FISH MYXOSPOREANS FROM THE OKAVANGO DELTA, BOTSWANA AND THE SOUTH COAST OF SOUTH AFRICA

by

Cecilé Catharine Reed

Thesis submitted in fulfilment of the requirement
for the degree Philosophiae Doctor
in the Faculty of Natural and Agricultural Sciences,
Department of Zoology and Entomology,
University of the Free State

Promotor: Prof. Linda Basson
Co-promotor: Dr. Liesl L. Van As
Co-promotor: Prof. Iva Dyková

December 2003

Fish Myxosporeans from the Okavango Delta, Botswana and the South Coast of South Africa

1. Introduction

Myxozoans may be described as an incredibly specious and economically important group of entirely endo-parasitic metazoan animals (Kent, Andree, Bartholomew, El-Matbouli, Desser, Devlin, Feist, Hedrick, Hoffmann, Khattra, Hallett, Lester, Longshaw, Palenzuela, Siddall and Xiao 2001). These complex and minute parasites were originally described during the early 1800's (Müller 1838) and have ever since intrigued scientists. Since their initial discovery, descriptions of new species have proliferated as the pathogenic potential of these organisms has been recognised in fishing industries throughout the world (Bartholomew 1998). Furthermore, myxosporeans were originally thought to be primarily parasites of teleost fishes, but they have since been found in a wide variety of hosts including bryozoans, oligochaetes, plathyhelminths, insects, elasmobranchs, lampreys, amphibians, reptiles and mammals (see Chapter 2). Today, 165 years since their discovery, myxozoans are represented by more than 1300 species, assigned to about 54 genera throughout the world (Kent *et al.* 2001). During the past two decades increasing attention has been paid to this group of parasites, mainly because of their already notorious pathogenicity, their peculiar life cycle first elucidated by Wolf and Markiw (1984), as well as the assignment of the previously protozoan myxozoans to the Metazoa (see Chapter 2), and the recent reappraisal of the genus *Buddenbrockia* Schröder, 1910, a probable ancestor of myxosporeans.

Myxosporeans are best known for the diseases they cause in commercially important fish hosts and the devastating effects some species have had on fishing industries. As a result, this group of parasites has been extensively researched in many parts of the world. However, in Africa research on fish-infecting myxosporeans is limited to just a few countries where these parasites are also considered to be economically important. Most research on myxosporeans is concentrated in Central, West and North Africa, with large parts of the continent remaining entirely unexplored. Fortunately during the last decade myxosporean research in Africa has increased and to date more than 140 species have been described from freshwater, marine and estuarine fishes in Benin, Botswana, Burkina Faso, Cameroon, Chad, Egypt, Ghana, Namibia, Nigeria, Senegal, South Africa, Tunisia and Uganda. Considering that more than 2500 species of fish are known from freshwater and marine environments in Africa, many of which are endemic, the number of known myxosporea infecting these fishes is remarkably small and it can safely be expected that many more remain to be discovered (Ali 1999).

In southern Africa very little research has been conducted in this field and as a result, hardly any literature exists regarding the biodiversity of myxospores in both freshwater and marine environments. Apart from a few publications from the Cape east, south and west coasts in South Africa (Fantham 1919; Gilchrist 1924; Fantham 1930; Van Wyk 1968; Paperna, Hartley and Cross 1985, Ali 2000) and the Okavango Delta in Botswana (Peters 1971; Reed, Basson and Van As 2002b; 2003a), fishes in the majority of southern Africa's freshwater and marine ecosystems are yet to be examined for the presence of myxozoan parasites.

Although the success of freshwater and marine aquaculture and fishing industries in North and Central African countries have been tremendous, the pathogenic potential of fish-infecting myxosporean parasites have repeatedly been recognised as being a serious problem (Sakiti, Tarer, Jaquemini and Marques 1996; Negm-Eldin, Govedich and Davies 1999; Gbankoto, Pampoulie, Marques and Sakiti 2001a,b). Freshwater and marine aquaculture and fishing industries are growing at a considerable rate in southern Africa and have the potential to reach the same extent as those industries in Central and North Africa.

