysporous trophozoites, histozoic in freshwater fishes. — Type species *P. mysti* Qadri, 1962.

Genus *Neohenneguya* Tripathi, 1953. — Spores spindle-shaped in valvular view, and flattened spindle-shaped in sutural view; two fine, equal prolongations both at anterior and posterior end. Two spherical polar capsules, tandem in position, at a distance from the anterior end. Sporoplasm with polysaccharide reserves in form of a spherical inclusion. Large polysporous trophozoites, histozoic in freshwater fishes. — Type species *N. tetraradiata* Tripathi, 1953.

Genus *Trigonosporus* Hoshino, 1952. — Spores broadly triangular, with rounded anterior and flattened posterior ends in valvular view. Two polar capsules. Each shell-valve drawn out into two long filamentous processes on each side, each pair connected by a filament. Binucleate sporoplasm with polysaccharide reserves in form of a spherical inclusion. Polysporous trophozoites, histozoic in marine fishes. Type species *T. acanthogobii* Hoshino, 1952.

Genus *Hoferellus* Berg, 1898. — Spores pyramidal or ovoid with pointed anterior end in valvular view, biconvex in sutural view. Shell valves with ridges bear posteriorly two spinous processes arising from the lateral faces of the valves. Between these processes many rigid short filaments extend from the posterior surface. Binucleate sporoplasm with an "iodinophile vacuole"; coelozoic in freshwater fishes. — Type species *H. carassii* Achmerov, 1960.

Order Multivalvulida Schulman, 1959.

The shell of radially symmetrical spores is composed of 3 to 7 valves meeting in three to seven sutures; polar capsules one to each valve are grouped together at the apex of the spore.

13. Family **Trilosporidae** Schulman, 1959. — Spore shell consists of three valves; three polar capsules.

Genus *Trilospora* Noble, 1939. — Spores with three elongated shell-valves, one spherical polar capsule in each valve; appears in apical view as a triradiated star with rounded points. Sporoplasm in the central cavity of the spore. Small mono- and disporous trophozoites, coelozoic in gall bladder of marine fishes. — The only and type species *T. californica* Noble, 1939.

Genus *Unicapsula* Davis, 1924. — Subspherical spores with three unequal shell valves; one small valve covers a single spherical polar capsule, two larger, bilaterally symmetrically arranged valves contain two capsular rudiments difficult to distinguish by light microscopy, and two uninucleate sporoplasms, one enveloping the other. Large polysporous trophozoites, no pansporoblast formation. Histozoic (intracellular) in muscles of marine fishes. — Type species *U. muscularis* Davis, 1934.

14. Family **Kudoidae** Meglitsch, 1960. — Spores with four shell valves each containing one polar capsule.

Genus *Kudoa* Meglitsch, 1947. — Spores stellate, quadrate or rounded quadrate in apical view with a suture line often indistinct. Polar capsules pyriform. Two uninucleate sporoplasms, one enveloping the other. Trophozoites small, producing one to seven spores, and large, polysporous; no pansporoblast formation observed. Histozoic, mostly intracellular in muscles, exceptionally coelozoic in marine fishes. — Type species *K. clupeidae* (Hahn, 1917) Meglitsch, 1960.

15. Family **Pentacapsulidae** Naidenova et Zaika, 1970. — Five shell valves each containing one polar capsule.

Genus *Pentacapsula* Naidenova et Zaika, 1970. — Spores stellate in a pentaradiate form in apical view. Large polysporous trophozoites histozoic in muscles of marine fishes. — Type species *P. schulmani* Naidenova et Zaika, 1970.

16. Family **Hexacapsulidae** Schulman, 1959. — Six shell valves each containing one polar capsule.

Genus *Hexacapsula* Arai et Matsumoto, 1953. — Spores in apical view have the form of a hexaradiate star. Trophozoites not described; histozoic in muscles of marine fishes. — Type species *H. neothunni* Arai et Matsumoto, 1953.

Yasunaga et al. (1981) reported an undescribed species with heptaradiate spores with seven polar capsules infecting brain tissue of *Lateolabrax japonicus*.

