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Studies on *Myxosoma cartilaginis* n. sp. (Protozoa: Myxosporidea) of Centrarchid Fish and a Synopsis of the *Myxosoma* of North American Freshwater Fishes

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SYNOPSIS. *Myxosoma cartilaginis* n. sp. is described from the cartilage of *Lepomis macrochirus* (bluegill), *L. cyanellus* (green sunfish) and *Micropterus salmoides* (largemouth black bass). The development of the parasite is described from naturally infected fish which were held in spore-free water after infection. The sporoplasm invades cartilage, and becomes a multinucleate trophozoite which forms pansporoblasts, each of which produces 2 to 4 spores. The first spores appear in 7 weeks.

The histopathology in the above fish consists at first of little cellular reaction, but after 4 to 5 months epithelioid granulomas appear around some of the spore masses. Cartilage liquefaction is present around the parasites for at least 5 weeks. Eosinophilic globules are present in cartilage cells adjacent to the lesions. Diffuse infiltration of the spores from the lesions is described.

Of 24 chemicals tested for polar filament extrusion, potassium hydroxide gave the best results.

An illustrated synopsis of the *Myxosoma* of North American fishes is given. Included is some additional information and illustrations of *M. hoffmani* Meglitsch, 1963. Also included is a table showing the hosts, site of infection, geographic location, spore and polar capsule sizes.

FORTY-SEVEN species of *Myxosoma* have been described, 29 of which are North American. Species descriptions and differentiating characteristics can be found in the following, arranged in chronological order: Kudo(20,21,25); Davis(6,7); Markewitsch (27); Meglitsch(28-30); Bond(3,4); Fantham, Porter & Richardson(9,10); Otto & Jahn(33); Rice & Jahn(35); Iversen(17); Dogiel, Petrushevski & Polyanski(8); Bychowsky(5); Ghittino(11); Guilford (12); Baker(1).

Myxosoma is differentiated from the very similar genus *Myxobolus* by the lack of an iodinophilous vacuole(24).

M. cartilaginis n. sp. was first noticed in bluegill fingerlings at Leetown in December 1960, and was found in a large percentage of the young fish that year and also in 1961, 1962, 1963. It was also found in young bluegills from the Izaak Walton pond at Leetown, White Sulphur Springs National Fish Hatchery, David Wright's farm pond at Inwood, the Shenandoah River at Millville, all in West Virginia, and the State Hatchery at Lewistown, Maryland. It was also found in *Micropterus salmoides* (largemouth black bass), but the cysts were very small and difficult to find.

Myxosoma cartilaginis n. sp. localizes in the cartilage of the head, particularly the gill arches, occasionally in the base of the largest fin rays, but never in the vertebrae of *Lepomis macrochirus* (bluegill) and *L. cyanellus* (green sunfish). We are not aware of any other group of organisms which invade cartilage as a normal part of their life cycle. Among the Myxosporidia the following have been reported from the cartilage of fishes: *Myxobolus aeglefini* from the head skeleton of marine fish(18); *M. dentium* from the base of the teeth of *Esox masquinongy*(9); *Myxosoma cerebralis* from the cartilage of salmonids(16); *M. hoffmani* from the cartilaginous sclera of the eye of *Pimephales promelas* (this paper); *M. scleroperca* from the cartilaginous sclera of the eye of *Perca flavescens* and *Percina caprodes*(12); *Henneguya brachyura* from the fin ray of *Notropis*(39); *H. schizura* from the sclera of the eye of *Esox lucius*(13); *Henneguya* sp. from the cartilage of the branchial arch of *Pomoxis* (6), and *Sphaerospora platessae* from the auditory capsule of flounders(40). In addition, *Myxobolus dentium* from the bases of the palatine teeth of *Esox masquinongy* and *M. hyborhynchi* from the bone of *Hyborhynchus notatus*(9) may actually be cartilage parasites. We believe that these species are specific for cartilage; Kudo(26) has stated that Myxosporidea are more specific for tissues and organs than for host species; e.g., *Myxosoma cartilaginis* n. sp. was found growing in the cartilage only. It was found in the cartilage of 3 species of centrarchid fish but not in 7 other fish of different families in the same habitat, so it has host specificity as well as tissue specificity.

Myxosoma cartilaginis n. sp.
(Figs. 1-9, 50, 51)

Vegetative form. Cysts in head cartilage, 420-1500 μ in greatest diameter, 2-4 spores formed in pansporoblasts (see "Development" for further details).

Spore. Subspherical in front view, lenticular in side and end view. The shell valves are symmetrical, and the sutural ridge is narrow, about 1 μ. Three to 8 triangular thickenings present along the posterior half of the shell in many spores. The two polar capsules of equal size are broadly piriform with very short convergent ducts. Five to seven turns of capsular filament can be seen in each capsule without staining. Maximum length of extruded polar filaments, 83 μ. Sporoplasm comparatively large, uniformly granulated and without an iodinophilous vacuole. Dimensions of ten formalin-preserved spores: length 10.8 (10-12) μ, breadth 9.5 (9-11) μ, thickness 6.1 (6-7)

μ, polar capsules 5.3 (5-6) μ by 3.1 (3-4) μ. Ten fresh spores: length 10.2 (9.5-10.5) μ, breadth 8.9 (8.4-9.5) μ, thickness 6.4 (6.3-7.3) μ, polar capsules 5.3 (5.2-5.6) μ by 3.3 (3-3.5) μ.

Habitat. In the cartilage, particularly the branchial arches, occasionally in the base of the largest fin rays, never in the vertebrae of *Lepomis macrochirus,* and *L. cyanellus.* Also in *Micropterus salmoides,* but cysts small and difficult to find; Leetown (Kearneysville), West Virginia.

Identification. Since Myxosporidea appear to be highly specific for tissue and organ as well as host, *M. cartilaginis* n. sp. is here compared with cartilage-dwelling species only. It very closely resembles *M. cerebralis*; the spore is only slightly larger (*M. cerebralis* is 8.9 μ long, 7.6 μ wide, 6 μ thick, polar capsules 3.9 $\times$ 2.8 μ), and the vegetative form is very similar—the most notable differences are in host specificity and pathology. *M. cartilaginis* was found in nearly 100% of the young bluegills at this station, but trout were never found infected. To test this further, 200 rainbow trout, 3 mo. old, were held in a screen livebox in the bluegill pond from March 15, 1963, till May 9, 1963, and then kept in trout troughs until July; no *Myxosoma* was found. Further evidence of the difference in host specificity between *M. cartilaginis* and *M. cerebralis* is that no infected bluegills could be found at the National Fish Hatchery, Lamar, Pennsylvania, although *M. cerebralis* was present in the trout. Although the histopathology appears very similar in both, trout infected with *M. cerebralis* demonstrate dramatic symptoms (whirling, black-tail, spinal curvature, misshapen heads), whereas no symptoms could be attributed to *M. cartilaginis* in bluegills.

The spore of *M. cartilaginis* n. sp. also resembles that of *M. hoffmani* but is slightly larger; vegetative stages of the latter were not described. Because of its specific location in the fish, and because no other species of fish were found infected in the Grand Forks, North Dakota area, we consider *M. hoffmani* a different species.

DEVELOPMENT OF *MYXOSOMA CARTILAGINIS* N. SP. (Figs. 1-9, 61)

Until recently no one had succeeded in achieving experimental infection with histozoic Myxosporidea (16,23). However, Uspenskaya(37), has infected trout with *Myxosoma cerebralis* by introducing into the stomach spores that had been "aged" in water 4 months. Wagh(38) transplanted spores of *M. ovalis* by hypodermic injection. In 1961 we attempted to infect yearling bluegills by feeding the spores to them in small pieces of tissue; none became infected. In 1963, about 200 bluegills, 18-25 mm long, were transferred to our laboratory from the National Fish Hatchery, Lamar, Pennsylvania where *M. cartilaginis* n. sp. does not exist. They were distributed in 3 aquaria; those in No. 1 and 2 were fed tissue containing spores, whereas those in No. 3 were supplied with a large amount of freed spores, algal bloom and small *Cladocera.* Since there is a possibility that small invertebrates are a necessary transport host, we expected the fish in No. 3, at least, to become infected. No infected fish were recovered from the experiment.