It has already been recognised that some disease-causing parasites have had a great impact on the growing southern African aquaculture industry, causing serious losses for fish keepers and aquarium traders (Skelton 2001). Before the aquaculture fishing industry in southern Africa develops to its full potential, it would be valuable to have a thorough knowledge and understanding of potential disease-causing parasites such as myxosporeans occurring naturally in southern Africa's marine and freshwater environments. Furthermore, it is well known that a comprehensive approach to the study of fishery science must also include an examination of fish parasites, because of the influence they have on the general well-being of fish stocks and in turn, the overall management of the fisheries. Such a study also involves the assessment of possible damages the parasites can cause to the host, which are affected by the environment, or a combination of parasite-host-environmental relationships. It therefore becomes essential to undertake a systematic survey of fish parasites of fishes living under different ecological conditions (Narasimhamurti, Kalavati, Anuradha and Padma Dorothy 1990).

In recognition of the need to investigate the presence of fish-infecting myxosporeans in both the freshwater and marine environments of southern Africa, the Aquatic Parasitology research group in the Department of Zoology and Entomology, University of the Free State, Bloemfontein, South Africa initiated a study on the biodiversity of myxosporeans infecting southern African freshwater and marine fishes in 1997. This research, conducted by the author, formed part of two major projects currently undertaken by the Aquatic Parasitology group. The *Okavango Fish Parasite Project* was funded by the Debswana Diamond Company in Botswana for a period of five years, and is continually funded by the National Research Foundation (NRF) in South Africa. This ongoing project examines the prevalence and biodiversity of fish parasites in the Okavango River and Delta in Botswana. A second project, entitled: *Intertidal Symbionts and Parasites of the South African Coast*, which is funded by the National Research Foundation (NRF), investigates the biodiversity and prevalence of symbionts and parasites associated with intertidal organisms along the coast of South Africa. These projects have allowed the study of fish-infecting myxosporeans in two of the most unique regions in the world (see Chapters 5 and 6).

Once it has been established which myxosporean species are found in southern Africa's natural environments, it will be possible to determine the pathogenic potential of these species. Determining the presence of any alien myxosporeans that might have been introduced together with the many alien host species would also give an indication of the potential threats these parasites might hold for our natural fish populations.

The first major results on fish-infecting myxosporeans in southern Africa obtained since the onset of the study were from extensive surveys conducted in the Okavango River and Delta during 1998 and 1999. The research conducted during that time led to the completion of the author's M.Sc. dissertation, entitled: "*Myxosporean parasites (Myxozoa: Myxosporea) infecting fishes in the Okavango River system, Botswana*" (Reed 2000). The main aims of the study were to investigate the available literature regarding African myxosporeans and to determine the taxonomic status, species biodiversity and prevalence of myxosporeans infecting fishes in the Okavango River and Delta in Botswana. The results of this study have led to the publication of two scientific papers (Reed *et al.* 2002b; 2003a) in international journals (see Appendix I). These papers represent the first publications on southern African freshwater fish-infecting

myxosporeans. Furthermore, the results have also been presented at several national (Reed, Kruger, Van As and Basson 1999; Christison, Reed, Smit, Basson and Jansen van Rensburg 2000; Reed, Basson and Van As 2001; Reed, Smit, Christison and Basson 2001; Reed, Basson and Van As 2002a) and one international conference (Reed and Van As 1999).

Research on marine fish-infecting myxosporeans along the Cape south coast of South Africa was initiated in 1998, a year after the Okavango Fish Parasites Project. The preliminary results obtained from the marine surveys have been presented at several national (Reed, Van As and Basson 1998; Grobler, Christison, Jansen van Rensburg, Reed, Smit and Basson 2001) and two international conferences (Reed, Basson, Van As and Dyková 2002; Reed, Basson and Van As 2003b).