Important synonyms:

Conispora Sancurathri, 1976 = *Myxoproteus*
Cystodiscus Lutz, 1889 = *Myxidium*
Disparospora Akhmerov, 1954 = *Myxobolus*
Facieplatycauda Wyatt, 1979 = *Myxobolus*
Gyrospora Qadri, 1962 = *Myxobolus*
Hoferia Doflein, 1898 = *Hoferellus*
Lentospora Plehn, 1905 = *Myxobolus*
Myxosoma Thélohan, 1892 = *Myxobolus*
Neochloromyxum Matsumoto, 1954 = *Kudoa*
Parapileispora Naidenova et Zaika, 1970 = *Unicapsula*
Pileispora Naidenova et Zaika, 1970 = *Unicapsula*
Symmetrula Rajula et Radha, 1966 = most probably not a myxosporean

РЕВИЗИЯ КЛАССИФИКАЦИИ КЛАССА MYXOSPOREA BÜTSCHLI, 1881

Й. Лом и Е. Р. Ноубл

Резюме. На основе нового обсуждения признаков, имеющих значение для классификации миксоспоридий, была сделана новая ревизия таксонов класса Myxosporea Bütschli, 1881. Эта ревизия учитывает главные линии классификации, предложенные комитетом Левайна (Levine 1980), включающие системы Шульмана (Shulman 1966) для класса Myxosporea. Были сделаны следующие надродовые изменения: подотряды Bipolarina Tripathi, 1948 и Eurysporina Kudo, 1919 и семейство Myxosomatidae Poche, 1913 были подавлены и были предложены новые категории: подотряды Sphaeromyxina subord. n. и Variisporina subord. n. и семейства Sphaeromyxidae fam. n. и Ortholineidae fam. n. Род *Myxosoma* Thélohan, 1892 считается младшим синонимом *Myxobolus* Bütschli, 1881 и приводятся причины этого изменения. Новая ревизия основана, также как и предыдущая, на морфологии спор. Обсуждается опасность арбитрарного решения при определении видов, споры которых имеют признаки сходных родов. Для полного использования морфологии трофозоитов, стадий жизненного цикла и способа спорогонии в классификации миксоспоридий необходимы дальнейшие исследования.