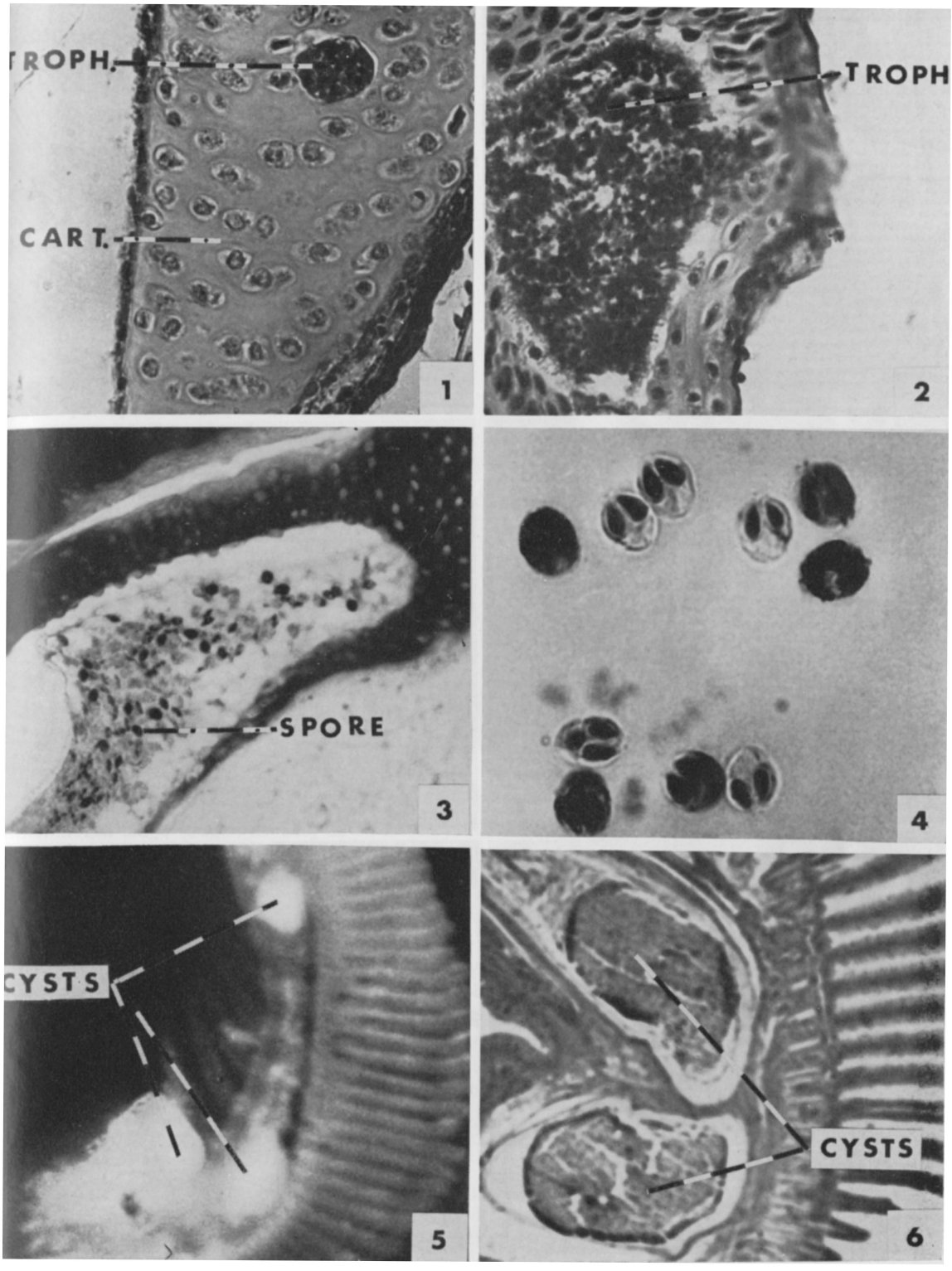
To study the development of the parasite, we collected one lot of bluegills, about 3 weeks old (16-18 mm long), on June 20, 1962, from one of the hatchery ponds containing heavily infected bluegills. At the time of collection the fish had been feeding on phyto- and zooplankton and presumably had been exposed to infection. Since younger fish were not found infected, we presume that they became infected at about 2 weeks of age. These fish were kept in aquaria supplied with spore-free water at 15-26°C (avg. 22). Samples of the fish were examined at intervals, and the smallest parasites found were assumed to be the youngest and approximately as old as the time the fish had been held in spore-free water.

Approximate 1-week stage (Fig. 1). Of 20 trophozoites measured from the fish which had been in the laboratory 7 days, the sizes range from 15-76 μ in greatest diameter with the two smallest ones being 15 and 20 μ respectively. We assume that these smallest trophozoites are approximately one week of age. This corresponds to the size of the youngest stage found for *Myxosoma ovalis* in the gill capillaries by Davis(6) and *M. cerebralis* in the cartilage of trout (16).

The trophozoite is light yellow-brown, round to oval, and appears multicellular in fresh material; in sectioned material this is not so obvious. The "cells" are 5-7 μ in diameter and the nuclei (20 counted in one whole mount) are 3-4 μ in diameter. There is a zone of cartilage liquefaction 1-10 μ thick around the parasite; this is apparent in wet mounts as well as sections.

Approximate 2-week stage. The smallest trophozoite from the fish which had been in the laboratory 2 weeks measured 21 μ in diameter; we assume it to be approximately 2 weeks old. Nuclei are 3 and 5 μ in diameter.

Approximate 4-week stage (Figs. 2, 61). Of 13 trophozoites measured, the smallest was 23 $\times$ 30 μ in diameter. In the fresh preparations the parasite appears multicellular. In cross sections there are 2 sizes of nuclei, about 2 and 4 μ in diameter. It is probable that both vegetative and generative nuclei as described by Kudo(22,23) are present but we were not able to determine any morphological differences in our sections. Some pansporoblasts have formed and are in the process of producing spores; unfortunately the only details to be seen are round objects about 8 μ in diameter which resemble spores. In



Figs. 1-6. All photomicrographs of *Myxosoma cartilaginis* n. sp. in the bluegill, *Lepomis macrochirus*. Fig. 1. Trophozoite, about one week old, in the infraorbitalis (anterior to eye). Hematoxylin and eosin stained section. Magnification 870 ×. Fig. 2. Trophozoite, about 4 weeks old in cartilage of ventral cranium. Note the numerous nuclei. Magnification 870 ×. Fig. 3. Trophozoite, about 7 weeks old, containing a few spores. Note thin "bone ring" around cartilage. Giemsa's stain. Magnification 200 ×. Fig. 4. Spores stained with Giemsa's. Magnification 1000 ×. Fig. 5. Mature, spore bearing cysts of *M. cartilaginis* n. sp. in the gill arch. Magnification 10 ×. Fig. 6. Section through gill arch containing 2 large mature cysts. Stained with hematoxylin and eosin. Magnification 27 ×.