In order to provide a complete overview of the research conducted on southern African fish-infecting myxosporeans from 1997 to 2001, the results presented in this thesis will be divided into two major 'results' chapters (see Chapters 5 and 6). Since the two regions Okavango River and Delta, and Cape South Coast) differ considerably in most aspects (freshwater versus marine habitats), each of these chapters should be seen as an entity, largely unrelated to the other.

The study of the diversity of fish-infecting myxosporeans in the Okavango River and Delta, Botswana is based on material collected from 1997 to 2001. The data collected during 1998 and 1999 was presented in the author's M.Sc. dissertation (Reed 2000). Results presented in this Ph.D. thesis subsequently include material collected during 1997, 2000 and 2001. Material collected during 1997 did not form part of the author's M.Sc. since she had only started her research in 1998. Hence, material and data collected during 1997 was sampled by other researchers from the Aquatic Parasitology Research Group at the University of the Free State.

Results on myxosporeans infecting intertidal and surf zone fishes along the Cape south coast, South Africa, provides complete species descriptions, infection statistics and pathological effects of these myxosporean species. These results are presented for the first time in this thesis and form the first truly comprehensive study on fish-infecting myxosporeans along the Cape south coast of South Africa.

In brief, the main aims of this study are to:

- Review of all existing literature concerning freshwater and marine fish-infecting myxosporeans in Africa.
- Report on the biodiversity and prevalence of fish-infecting myxosporeans in the Okavango River and Delta, Botswana.
- Investigate the pathogenic potential of the myxosporeans infecting fishes in the Okavango River and Delta, Botswana.
- Determine the taxonomic status, species biodiversity and prevalence of myxosporeans infecting intertidal and surf zone fishes along the Cape south coast, South Africa.
- Investigate the pathogenic potential of myxosporeans infecting intertidal and surf zone fishes along the Cape south coast of South Africa.
- Discuss possible life cycles of these fish-infecting myxosporeans and determine the potential for future research on the life cycles of these myxosporeans.
- Provide a complete key to the freshwater, marine and estuarine fish-infecting myxosporeans in Africa.

On completion of this short introduction (Chapter 1), this thesis will provide an in-depth review of the Myxozoa Grassé, 1970 (Chapter 2), discussing the complexities of their origin, spores, classification and life cycle, phylogeny, development and hosts, as well as reporting on hyperparasitism and pathology associated with this group of parasites. A complete literature review on freshwater and marine African myxosporeans (Chapter 3) will be followed by a detailed description of the collection localities, materials and methods used during this study (Chapter 4). The results of the diversity of fish-infecting myxosporeans from the Okavango Delta, Botswana (Chapter 5) will precede the study of the myxosporeans infecting intertidal and surf zone fishes along the Cape south coast, South Africa (Chapter 6). Keys to the freshwater and marine fish-infecting myxosporeans in Africa (Chapter 7) will be followed by a brief discussion and concluding remarks (Chapter 8). The literature cited for the purpose of this study will be provided (Chapter 9) and followed by the abstracts and acknowledgements. Appendix I contains two papers published during the course of this study. Appendix II shows the required permits for collecting fishes in the Okavango Delta, Botswana and along the Cape south coast, South Africa. Appendix III contains two tables (7.1 and 7.2) illustrating the articles from which all the sketches in the respective keys were redrawn.

2. The Phylum Myxozoa Grassé, 1970

Members of the Myxozoa undeniably have one of the most intricate and complicated life histories of all the animals in the Kingdom Animalia. In order to fully understand these parasites, it is essential to have a thorough knowledge of the biology, taxonomy, phylogeny and life cycles of these unique animals. This chapter is dedicated to explaining the many incredible discoveries made by scientists whilst researching these parasites throughout the years.

Origins

It is believed that the first myxosporeans were coelozoic, inhabiting the gall bladders and later urinary bladders of marine teleost fishes during the Cretaceous Period and eventually evolving to infect other tissues (Shulman 1966). Shulman (1966) also suggested that the first myxosporeans were bipolarids with polar capsules situated at opposite sides of the spore ends, which eventually gave rise to platysporinids with polar capsules situated in the anterior of the spores (Kent *et al.* 2001).