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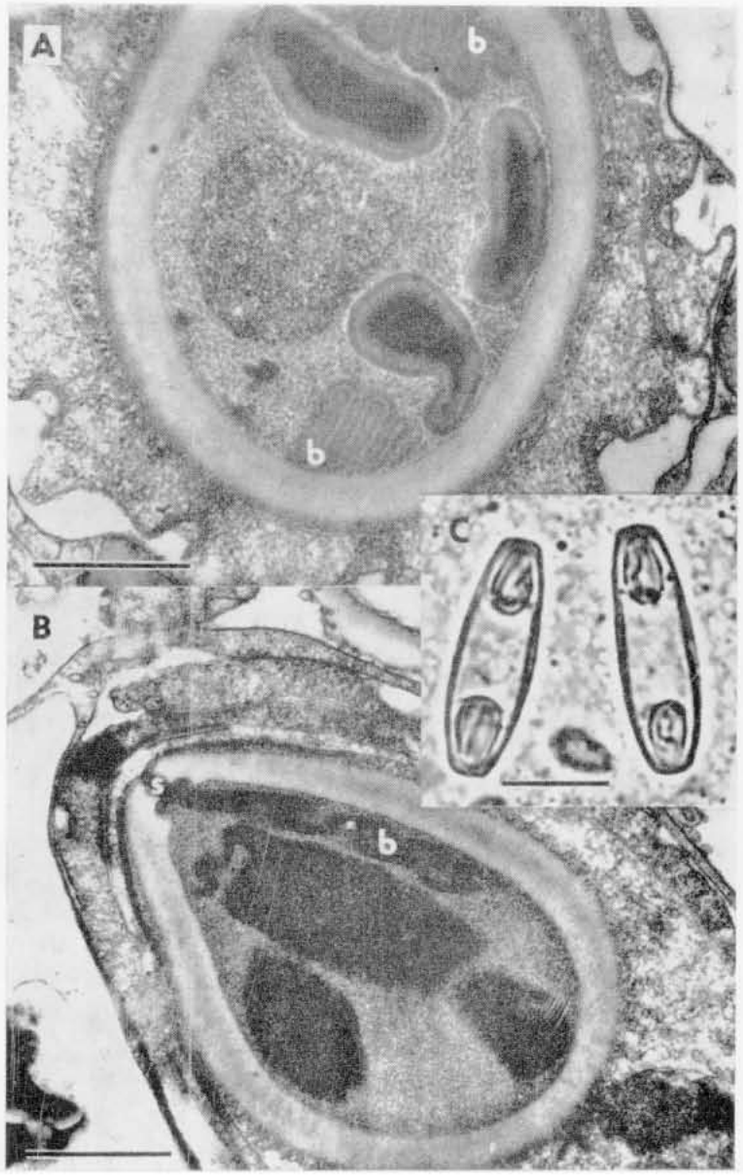
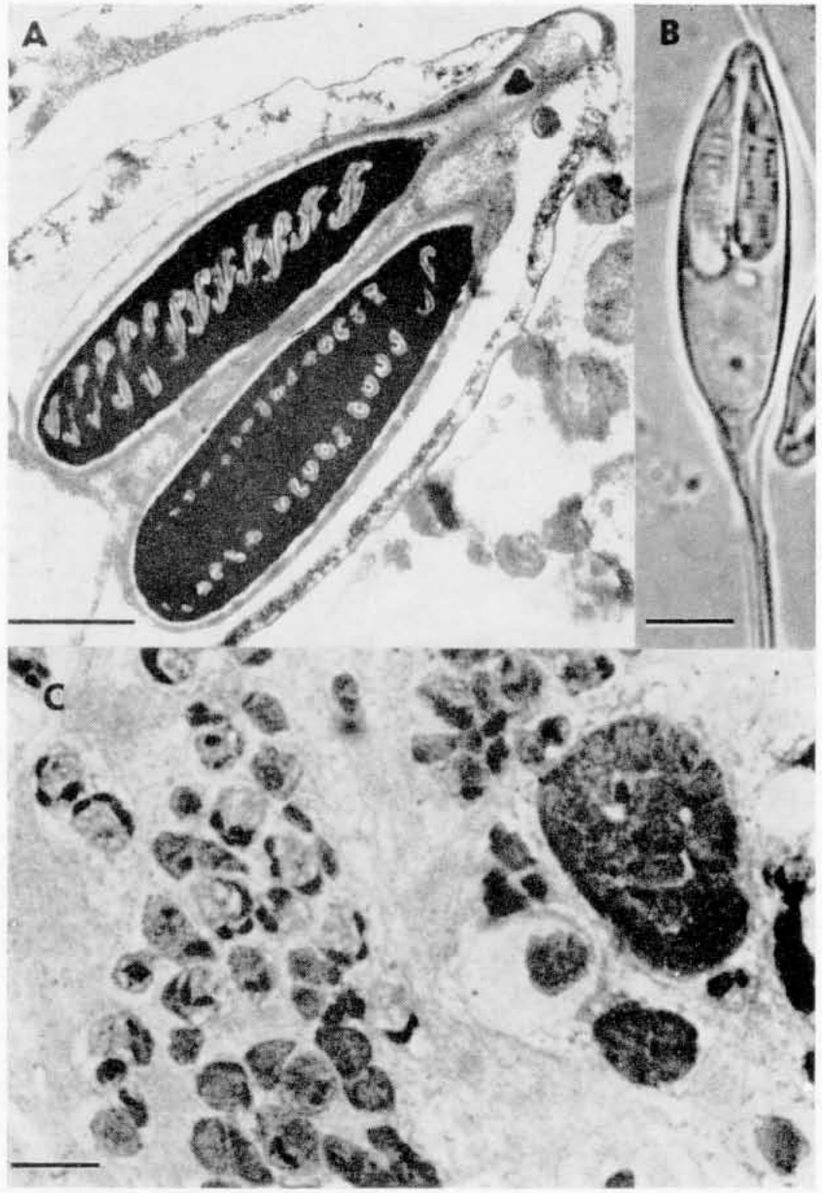
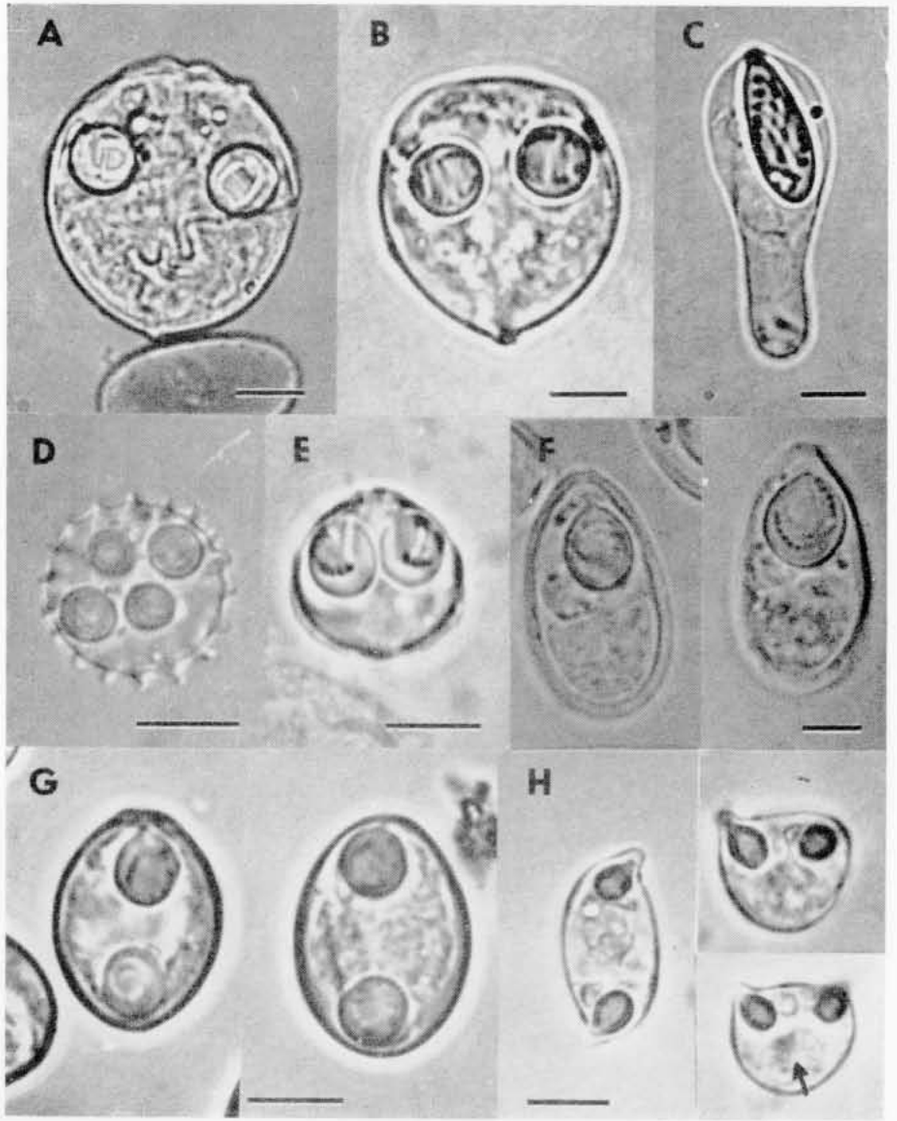