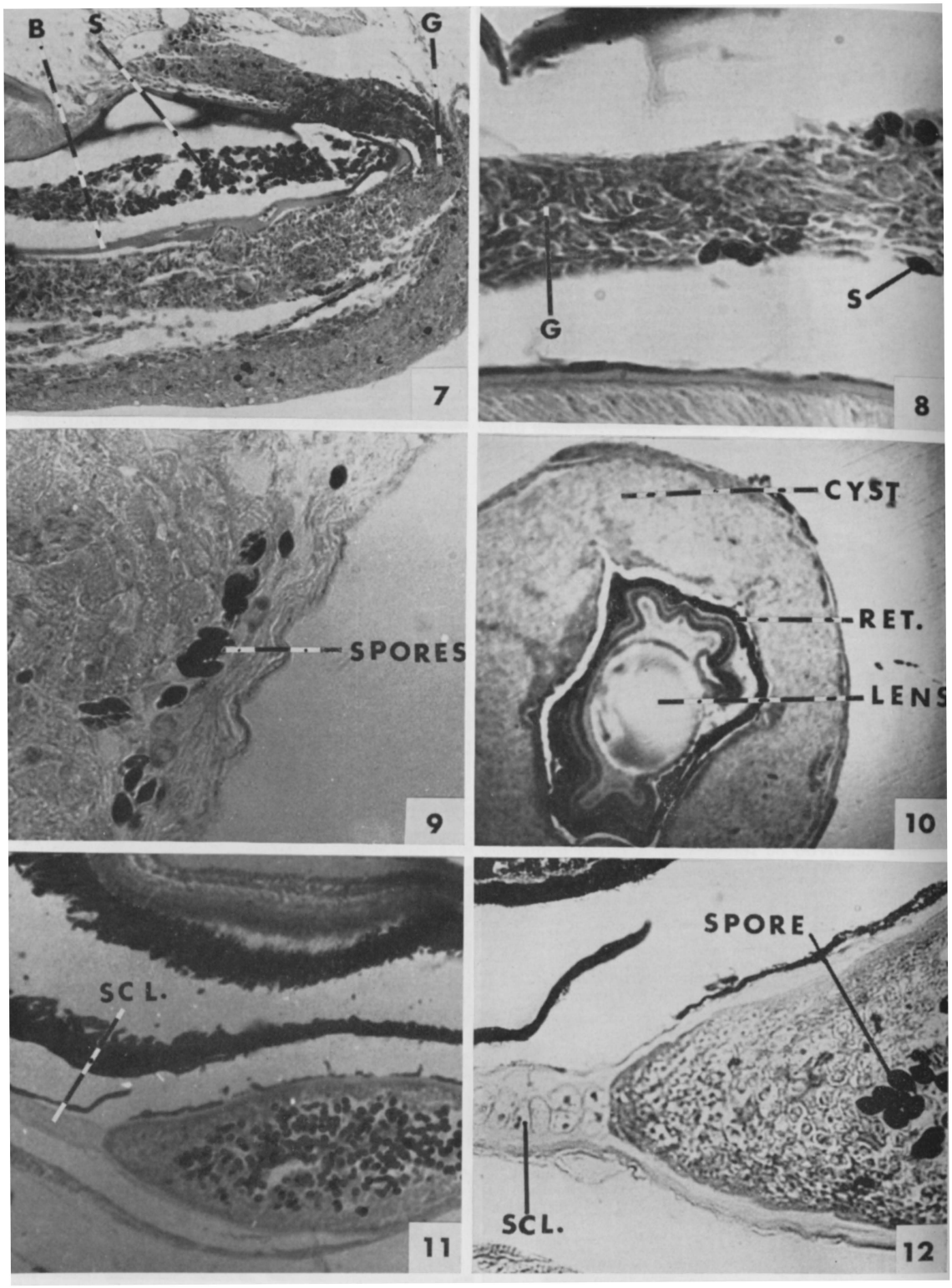


Fig. 7. Remains of cyst of *M. cartilaginis* n. sp. in opercular bone at 5 months post infection. Granuloma extends into the cyst area, around the bone, and darkly staining spores have moved nearly to the mucosa at the bottom. Giemsa's stain. Magnification 120 ×. Fig. 8. Part of Fig. 7 but magnification 250 ×. Granuloma extending into area of cyst. Fig. 9. Darkly stained spores of *M. cartilaginis* n. sp. have moved into the side of the pseudobranch from a cyst which was located above and to the right. Giemsa stain. Magnification 400 ×. Fig. 10. Section through entire eye showing large cyst of *M. hoffmani* completely encircling and compressing retina. Hematoxylin and eosin stain. Magnification 40 ×. Fig. 11. Spore bearing cyst of *M. hoffmani* in cartilaginous sclera of eye. Giemsa's stain. Magnification 150 ×. Fig. 12. As Fig 11 but magnification 500 ×.

Abbreviations: B = bone, G = granuloma, RET = retina, S = spore, SCL = sclera.

stained smears the young spores (Fig. 61) with their parent nuclei are easily seen. There are 2 nuclei "perched" on the outside of the valves, one at the base of each polar filament and 2 in the sporoplasm. These nuclei measure about 1.5 μ in diameter.

Approximate 5-week stage. Of 14 trophozoites measured, the smallest was 60 μ in diameter. In cross sections the nuclei appear similar to the earlier stages. The zone of cartilage liquefaction is still prominent around the parasite.

The bone "shell" around the head cartilage is now about 1 μ thick in most places and many parasites appear to be trapped therein.

Approximate 7-week stage (Figs. 3, 4). The parasites are now 100-200 μ in diameter and some spores were present in cross sections of all parasites examined, but spore production is not completed.

To determine the number of spores in the pansporoblasts, the cyst was ruptured and the material examined in wet mounts; 2, 3 and 4 spores were seen in individual pansporoblasts. Spores are not all formed simultaneously, and the earlier spores are produced throughout the cyst, not centrally as in some *Myxosoma* species(6).

Three-month stage (Figs. 5, 6). Spore production appears to be nearly complete and most, if not all, spores are still contained in the cysts.

Five- to 6-month stage (Figs. 7, 8). The cysts are now 420-790 μ in diameter and round to oval. Spore production is completed. Many cysts appear to have ruptured and many of the spores have "leaked" out into adjacent tissue in spite of partial ossification of the skeleton (see section on histopathology).

Seven-month stage (Fig. 9). Very few intact cysts can now be found. Most have ruptured and lost most of their spores (see histopathology).

HISTOPATHOLOGY

The mature opaque white cysts can be seen easily in the gill arches and opercula of small bluegills at 10× magnification with the dissection microscope (Figs. 5, 6). Young developing stages can be seen with the compound microscope, but the remains of older cysts which have lost most of their spores can be detected only in histological sections stained with Giemsa's or other stains which stain the spores (Figs. 7-9).

There are few reports concerning the histopathology associated with cartilage parasites. Kabata(18) stated that the cartilage seemed hypertrophied and full of white splotches in *Pleuronectes platessa* infected with *Myxobolus aeglefini*. Plehn(34) gave a detailed description of the granulomas extending from the head cartilage in trout infected with *Myxosoma cerebralis*. Woodcock(40) [quoted by Kudo,(20)] described *Sphaerospora platessae* from the cartilage of *Pleuronectes platessa* and notes hypertrophy of the head cartilage. We don't know whether the "hypertrophied cartilage" was actually hypertrophy of cartilage or granulomas growing from the skeletal parts as in *M. cerebralis* and *M. cartilaginis* n. sp. infections; we have not seen the original publication.

Approximate 1-week stage (Fig. 1). There is no evidence of cellular destruction or tissue response; the parasite appears to be located innocuously in the cartilage.

Two to 5 weeks (Fig. 2). There is no tissue reaction, but there is a distinct clear zone of cartilage liquefaction, 1-10 μ thick, around the trophozoite. There are eosinophilic globules in adjacent cartilage cells from about 2 weeks on.

Six weeks to 3 months (Figs. 3-4). Spores are present in the lesions from about 7 weeks on. There is very little tissue reaction around the cysts, which can be recognized by the large number of spores present. A thin layer of bone, a few microns thick, can be seen around most of the head skeletal parts when the bluegills are about 6 weeks old. Some of the cysts become trapped in the skeleton, but the spores from most of the cysts are apparently forced out later on, particularly those in the gill arches and opercula where the cysts did not become enclosed by bone.

Four to 5 months (Figs. 7, 8). Epithelioid proliferation is present around many of the cysts. In one instance the granuloma extended into the cranium along with an emerging nerve. Spores have been moved out of the cysts into the proliferating granulomas. Apparently most, or all, of the cysts rupture during this period and spores disperse into adjacent tissue and probably even out of the fish. Spores were found, apparently migrating through tissue, in connective tissue adjacent to lesions and in the epithelium of the opercula, mouth, base of gills and gill filaments. None were found in the kidney, liver, spleen, brain or blood vessels although it is probable that some are carried to these organs by the vascular system. Similar movement of spores has been recorded for *Myxosoma cerebralis*(36), and *Myxobolus insidiosus*(41); earlier references are discussed in Kudo(23) under problems of "diffuse infiltration."

Seven months (Fig. 9). Most of the spores have been forced out of the cysts, many of which are surrounded by an epithelioid proliferation which still contains some of the spores. There has been connective tissue repair of the cyst region in many cases, and some are completely encased in bone.

EXTRUSION OF POLAR FILAMENTS OF *M. CARTILAGINIS* N. SP.

The purpose of this work was to determine which

chemicals were most effective in causing the extrusion of the polar filaments. Myxosporidean spores extrude their filaments in the intestine of fish, a process assumed to aid in attachment to the epithelium(23). It is possible that the forced extrusion of the filaments by chemical action will render the spores non-infective. If so, such a chemical, if effective in dilute amounts, would be very useful in hatchery and aquarium disinfection.

Kudo(19,23) listed the following chemicals which have been shown to cause polar filament extrusion of Myxosporidea: acetic acid, alkalies (KOH and NaOH), ammonia, boiling water, distilled water, ether, glycerin, hydrochloric acid, iodine-alcohol, iodine-water, nitric acid, and sulfuric acid. Plehn(34) reported that acid, (kind not listed), glycerin, alcohol and ether did not cause extrusion of the polar filaments of *Myxosoma cerebralis* (*Lentospora c.*). Herrick(14) caused the extrusion of polar filaments of *Myxobolus osburni* by allowing a physiological saline solution, containing spores, to dry and then adding distilled water. Herrick(15) could not repeat the above with *Henneguya rupestris*. Noble(32) caused the extrusion of the polar filaments of *Myxidium gasterostoi* with KOH. Uspenskaya(36) caused the extrusion of the filaments of *Myxosoma cerebralis* with 1-2% KOH, but not with acids and artificial gastric juices. Yasutake and Wood(42) extruded the filaments of *Myxidium minteri, Chloromyxum majori* and *Myxobolus kisutchi* with 5% KOH, but not with acids and artificial gastric juices. Guilford(12) used pressure in water mounts successfully for *Myxosoma neurophila, M. scleroperca* and *Henneguya doori.*

Methods. The cysts containing the spores were dissected from the head cartilage of the bluegill, *Lepomis macrochirus.* The spores were placed in vials containing physiological saline (0.85% NaCl) and stored in the refrigerator at 6°C. Some of these spores were kept in good condition for as long as 4 months.

A drop of spore solution was placed on a slide and an equal volume of the reagent to be tested was added. A cover slip was placed over the mixture and the slides examined under the high dry (430 ×) lens of the microscope. In some instances the slide was examined for an hour or less. Pressure from drying might have been a factor beyond an hour and before additional fluid was added.

Most slides were prepared at room temperature (22°C approx.), but heat from an electric light bulb was applied to several slides to try to determine whether temperature was a factor in polar filament extrusion. Also, some slides were made with the spore solution and reagent at refrigerator temperature (6°C approx.).

Results. Potassium hydroxide gave the best results for spore polar filament extrusion of *M. cartilaginis* n. sp. The 2% solution appeared to be the weakest which would generally cause the expulsion of the polar filaments. Even at the 2% level and at the same temperatures, results could not always be duplicated. The spores had been held over a 4-month period and this fact may have a bearing on the relative effectiveness of a reagent at any given concentration.