Spores

The most obvious characteristic of members of the myxosporeans is the production of many tiny spores at certain stages of their life cycle in the fish host (Fig. 2.1a). Myxosporean spores are the infective stages of the parasites and range in length from 8µm to 100µm. The spores are multi-cellular and consist of several (4 to 16) cells, which are transformed during sporogenesis into the various components of the spore (Lom and Dyková 1995). There may be one to seven capsulogenic cells that will produce the polar capsules, two to seven valvogenic cells forming the shell valves and one to two cells developing into the infective sporoplasm. The shell valves join at a sutural plane that may be twisted or straight (Roberts and Janovy 2000) and enclose the polar capsules that are usually situated in the spore apex or at opposite ends of the spore. The sporoplasm is situated in the anterior end of the spores and may consist of a single binucleate sporoplasm or two uninucleate sporoplasms (Lom and Dyková 1995). Some species have large vacuoles that stain readily with iodine and are subsequently known as iodinophilous vacuoles (Roberts and Janovy 2000). The spore shell valves may be smooth or ridged and may even have various projections or be invested with a transient mucous envelope. These structures are presumed to increase the buoyancy of the spores and thus enhance distribution in the aquatic environment (Lom and Dyková 1995). The polar capsules

contain a coiled polar filament (Fig. 2.1a), which is a hollow tube spirally twisted along its length. The polar filament is capable of rapid extrusion and is probably used to attach the hatching spore to the definitive host's (e.g. oligochaete) body surface (Lom and Dyková 1995).

Myxosporeans are capable of infecting any organ of the host in which they are found and may be divided into two groups based on the site preference within the host. Coelozoic species live in body cavities such as gall- or urinary bladders and histozoic species are found within various tissues (Lom and Dyková 1992). Most histozoic species are found intercellularly, but may occasionally be found intracellularly. Mature spores of histozoic species are sometimes housed in large macroscopic 'cysts' or plasmodia.

Classification and life cycle

Since the discovery of myxosporeans during the late 1800's, the classification of these animals has been the cause of much confusion and frustration amongst scientists. The classification of this group from its higher taxonomic categories right down to species level has forever been problematic (Lom and Arthur 1989), the main reason being that the vegetative stages of these parasites provide no distinctive morphological features on which to base differences amongst species. Thus, the classification of myxosporeans has generally been based entirely on the morphological structure of the spores.

Since the spores are so tiny and largely exhibit protozoan characteristics and habits, the myxosporeans were originally classified together with other protists. The phylum Myxozoa was divided into two main classes, i.e. Myxosporea (Bütschli, 1882), infecting mostly freshwater and marine teleosts and Actinosporea (Štolc, 1899) (Fig. 2.1b.), infecting annelid worms. This classification seemed to make sense since the final development in both hosts was a spore containing the distinct polar capsules, with the smaller, simpler, bilateral myxosporeans parasitising vertebrate hosts and the larger, ornate actinosporeans found exclusively in annelid hosts (Kent *et al.* 2001).

Actinosporeans infecting aquatic oligochaetes were discovered at the turn of the 19th century and although numerous species have been described, the numbers do not nearly parallel that of the myxosporeans, mainly due to the relative economic importance of fish compared with aquatic oligochaetes (Bartholomew 1998). Only 45 species of

actinosporeans have been described compared to the more than 1300 myxosporean species (Lin, Hanson and Pote 1999).