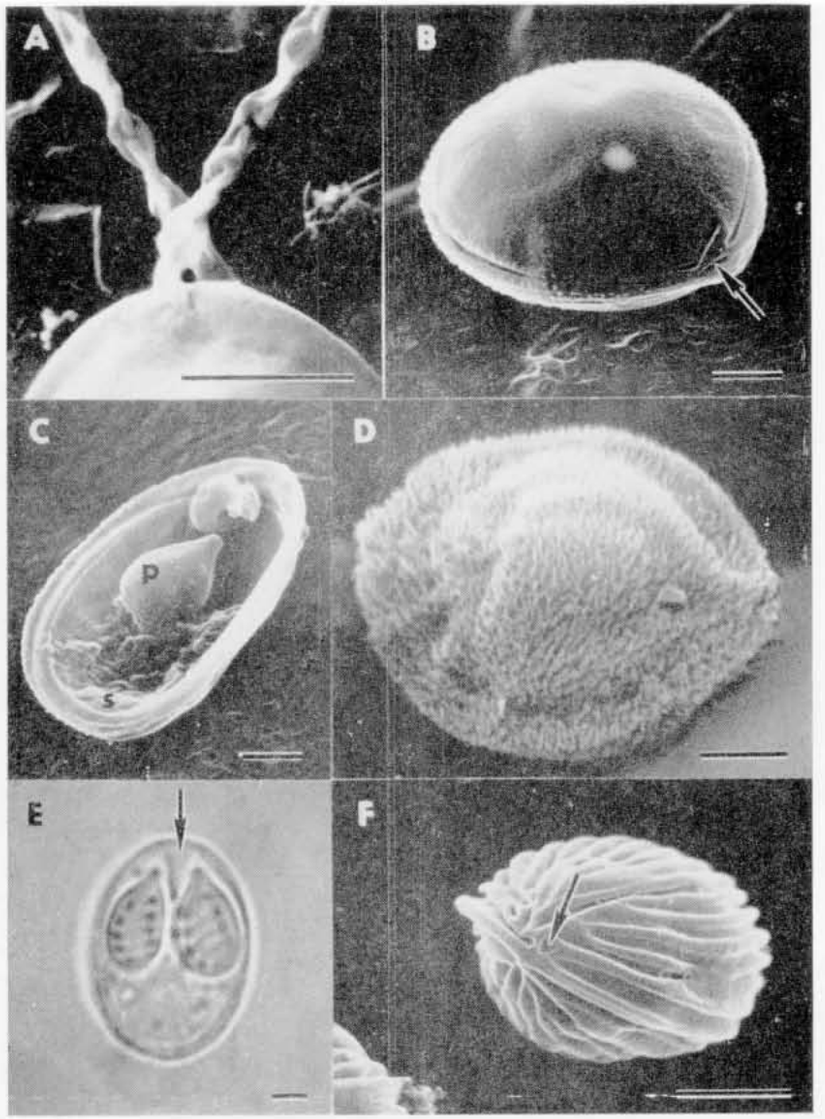
Structure and arrangement of the polar filament in the spore of *Sphaeromyxa magna* Zhukov, 1964. A — transmission electron micrograph of a transverse section through a maturing polar capsule; the loops of the filament occupy already their final position. b — the basal, wide stretch of the filament is richly folded to fit easily into the capsule. B — oblique section of the anterior part of an almost mature polar capsule. The folded basal part of the filament (b) is attached to the slit-like opening (s) in the thick capsular wall. C — light micrograph of fresh spores to show the appearance of the filament. (Compare with Pl. 3A and B.) Bar equals 1 μm in A and B, and 10 μm in C.