Temperature of the solutions affected polar filament extrusion. Two slides were made using 1.5% KOH at room temperature (23°C). One slide was subjected to heat from a lamp and the other remained at room temperature. In 30 min the slide which was heated (40°C) had 96% of the spore filaments extruded (based on a count of 55 spores). The slide which remained at room temperature had only 57% at the end of 30 min (based on a count of 45 spores). After letting the same reagent (1.5% KOH) solution cool for 2.5 hr, a slide was made up and kept at room temperature. At the end of 30 min, 51% of the spores had extruded one or more filaments (based on a count of 144 spores). Cold apparently retards the effectiveness of KOH on spores. Using 1.5% KOH solution at 6°C there was no evidence of polar filament extrusion in 20 min. Spores held in distilled water at 24°C and then raised to a temperature of 39.5° for an hour failed to expel their filaments.

Sodium hypochlorite (0.45%) was the most effective agent tested for destruction of the spore. In sufficient strength it caused the polar filaments to extrude; the spore split at the sutural line, the polar capsules floated out and then the entire spore dissolved. Once extruded, the polar filaments dissolved so fast that it was difficult to determine filament extrusion. Using 0.26% NaOCl (5% bleach) the result was more of a general spore dissolution.

The following is a list of chemicals found to be effective in forcing the expulsion of polar filaments:

Potassium hydroxide

10% solution: 90% polar filaments extruded (estimate).
5% solution: 90% polar filaments extruded (estimate).
2.5% solution: 95% polar filaments extruded (actual count).
2% solution: 93% polar filaments extruded (based on a count of 55 spores).
1.5% solution: 50% polar filaments extruded (15 min).
67% polar filaments extruded (20 min, based on a count of 126 spores).
1% solution: 9% polar filaments extruded (20 min, actual count of 92 spores).

Roccal (alkyl-dimethyl-benzyl-ammonium chloride)

0.5% Roccal: 6% polar filaments extruded (20 min).
0.05% Roccal: few polar filaments extruded (50 min).

Sodium hypochlorite (household bleach)

1.3% NaOCl; almost immediate extrusion of polar filaments, spores dissolve quickly.

0.45% NaOCl; polar filaments extruded quickly, the spores split and dissolve.

0.26% NaOCl; polar filaments extruded soon, the spore gradually dissolves, but it does not split (25 min).

0.05% NaOCl; variable results; generally not reliable.

Following is a list of the percentages of sodium hypochlorite and the corresponding parts per million of available chlorine: 5% NaOCl = 1233 ppm, 2.5% NaOCl = 617 ppm, 2%

NaOCl = 494 ppm, 1.5% NaOCl = 370 ppm, 1% NaOCl = 247 ppm.

The list which follows gives the reagents, concentrations and times used *unsuccessfully* in attempts to force polar filament extrusion: *Acetic acid:* 50% solution, 15 min; 10% solution, 25 min. *Acetone:* 5% solution, 60 min. *Calcium cyanamide:* 10% suspension, some effect visible in 15 min, a few polar filaments may have extruded; 5% solution (sealed in petrolatum), little effect noted in 5 hr, in 50 hr the spore appeared normal except that the polar capsules appeared empty. *Calomel:* 2.5% solution, 30 min. *Carbarsone:* 2.5% solution, 30 min. *Formalin:* 50% solution, 30 min. *Furoxone* (furazolidone): 2% solution, 45 min. *Glycerin:* 10% solution, 23 min. *Hydrogen peroxide:* 10% solution, 30 min. *Lux liquid detergent* (active ingredient not stated): 4% solution, 73 min. *Malachite green* (technical grade): 2500 ppm, 30 min; 830 ppm, 25 min; 500 ppm, 45 min; 25 ppm, 70 min. *Merthiolate* (sodium ethyl mercurithiosalicylate): 10% solution, 30 min. *Picric acid:* 50% solution, 25 min. *Potassium permanganate:* 5% solution, 25 min. *Pyridylmercuric acetate* (PMA): 10% solution, 60 min; 5% solution, 30 min. *Quinine sulfate:* 1.25% solution, 20 min. *Sodium bicarbonate plus trypsin:* 5% solution of $NaHCO_3$ plus 0.025% trypsin, 60 min; 1% solution $NaHCO_3$ plus 0.025% trypsin, 27 min; 1% solution $NaHCO_3$, plus 0.1% trypsin, 145 min. *Sodium chloride:* 10% solution, 60 min; 3% solution, 35 min. *Tri-sodium phosphate* (detergent): 10% solution; 1% solution; 0.1% solution. *Tween 40 (Polyoxyethylene sorbitan monopalmitate):* 10% solution, 30 min; 0.5% solution, 25 min. *Versene (chelating agent):* 50% solution, 30 min; 5% solution, 68 min; 0.01% solution, 45 min.

SYNOPSIS OF THE *MYXOSOMA* OF NORTH AMERICAN FRESHWATER FISHES
(Figs. 13-61, Table 1)

The object of this review is to bring together the drawings and information necessary for the identification of the known *Myxosoma* species which parasitize freshwater fishes of North America.

Because the morphology and size of the spore are the most useful criteria for identifying *Myxosoma* species, this synopsis includes little else except the host species, site of infections, geographical locations (in Table 1), and brief notes concerning the pathology. There are few records concerning the host specificity and tissue specificity of *Myxosoma*, but if the rather strict host and tissue specificity of *M. cartiliginis* n. sp. and *M. cerebralis* which we have studied is any indication, these criteria will prove to be very useful in species identification. All reports concerning the sporulating stages of *Myxosoma* indicate that most, or all, are disporoblastic and polysporous so this information would be of little help in determining species; however, the developmental stages should be included in species descriptions.

Drawings shown in Figs. 13-61 were projected and traced to scale from original papers except for *M. cartilaginis* n. sp., *M. cerebralis*, and *M. hoffmani*, which are originals. The *Myxosoma* species are arranged from largest to smallest (top left to bottom right) and are not in alphabetical order.

Table 1 lists *Myxosoma* species, hosts, site of infection, geographic location, spore and polar capsule sizes in microns. All are taken from original sources except for the above mentioned 3 species which are originals.

In the following synopsis the species are listed in alphabetical order, and a brief description of the spores is given (host, site of infection, geographical location and biometry are given in Table 1). Few references prior to Kudo's synopsis(20) will be given in our bibliography. Descriptions of *M. cartilaginis* n. sp., *M. cerebralis*, and *M. hoffmani* are mostly from our own observations.

Genus MYXOSOMA (Thélohan, 1892) emend. Kudo, 1933
(syn., *Lentospora* Plehn, 1905)

Spore ovoidal (front view); flattened (side view). Two piriform polar capsules at anterior end. Histozoic in freshwater and marine fish. 31 species. Type species: *M. dujardini* Thélohan.

In addition to Kudo's diagnosis above, the spores are usually lenticular in side view, and the trophozoites of those species studied usually produce numerous pansporoblasts which are disporoblastic, rarely monosporoblastic or quadrisporoblastic.

M. bibullatum, Kudo, 1934
(Figs. 34, 35)

The cyst was a hemispherical tumor, 1.25 mm in diameter on the ventral side close to the left pectoral fin of *Catostomus commersonii,* Rock R., Ill. Nigrelli(31) reported a similar parasite in the gills of *Catostomus commersonii* in the New York Aquarium.

Spore oval in front view; lenticular with somewhat drawn-out ends in side and end views. Valves relatively thick, and both the sutural ridge and line are distinct. Two or rarely 3 radiating thickenings on the valves give a characteristic appearance to the spore. The polar capsules are broadly piriform with often a long drawn-out duct.

M. cartilaginis n. sp.
(Figs. 1-9, 50, 51, 61)

The cysts, up to 1.5 mm in diameter, are primarily in the head skeleton but may extend from it; those in the gill arches and inner side of the opercula are easily seen. Primarily in *Lepomis macrochirus,* but also in *L. cyanellus* and *Micropterus salmoides*; Northwest West Va. and adjacent Maryland.

Spore subspherical in front view; lenticular in side and end views. Valves relatively thick, sutural ridge but not line, is distinct. Three to 8 triangular thickenings on the shell. Polar capsules broadly piriform with short convergent ducts. Pansporoblast produces 2-4 spores.

M. catostomi Kudo, 1923 (*cf.* Kudo, 22)
(Figs. 32, 33)

Cysts in protruding tumor in muscle of *Catostomus commersonii*; Douglas L., Mich. Also reported from Quebec(9). Spore ovoid to almost rounded. Valves of the Canadian form show a series of folds or thickenings, though they do not have the regularity of numbers, 6-8, described by Kudo, nor can the thickenings or folds be described as triangular. The sutural ridge is very slightly curved, and the 2 valves are not quite the same size. The polar capsules are piriform.