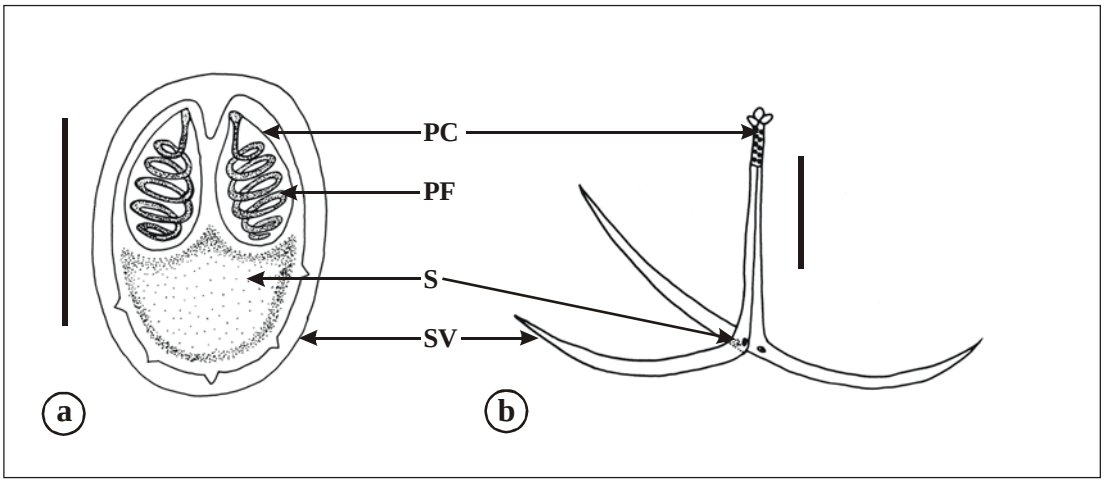


Figure 2.1. Diagrams of examples of myxosporean (a) and actinosporean (b) spores. Redrawn from Lom and Dyková (1992). PC- Polar capsules; PF- Polar filament; S- Sporoplasm; SV- Shell valves. Scale bars: 10μm.

A direct mode of transmission, via the spores, was previously assumed to be the life strategy of myxosporeans. This conventional strategy involved hatching of the spore in the digestive tract of the fish, extrusion of the polar filaments and release of the sporoplasm. The sporoplasm then underwent autogamy to produce the only uninucleate stage in the life cycle. This cell migrated to the final site of infection and eventually developed into the mature spores (Bartholomew 1998). This interpretation could, however, never be truly demonstrated under laboratory conditions and had always been rather controversial (Bartholomew 1998).

Together with their classification, the life cycle of myxozoans has also always been enigmatic to scientists. Ironically, whilst investigating the life cycle of a specific pathogenic myxosporean, a remarkable discovery was made regarding the classification of these animals. The entire classification of the myxosporeans was completely overthrown in 1984 when Wolf and Markiw discovered that myxosporeans and actinosporeans were, in fact, alternating life forms in a single life cycle. Wolf and Markiw (1984) were investigating the life cycle of *Myxobolus cerebralis* Höfer, 1903 when they discovered that this particular myxosporean had an actinosporean stage, parasitising an oligochaete, as an alternating life form. The life cycle of *M. cerebralis* was proposed by Wolf and Markiw (1984) as follows: the spores of *M. cerebralis* infect

tubificid oligochaetes and initiate the actinosporean stage. Young salmonid fish ingest the worms, or, a water borne actinosporean infects the fish via the gut or the branchial route. These events begin the myxosporean phase. After three to four months the myxosporean stage is complete with mature spores occurring in the cartilage of the fish. The myxosporean phase is not capable of infecting other fishes and likewise, the actinosporean stage is not capable of infecting other oligochaetes.

Although it is now generally accepted that myxosporeans undergo a two-host life cycle, there have been several reports of direct fish-to-fish transmission of these parasites. Diamant (1997) reported a direct fish-to-fish transmission for the marine myxosporean, *Enteromyxum leei* (Diamant, Lom and Dyková, 1994), a histozoic myxosporean infecting the intestine of gilthead bream *Sparus aurata*. His reports indicated that the myxosporean is transmitted between fish via the ingestion of infected fish tissue and through water borne contamination. Yasuda, Ooyama, Iwata, Tun, Yokoyama and Ogawa (2002) also reported direct fish-to-fish transmission of two *Myxidium* Bütschli, 1882 species infecting the tiger puffer, *Takifugu rubripes* in Japan. In a net-pen of cultured tiger puffer, the authors observed fish trailing their reversed and extruded hindgut, which was probably pecked by other fish. This observation led to the suspicion that direct fish-to-fish transmission of these gut parasites was taking place. Experimental transmission of this parasite confirmed their hypothesis. Although alternate invertebrate hosts and actinosporean stages may be involved in the natural life cycles of both these myxosporeans, it was evident that developmental stages excreted from infected fish were transmittable to other fish.