A — Transmission electron micrograph of longitudinal section of the mature polar capsules of *Henneguya psorospermica* Thél., 1895. In the upper left capsules, the threads of the polar filament are caught in a grazing section. B — Spore of *H. creplini* (Gurley, 1893); capsules with spirally wound filament. C — Giemsa-stained smear of the tissue of the swim bladder of a yearling carp shows various stages of the presporogonic cycle of *Sphaerospora renicola* Dyková et Lom, 1982. Future improvement of myxosporean classification depends also on the success with which the characters of vegetative stages will be incorporated into the system. Bar equals 2 μm in A, 5 μm in B, and 10 μm in C.



Various types of myxosporean spores (light micrographs of fresh specimens). A — *Sinuolinea* sp. from *Myoxocephalus scorpius*. B — *Myxoproteus* sp. from *Rheinhardtius hippoglossoideus* is transient form between *Sinuolinea* and "typical" *Myxoproteus* spores of pyramidal or triangular shape. In both A and B, polar capsules open in opposite directions. C — *Auerbachia pulchra* Lom, Noble et Laird. D — *Chloromyxum barbi* Dogiel; four capsules of two sizes. E — *Sphaerospora molnari* Lom, Dyková, Pavlásková et Grupcheva; polar capsules are subspherical. F — ***Thelohanellus nikolskyi*** Akhmerov; polar filament makes several threads inside its outer coils (spore at right). G — *Zschokkella* sp. from *Gadus morhua*. Ellipsoid *Zschokkella*-spores are difficult to tell apart from ellipsoid spores of *Myxidium*, especially if polar capsules open terminally (spore at left). H — ***Myxidium gadi*** Géorgevitch; "aberrant" spores with capsules shifted to one side and sporoplasm to the other (arrow) are quite frequent. Bar equals 5 μm.



A — Anterior part of a *Myxobolus*-spore with fully extruded polar filaments; filaments from converging capsules in Platysporina always cross. B — Spore surface of *Myxobolus macrocapsularis* Reuss is not quite smooth; arrow indicates the future capsular foramen. C — the inside of a detached shell valve of *M. macrocapsularis* showing one polar capsule (p) and remnants of the sporoplasm (s). D — *Myxobolus* sp. from the gills of *Ictiobus cyprinellus*; compare the surface with (B); such differences should also be exploited in the taxonomy of this genus. E — light micrograph of the spore of *M. muelleri* from a population with an extremely distinct intercapsular appendix (arrow). F — ***Myxidium giardi*** — spore with characteristic pattern of ridges; sutural line and capsular foramen (arrow). A to D and F — scanning electron micrographs. Bar equals 2 μm in all figures.