M. cerebralis (Hofer) Plehn, 1905 emend. Kudo, 1933
(syn., *Lentospora c.* (Hofer) Plehn, 1905)
(Fig. 60)

The cysts are located mostly within the head skeleton, but may extend from it in the form of granulomas which can be found by dissecting under the dissection microscope. Pre-spore stages can be found in the cartilage in histological sections. This European species has become a serious disease agent in rainbow trout hatcheries in Eastern U.S. where it severely cripples the fish(16). It causes serious disease in *Salmo gairdneri* and *Salvelinus fontinalis* but also infects other salmonids. Pansporoblast diplosporous. Spore subspherical, slightly longer than broad; lenticular in side view. Sutural ridge relatively narrow. Polar capsules piriform, equal and convergent. This is the smallest known *Myxosoma.*

M. commersonii Fantham, Porter and Richardson, 1939
(Fig. 45)

A very small cyst was found in the skin of a *Catostomus commersonii*; Stoke R., Quebec. Spore oval. Valves smooth with neither folds nor thickenings. Sutural ridge thin, curved, and uniform. Sutural line indistinct. Polar capsules elongate piriform bodies and almost half the length of the spore.

M. cuneata Bond, 1939
(Figs. 52, 53)

Cysts 2-3 mm in diameter are found under the dermis of the inner surface of the gill arch of *Esox masquinongy*; Chautauqua L., N. Y. Spore ovate, piriform in face view, lenticular in side view. Valves of medium thickness with a wedge-shaped marking arising from the base of the spore and extending to about the center of the sporoplasm. This marking is characteristically asymmetrical, the point terminating to the left of the mid-line of the spore as viewed in face view. Sutural ridge heavy with a definite sutural line present. Polar capsules subequal, convergent; they occupy between one-third and one-half of the spore.

M. diaphana Fantham, Porter and Richardson, 1940
(Figs. 13, 14)

Small cyst in the testis of one *Fundulus diaphanus*; Salmon R., Nova Scotia. Spore elongate-ovoid to piriform in shape. Valves fairly thick, with an inconstant number of folds at the posterior end. Sutural ridge almost straight, sometimes slightly curved. Polar capsules subequal, elongate, piriform bodies, with distinct convergent ducts. This is the largest *Myxosoma.*

M. ellipticoides Fantham, Porter and Richardson, 1939
(Fig. 44)

Cysts, 5-8 mm in diameter, on cleithrum of operculum of one *Catostomus commersonii*; Coaticook R., Quebec. Ovoid and ellipsoidal in outline. Valves smooth, without thickenings or folds. Polar capsules flask-like, have relatively long ducts and are less than half the spore length.

M. endovasa Davis, 1947
(Fig. 57)

Trophozoites in the capillaries of the gill lamellae—no large cysts seen. In *Ictiobus bubalus*; Mississippi R., Fairport, Iowa. Spore nearly spherical. Valves thin, without markings. Polar capsules large and piriform.

M. funduli Kudo, 1918
(Figs. 30, 31)

Cysts small, 150-360 μ, in gills. Also recorded by Bond(3). In *Fundulus heteroclitus, F. majalis* and *F. diaphanus*; Woods Hole, Mass. and Chesapeake Bay, Md. Spore piriform. Valves usually uniform in thickness, with 7 to 10 markings on the posterior half of their surfaces. Polar capsules piriform.

M. grandis Kudo, 1934
(Figs. 22, 23)

Infected fish, *Ericymba buccata,* had tremendously enlarged livers; Vermillion R., Ill. Also reported from *Notropis hudsonius* and *Rhinichthys atronasus*; Hudson R. Drainage, N. Y. (2). Spores are ellipsoidal with bluntly drawn-out anterior and broadly rounded posterior end in front view; piriform in side view; lenticular in end view. Valves symmetrical, sutural ridge broad. Five to 10 triangular markings are observable along the posterior half of the valves in the majority of spores. Polar capsules elongate, piriform and convergent.

M. hoffmani Meglitsch, 1963
(Figs. 10-12, 54-56)

The only material studied was collected by one of us (GLH) and described by Meglitsch(30). Unfortunately there was a mixup of host names—the infected fish were *Pimephales promelas,* not *P. notata.* Subsequent to sending material to Meglitsch we have studied additional preserved material, as well as our notes, and can add additional detail. *M. hoffmani* was found in 10 of 50 young-of-the-year *P. promelas* from the English Coulee, Grand Forks, North Dakota in October, 1951. The cysts were opaque white and very obvious; 3 of the fish had both eyes affected and in one, the cysts completely covered the visible part of the eye. Subsequent collections in May and September, 1952, October, 1953, November, 1954, and November, 1956 yielded no more eye cysts. We have examined additional sectioned material and can add that the infection starts in the cartilaginous sclera of the eye (Figs. 11, 12), which it digests almost completely, leaving a huge cyst which may nearly encircle the eye. The retina is displaced and the cavity of the eye markedly reduced (Fig. 10). Such severely affected fish are doubtless blinded. We believe that the primary habitat of *M. hoffmani* is cartilage. Only two other species, *M. scleroperca* and *Myxobolus aeglefini* have been recorded from the sclera of the eye of fishes.

Spores nearly circular to oval in front view and lenticular in side and end views. Valves with 5-15 sutural thickenings. Polar capsules elongate, somewhat inflated posteriorly and terminating in a rather broad neck region. The 2 foramina are distinct.

While examining fresh spores we noted caudal appendages, measuring 18-26 μ by 1.5-3 μ on some of the spores (Fig. 55); 30 of 800 spores were affected. The appendages were not a part of the valves. Also noted was an occasional spore containing 3 polar capsules (Fig. 54).

M. hudsonis Bond, 1938
(Figs. 46, 47)

Cysts between the surfaces of the scales that cover the bases of the fins of *Fundulus heteroclitus*; N. Y. The spores divided into 2 general types, 40-75% of spores examined were Type A, and 26-60% of the spores were Type B.

Type A: Spore piriform in face view, lenticular in side view and with medium thick valves. The most distinctive feature is the opening of the polar capsules. Polar capsules piriform and open at one side or the other at the midline of the spore. One

valve of the spore is flattened toward the capsular end.

Type B: This form is of varying shape but on the average is characterized by the elongation of the spore base. The spore is of greatest width on a line with the base of the capsules, and while rounded at the capsular end, gradually becomes narrower toward the base. The polar capsules are of the same size as in the first form and also open in the same manner. This type of spore is an elongated oval, more rounded at the capsular end and with the base narrow.

M. media Fantham, Porter and Richardson, 1939
(Fig. 41)

Large abdominal cyst in one *Notropis cornutus*; Missisquoi

TABLE 1. *Species of Myxosoma, with spore size and polar capsule sizes (in μ), host, site of infection and geographic location.*

M. bibullatum (Figs. 34, 35); 14-15 × 11.5-12.5, thickness 6-7.5; polar capsules 7 × 3.5; *Catostomus commersonii*; skin; Rock River, Beloit, Ill.; New York Aquarium.

M. cartilaginis (Figs. 50, 51); 9.5-10.5 × 8.4-9.5, thickness 6.3-7.3; polar capsules 5 × 3; *Lepomis macrochirus*; cartilage of head, occasionally fins; National Fish Hatchery vicinity, Kearneysville, West Va.; Shenandoah R., Millville, West Va.

M. catostomi (Figs. 32, 33); 13-15 × 10-11.5, thickness 8-8.5; polar capsules 5-6 × 2.5-3.3; *Catostomus commersonii*; muscle and connective tissue; Douglas Lake, Mich.; Francoeur Brook, Nicolet Watershed, Canada.

M. cerebralis (Fig. 60); 8.9 × 7.6, thickness 6.7; 3.9 × 2.8; salmonids; cartilage; Eastern United States and Europe.

M. commersonii (Fig. 45); 9.5-16.5 × 7-11.4, thickness not given; polar capsules 7.7 × 3.2; *Catostomus commersonii*; skin; Stoke River, Quebec, Canada.

M. cuneata (Figs. 52, 53); 9-10 × 5-7, thickness 4.5; polar capsules subequal, 4-6 × 1.5-3; *Esox masquinongy*; gill arch; Chautauqua Lake, N. Y.

M. diaphana (Figs. 13, 14); 15.5-20 × 5.2-7.6; polar capsules subequal, 7.4 × 9.6, 6.6 × 8.9; *Fundulus diaphanus*; cyst in testis; Salmon River, Guysborough County, Nova Scotia.

M. ellipticoides (Fig. 44); 11.4-14.1 × 6.8-8.2, thickness not given; polar capsules 4.5-5.9 × 1.8-3.2; *Catostomus commersonii*; skin (?) behind operculum; Coaticook River, St. Francis Watershed, Quebec.

M. endovasa (Fig. 57); 9 × 8, thickness not given; polar capsules 5 × 3.5; *Ictiobus bubalus*; gill capillaries; Mississippi River, Fairport, Iowa.

M. funduli (Figs. 30, 31); 14 × 8, thickness 6; polar capsules 8 × 12; *Fundulus heteroclitus, F. diaphanus* and *F. majalis*; branchial lamellae and connective tissue of gill filaments; Woods Hole, Mass.; Chesapeake Bay, Md.

M. grandis (Figs. 22, 23); 15-16 × 9-11, thickness 6.8; polar capsules 6-7 × 2.5-3; *Ericymba buccata, Notropis hudsonius, Rhinichthys atronasus*; liver; Salt Fork tributary, Vermillion River, Ill.; Hudson River Drainage, N. Y.

M. hoffmani (Figs. 54, 56); 9.8-10 × 8.4-9.8; thickness 6.2; polar capsules 5.6 × 2.8; *Pimephales promelas*; cartilaginous sclera of eye; English Coulee, Grand Forks, N. D.

M. hudsonis (Figs. 46, 47); 11.5-12.5 × 7, thickness not given; polar capsules 4.5 × 2-2.5; *Fundulus heteroclitus*; between surfaces of scales covering base of fins; Hudson River, Peekskill Bay, N. Y.; Dobbs Ferry, N. Y.

M. media (Fig. 41); 11-16.8 × 7.7-10.4, thickness not given; polar capsules 5-8.2 × 1.8-3.2; *Notropis cornutus*; dorsal portion of abdomen; Middle branch Missisquoi River, Abercorn Village, Quebec.

M. microthecum (Fig. 48); 10-12.5 × 8.3-11.4, thickness 4.3-5.2; polar capsules 5.5 (3.8-6.3) × 2.4 (1.9-3.2), *Minytrema melanops*; mesenteries; Ohio River, Ill.

M. muelleri (Figs. 42, 43); 12-13 × 5-7, valves subequal, thickness 4.5; polar capsules 7 × 2.5-3; *Esox masquinongy*, connective tissue between branchial lamellae; Chautauqua Lake, N. Y.

M. multiplicata (Fig. 49); 10-12 × 9.5, thickness 6; polar capsules 4 × 2.25; *Idus melanotus, Ictiobus bubalis*; Gills; Russia; Lake Okoboji, Ia.

M. neurophila (Fig. 36); 12-16 × 6-8.5, thickness 4-6; polar capsules 6.8 × 1.4-2.4; *Perca flavescens, Etheostoma nigrum*; brain; Green Bay, Lake Michigan.

M. notropis (Fig. 29); 13.3-16.6 × 6.4-11, thickness not given; polar capsules 4-6.4 × 1.3-3.2, sometimes subequal; *Notropis cornutus*; abdominal cavity and liver; First Brook south of Haseville, Yamasica Watershed, Quebec.

M. okobojiensis (Fig. 40); 16.3 × 13.2, thickness not given; polar capsules 7.8 × 6.2; *Ictiobus bubalis*; gills; West Okoboji Lake, Ia.

M. orbitalis (Fig. 28); 13.3-17.5 × 8.2, thickness not given; polar capsules 4.1-6.4 × 1.3-3; *Notropis cornutus*, in eye orbit; Middle Branch, Missisquoi River below Abercorn, Quebec.

M. ovalis (Figs. 18, 19); 15-17 × 15, thickness 11; polar capsules 8-9 × 6; *Ictiobus bubalis, I. cyprinella*; gills; Mississippi River, Fairport, Iowa; Wolf L., Ill.; East Okoboji Lake, Okoboji, Ia.

M. parellipticoides (Fig. 39); 11.4-16.4 × 7.3-10, thickness not given; polar capsules 4.1-5.5 × 2.3-3.2; *Pfrille neogaeus*; abdomen; Ulverton River, St. Francis Watershed, Quebec.

M. pfrille (Figs. 24, 25); 12.7-19.1 × 7.7-11.4, thickness not given; polar capsules 4.5-6.4 × 1.8-3.2; *P. neogaeus*; abdomen; Ulverton River, St. Francis Watershed, Quebec.

M. procerum (Figs. 20, 21); 15-17 × 6.5-7, thickness 5-6, polar capsules 7-9 × 1.5-2; *Percopsis guttatus*; skin; Illinois River, Meredosia, Ill.; Quiver Lake, Havana, Ill.

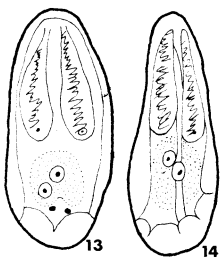
M. robustum (Figs. 26, 27); 14-16 × 10-11, thickness 7-8; polar capsules 6.5-7.5 × 2.5; *Notropis cornutus*; connective tissue of skin; Rick River, Newburry, Ill.

M. rotundum (Figs. 37, 38); 12-14 × 11-13, thickness 7-8.5; polar capsules 6-7 × 3-4; *Carpoides cyprinus*; connective tissue of gill filaments; Embarass River, Villa Grove, Ill.

M. scleroperca (Fig. 17); 10-19.2 × 7.2-9.6, thickness 6-9.6; polar capsules subequal 10.8 and 9.5 × 2.4-3.6; *Perca flavescens, Percina caprodes*; cartilaginous sclera of eye; Green Bay, Lake Michigan, Wisc.

M. squamalis (Figs. 58, 59); 8.1-9.9 × 7.7-9.9, thickness 5.6-7.7; polar capsules 3.9-5.1 × 2.6-3.9; *Salmo gairdneri, Oncorhynchus kisutch, O. keta*; integument; Commercial trout farms, Seattle and Olympia, Wash.

M. subtecalis (Figs. 15, 16); 15-18 × 6.5-8, thickness 6; subequal, polar capsules 7-8 × 2; *Fundulus heteroclitus*; connective tissue of viscera; fatty tissue on dorsal surface of brain; Chesapeake Bay, Baltimore, Md.



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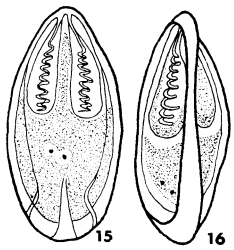
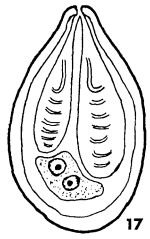


M. subtecalis



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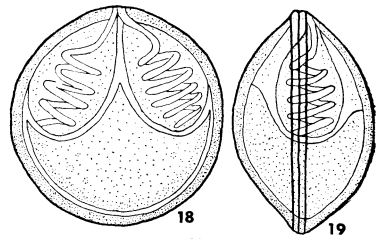

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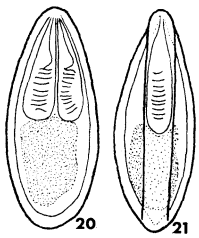

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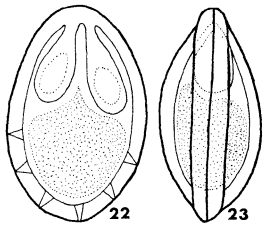

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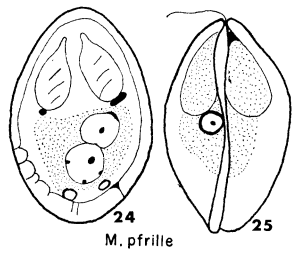
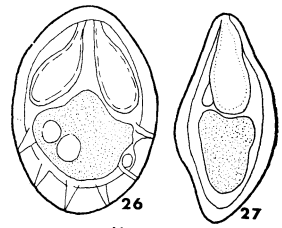
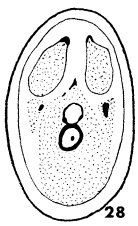


M. pfrille



M. robustum



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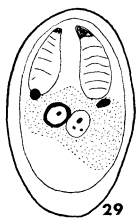

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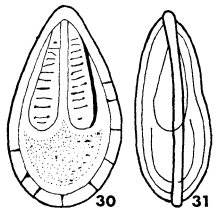

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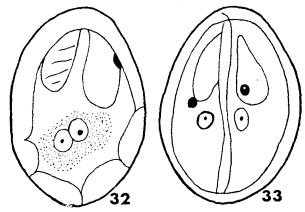

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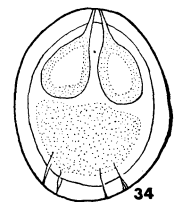
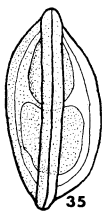


M. bibullatum



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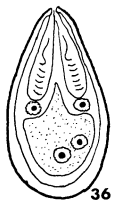

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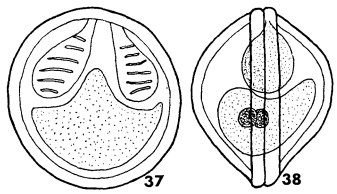
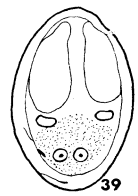


M. rotundum



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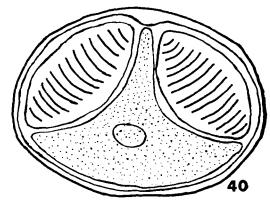

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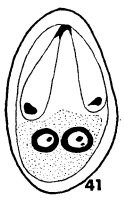
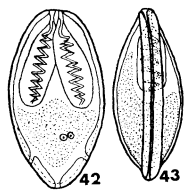


M. media



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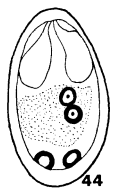

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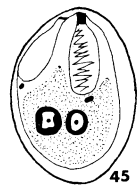
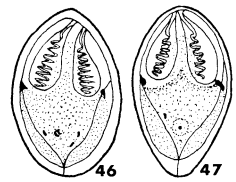
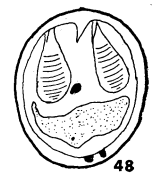


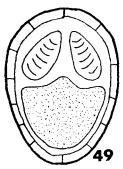
M. commersonii



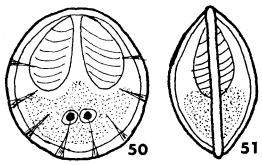
M. hudsonis



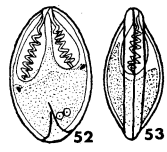
M. microthecum



M. multiplicata



M. cartilaginis n.sp.



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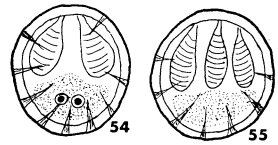
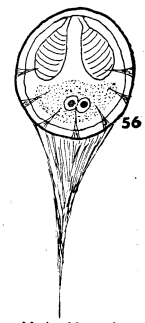
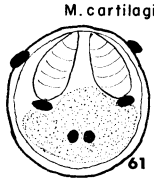
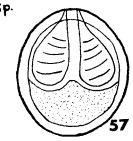


M. hoffmani

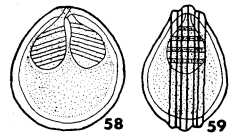


M. hoffmani

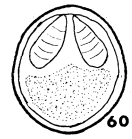




M. endovasa



M. squamalis



M. cerebralis

R., Quebec.

Spore usually ovoid but occasionally a more angular spore may be found. Valves smooth and without thickenings. Polar capsules elongate, piriform, and occupy about half the length of the spore.

M. microthecum Meglitsch, 1942
(Fig. 48)

Many minute (150-350 μ), oval to round cysts in mesenteries and peritoneum of *Minytrema melanops,* Ohio R., Ill.

Spore oval in front and lenticular in side views. Valves thin and smooth. Sutural ridge median and distinct, but sutural line not distinct. Capsular nuclei present in some spores. A slender intracapsular process present at anterior end. The two rather large nonconvergent polar capsules are elongate, piriform and constricted at the neck.

M. muelleri Bond, 1939
(Figs. 42, 43)

White oval cysts, 2 to 3 by 1 mm in the connective tissue between the branchial lamellae of *Esox masquinongy*; New York.

Spore bluntly ovate in face view, lenticular in side view with one valve somewhat larger. Valves medium thick; 2 lateral and one basal markings present so that 2 quadrilateral plaques are apparent at the base of the spore. Sutural ridge moderate, sutural line distinct; polar capsules equal, slightly convergent but not crossing when studied in face view. Polar capsules are large and occupy about half the spore.

M. multiplicata (Reuss) Rice and Jahn, 1943
(syn., *Lentospora multiplicatum* Reuss, 1906)
(Fig. 49)

This European parasite was reported from North America from the gills of *Ictiobus bubalis*; L. Okoboji, Ia.(35). The cysts were 200-492 μ in size and more or less oval.

Spores with 12-14 folds in the sutural ridge with the ones in the posterior region more distinct than the ones in the anterior region. Polar capsules uniform in size and egg shaped with the more pointed end anterior.

M. neurophila Guilford, 1963
(Fig. 36)

Spherical to oval cysts, 30-950 μ in size, found only in tissues of optic tectum and midbrain of *Perca flavescens* and *Etheostoma nigrum*; Green Bay, L. Michigan, Wis.

Front and side views of spore piriform, anterior view lenticular. Valves, unmarked and thin, except for posterior internal sutural folds, meet on a sutural ridge less than 1 μ thick. Polar capsules equal, narrow and piriform.

M. notropis Fantham, Porter and Richardson, 1939
(Fig. 29)

Large cyst filled and distended the anterior part of the abdomen. The liver had also been invaded and its structure had become almost obliterated by the parasite. One *Notropis cornutus* found infected; Yamaska Watershed, Quebec.

Spore oval in front view and ovoid in side view; anterior end narrower than posterior. Sutural ridge thin and slightly curved. Polar capsules elongate-piriform, with short ducts, may be equal or subequal. Very similar to *M. orbitalis.*

M. okobojiensis Rice and Jahn, 1943
(Fig. 40)

Cysts 175-200 μ long, in gills of *Ictiobus bubalis*; L. Okoboji, Ia.

Spore similar in shape to *M. ovalis,* but slightly broader. Valves thin, forming a small intercapsular appendix which appeared to meet the sporoplasm. Polar capsules considerably larger than in *M. ovalis* and having 14-16 turns to the polar filament. This is the widest *Myxosoma.* Figs. 2 and 3 in Rice and Jahn(35) are reversed.

M. orbitalis Fantham, Porter and Richardson, 1939
(Fig. 28)

Three cysts, situated deep in the eye orbit, extending down over the cheek, bulging outwards and upwards and forcing the eye out laterodorsally. In one *Notropis cornatus*; Missisquoi R., Quebec.

Spores oval to slightly ovoid and delicate in appearance. Valves transparent and without markings or thickenings. Polar capsules piriform. Very similar to *M. notropis.*

M. ovalis (Davis, 1923) Kudo, 1933
(syn., *Lentospora ovalis* Davis, 1923)
(Figs. 18, 19)

Cysts are small (500-700 μ), round to ovoid in the gill filaments of *Ictiobus bubalis* and *I. cyprinella*; Mississippi R., Fairport, Ia. Also reported from L. Okoboji, Ia.(35) and Wolfe L., Mississippi R., Ill.(38).

Figs. 13-61. Spores of *Myxosoma* of North American freshwater fishes. All were redrawn to scale except Figs. 50, 51, 54-56, and 60 which are original. The species are arranged in order of decreasing size. Figs. 13, 14. *M. diaphana,* two spores of different shape (after Fantham & Porter, 1940). Figs. 15, 16. *M. subtecalis,* front and side views, note subequal polar capsules (after Bond, 1938). Fig. 17. *M. scleroperca,* note subequal polar capsules (after Guilford, 1963). Figs. 18, 19. *M. ovalis,* front and side views (after Davis, 1923). Figs. 20, 21. *M. procerum,* front and side views (after Kudo, 1934). Figs. 22, 23. *M. grandis,* front and side views (after Kudo, 1934). Figs. 24, 25. *M. pfrille,* (after Fantham, Porter and Richardson, 1939). Figs. 26, 27. *M. robustum,* front and side views (after Kudo, 1934). Fig. 28. *M. orbitalis* (after Fantham, Porter and Richardson, 1939). Fig. 29. *M. notropis* (after Fantham, Porter and Richardson, 1939). Figs. 30, 31. *M. funduli,* front and side views (after Kudo, 1920). Figs. 32, 33. *M. catostomi,* note that the valves are subequal (after Fantham, Porter and Richardson, 1939). Figs. 34, 35. *M. bibullatum,* front and side views (after Kudo, 1934). Fig. 36. *M. neurophila* (after Guilford, 1963). Figs. 37, 38. *M. rotundum,* front and side views (after Meglitsch, 1937). Fig. 39. *M. parellipticoides* (after Fantham, Porter and Richardson, 1939). Fig. 40. *M. okobojiensis,* this is numbered incorrectly in the original (after Rice and Jahn, 1943). Fig. 41. *M. media* (after Fantham, Porter and Richardson, 1939). Figs. 42, 43. *M. muelleri,* front and side views (after Bond, 1939). Fig. 44. *M. ellipticoides* (after Fantham, Porter and Richardson, 1939). Fig. 45. *M. commersonii* (after Fantham, Porter and Richardson, 1939). Figs. 46, 47. *M. hudsonis,* both polar capsules open at one side of midline (after Bond, 1938). Fig. 48. *M. microthecum,* note anterior intracapsular appendix (after Meglitsch, 1942). Fig. 49. *M. multiplicata,* note broad anterior end (after Rice and Jahn, 1943). Figs. 50, 51. *M. cartilaginis* n. sp. (original). Figs. 52, 53. *M. cuneata,* note wedge-shaped thickening at posterior and subequal polar capsules (after Bond, 1939). Figs. 54-56. *M. hoffmani,* note tail-like process (original). Fig. 57. *M. endovasa* (after Davis, 1947). Figs. 58, 59. *M. squamalis,* note secondary ridges in side view (after Iversen, 1954). Fig. 60. *M. cerebralis* (original). Fig. 61. Newly formed spore of *M. cartilaginis* n. sp. with parent nuclei still present.

Spore usually circular to oval, but may be elongate. Valves rather uniform in thickness but slightly thickened posteriorly. Polar capsules fill the anterior two-thirds of the spore.

M. parellipticoides Fantham, Porter and Richardson, 1939
(Fig. 39)

Large cyst (10 mm long) in abdomen of one *Chrosomus neogaeus*; Ulverton R., Quebec.

Most spores oval in contour while others may be somewhat ovoid. Valves thin, transparent and without markings. Polar capsules piriform.

M. pfrille Fantham, Porter and Richardson, 1939
(Figs. 24, 25)

Large abdominal cyst in *Chrosomus neogaeus*; Ulverton R., Quebec.

Spores ovoid with folds or thickenings at the broader end. Valves smooth, suture very slightly curved. Polar capsules piriform.

M. procerum Kudo, 1934
(Figs. 20, 21)

Cysts (0.5-1.5 mm) in skin of *Percopsis guttatus*; Illinois R. and Quiver L., Ill.

Spores ellipsoid in front view and lenticular in side view. Valves relatively thin and symmetrical; sutural ridge broad, but sutural line indistinct. Polar capsules equally large and elongate piriform.

M. robustum Kudo, 1934
(Figs. 26, 27)

Cysts (1.3 cm) in integument of *Notropis cornutus*; Rock R., Ill.

Spore ellipsoidal in front view and fusiform in side view. Valves comparatively thick and showing 5-8 folds along the posterior margin in front view. Polar capsules elongate, piriform and convergent.

M. rotundum Meglitsch, 1937
(Figs. 37, 38)

Cysts small (0.5 mm) in connective tissue of gill filaments of *Carpiodes cyprinus;* Embarass R., Ill.

Spore circular or subcircular in front view, lenticular to oval in side view. Valves rather thick and smooth; sutural line distinct, and ridge is well developed, showing 2 distinct lips with a groove between them. Polar capsules broadly piriform with short necks.

M. scleroperca Guilford, 1963
(Fig. 17)

Conspicuous cysts (up to 5 mm) located predominantly in dorsal area of cartilaginous sclera of the eye of *Perca flavescens* and *Percina caprodes*; Green Bay L. Michigan, Wisc. Large cysts were accompanied by inflammation with leucocytic infiltration, capillary invasion, and increased connective tissue. Cartilage was hyperplastic.

Spore piriform in front and side views but lenticular in anterior view. Valves, thickened near posterior margin, meet at a sutural ridge less than 1 μ thick. Piriform polar capsules of unequal length extend into posterior of spore.

M. squamalis Iversen, 1954
(Figs. 58, 59)

Cysts develop within the scales of *Salmo gairdneri, Oncorhynchus tschawytscha* and *O. keta*; Seattle and Olympia, Wash.

Heavy infection of trout and salmon in hatcheries apparently contributes to mortalities. The skin pustules are unsightly and there is considerable tissue response adjacent to the pustules.

Spore rounded to slightly oblong in front view, piriform in side view, and lenticular in end view. Valves, devoid of appendages, are relatively thin throughout and of equal size. Sutural ridge, without sutural markings of any kind, narrow, the sutural line indistinct. Closely bounding either side of the sutural ridge is a narrow parallel ridge that runs completely around the valve. Polar capsules equal, convergent and piriform. This is a very small species.

M. subtecalis Bond, 1938
(Figs. 15, 16)

Cysts (50-300 μ) most numerous in connective tissue of fins and kidneys; also in most of the viscera and in the fatty tissue of the sub-tecal space of the optic lobes of the brain.

In heavily infected fish the glomeruli of the kidney are infected, the parasites occlude the glomeruli and eventually the parasites burst into surrounding tissue. The infection is found most often in the dorsal cranium, however.

Spore piriform in front view, lenticular in side view; valves fairly thick, not symmetrical, one side flattened anteriorly; sutural ridge broad, sutural line distinct. On the front view, the base of the spore appears to have 3 ridges, broad at the base and narrowing towards the middle of the spore. These are seen to consist of a definite central ridge and a lateral one on either side. The central ridge extends up the middle of the face view of the spore to about the middle of the sporoplasm, and there disappears. The lateral ridges are derived from the edges of the sutural ridge and, starting at equal distances from the central ridge, extend out onto the face of the spore for a distance equal to about one-fourth the width of the spore. They then curve back to meet the edge of the spore at a point approximately at the middle of the polar capsules. Polar capsules piriform, elongate and converging.

KEY TO *MYXOSOMA* SPECIES OF NORTH AMERICAN FRESHWATER FISHES

This key is artificial; the key characteristics are based on anything that we think might aid in identification.

1. Found in cartilage, or granulomas extending from it 2
1. Not found in cartilage 3
2. Found in Salmonidae ..... *M. cerebralis*
2. Found in the sclera of the eye of *Pimephales promelas* ..... *M. hoffmani*
2. Found in the sclera of the eye of *Perca flavescens* and *Percina caprodes* ..... *M. scleroperca*
2. Found in head cartilage of Centrarchidae ..... *M. cartilaginis* n. sp.
3. Spores distinctly oval or piriform 10
3. Spores nearly round or very short oval 4
4. In gills or gill capillaries 5
4. Not in gills 8
5. In gill capillaries of *Ictiobus*; spore small (9 $\times$ 8 μ) ..... *M. endovasa*

5. Not in gill capillaries; spore larger 6
6. Spore wider than long; small intercapsular appendix of valves; in gills of *Ictiobus* ..... *M. okobojiensis*
6. Spore round or slightly longer than wide 7
7. Spore larger (15-17 × 15 μ); in gills of *Ictiobus* ..... *M. ovalis*
7. Spore smaller (12-14 × 11-13 μ); in gills of *Carpiodes* ..... *M. rotundum*
8. In skin 9
8. In abdomen of *Minytrema*; spore with projection of valves into spore ..... *M. microthecum*
9. Spore larger (14-15 × 11.5 μ); in skin of *Catostomus* ..... *M. bibullatum*
9. Spore smaller (8.4-9.9 × 7.7-9.9 μ); in skin of salmonids ..... *M. squamalis*
10. In brain of *Perca* and *Etheostoma*; spore distinctly piriform ..... *M. neurophila*
10. Not in brain 11
11. In gill arch of *Esox*; small spore (9-10 × 5-7 μ); polar capsules subequal ..... *M. cuneata*
11. Not in gill arch 12
12. In skin 13
12. Not in skin 17
13. Polar capsules open on one valve only; in skin of *Fundulus*; spore 11.5-12.5 × 7 μ; length/width = 1.7 ..... *M. hudsonis*
13. Polar capsules open on each side 14
14. Very narrow spore, length/width 2.4; spore 15-17 × 6.5-7 μ; in skin of *Percopsis* ..... *M. procerum*
14. Spore not extremely narrow 15
15. Spore fairly narrow, length/width = 1.8; in skin (?) on cleithrum of operculum of *Catostomus* ..... *M. ellipticoides*
15. Spore not as narrow, length/width = 1.3-1.4 .. 16
16. Spore larger (14-16 × 10-11 μ); in skin of *Notropis* ..... *M. robustum*
16. Spore smaller (9.5-16.5 × 7-11 μ); in skin of *Catostomus* ..... *M. commersonii*
17. In gill filaments 18
17. Not in gill filaments 20
18. Spore piriform in front view, 14 × 8 μ; in filaments of *Fundulus* ..... *M. funduli*
18. Spore with anterior end more or less truncated.. 19
19. In gill filaments of *Esox*; spore 12-13.5 × 7 μ with length/width = 1.8; polar capsules 7 × 3 μ ..... *M. muelleri*
19. In gill filaments of *Ictiobus* (in *Idus* in Europe); spore 10-12 × 9.5 μ with length/width = 1.2; polar capsules 4 × 2.3 μ .... *M. multiplicata*
20. In musculature (connective tissue?) of *Catostomus*; spore 13-15 × 10-11.5 μ; polar capsules occasionally subequal, 5.6 × 2.5-3.3 μ .... *M. catostomi*
20. Not in musculature 21
21. Larger, spores 15-17.5 μ 22
21. Smaller, spores 13-14.5 μ 26
22. Very narrow in face view, length/width = 2.3-3 23
22. Not as narrow, length/width = 1.6-1.9 24
23. In testis of *Fundulus*; spore 15.5-20 × 5.2-7.6 μ, length /width = 3; polar capsules subequal 8.9-9.6 × 6.6-7.4 μ ..... *M. diaphana*
23. In connective tissue of viscera, and fat bodies in cranium of *Fundulus*; spore 15-18 × 6.5-8 μ, length/width = 2.3; capsules subequal 7-8 × 2(?) ..... *M. subtecalis*
24. In eye orbit of *Notropis*; spore 13.3-17.5 × 8.2 μ, length/width = 1.9; polar capsules 4.1-6.4 × 1.3-3 μ (very similar to *M. notropis* .... *M. orbitalis*
24. Not in eye orbit 25
25. In abdomen of *Pfrille*; spore 12.7-19.6 × 7.7-11.4 μ, length/width = 1.8; polar capsules 4.5-6.4 × 1.8-3.2 μ ..... *M. pfrille*
25. In liver of *Ericymba, Notropis, Rhinichthys*; spore 15-16 × 9-11 μ, length/width = 1.6; polar capsules 6-7 × 2.5-3 μ ..... *M. grandis*
26. In visceral cavity and liver of *Notropis*; spore 13.3-16.6 × 6.4-11 μ, length/width = 1.6; polar capsules 4-6.4 × 1.3-3.2 sometimes subequal, (very similar to *M. orbitalis*) .. *M. notropis*
26. In visceral cavity only 27
27. In *Notropis*; spore 11-16.8 × 7.7-10.4 μ, length/width = 1.5; polar capsules 5-8.2 × 1.8-3.2 μ .....*M. media*
27. In *Pfrille*; spore 11.4-16.4 × 7.3-10 μ, length/width = 1.5; polar capsules 4.1-5.5 × 2.3-3.2 μ ..... *M. parellipticoides*

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