Alternating myxosporean-actinosporean life cycles are now widely accepted and can almost certainly be regarded as being confirmed (Table 2.1) (Lom, McGeorge, Feist, Morris and Adams 1997). Future research will, however, have to determine whether a life cycle including myxosporean-actinosporean transformation takes place in all myxozoan genera, and to confirm whether it is applicable to marine as well as freshwater myxozoans.

Table 2.1. Summary of known myxozoan life cycles from Kent, Andree, Bartholomew, El-Matbouli, Desser, Devlin, Feist, Hedrick, Hoffmann, Khattra, Hallett, Lester, Longshaw, Palenzuela, Siddall and Xiao (2001) [Key: * Bryozoan host].

Myxosporean	Fish host	Actinosporean	Invertebrate host	References
Ceratomyxa shasta	*Oncorhynchus mykiss*	Tetractinomyxon	*Manayunkia speciosa*	Bartholomew, Whipple, Stevens and Fryer (1997)
Henneguya exilis	*Ictalurus punctatus*	*Aurantiactinomyxon janiszewskai*	*Dero digitata*	Lin, Hanson and Pote (1999)
Henneguya ictaluri	*Ictalurus punctatus*	Aurantiactinomyxon	*Dero digitata*	Burtle, Harrison and Styer (1991); Styer, Harrison and Burtle (1991); Pote, Hanson and Shivaji (2000)
Hoferellus carassii (Germany)	*Carassius auratus*	Aurantiactinomyxon	Mixed species	El-Matbouli, Fischer-Scherl and Hoffmann (1992)
Hoferellus carassii (Japan)	*Carassius auratus*	Neoactinomyxon	*Branchiura sowerbyi*	Yokoyama, Ogawa and Wakabayashi (1993)
Hoferellus cyprini	*Cyprinus carpio*	Aurantiactinomyxon	*Nais* sp.	Grossheider and Körting (1992)
Myxobolus arcticus (Canada)	*Oncorhynchus nerka*	Triactinomyxon	*Stylodrilus heringianus*	Kent, Whitaker and Margolis (1993)
Myxobolus arcticus (Japan)	*Oncorhynchus masu*	Triactinomyxon	*Lumbriculus variegatus*	Urawa (1994)
Myxobolus bramae	*Abramis brama*	Triactinomyxon	*Tubifex tubifex*	Eszterbauer, Székely, Molnár and Baska (2000)
Myxobolus carassii	*Leuciscus idus*	Triactinomyxon	*Tubifex tubifex*	El-Matbouli and Hoffmann (1993)
Myxobolus cerebralis	*Oncorhynchus mykiss*	Triactinomyxon	*Tubifex tubifex*	Wolf and Markiw (1984)
Myxobolus cotti	*Cottus gobio*	Triactinomyxon	Mixed oligochaetes	El-Matbouli and Hoffmann (1989)
Myxobolus cultus	*Carassius auratus*	Raabeia	*Branchiura sowerbyi*	Yokoyama, Ogawa and Wakabayashi (1995)
Myxobolus dispar	*Cyprinus carpio*	Raabeia	*Tubifex tubifex*	Molnár, El-Mansy, Székely and Baska (1999a)
Myxobolus drjagini	*Hypophthalmichthys molitrix*	Triactinomyxon	*Tubifex tubifex*	El-Mansy and Molnár (1997a)
Myxobolus hungaricus	*Abramis abramis*	Triactinomyxon	*Tubifex tubifex, Lumbriculus hoffmeisteri*	El-Mansy and Molnár (1997b)
Myxobolus pavlovskii	*Hypophthalmichthys molitrix*	Hexactinomyxon	Mixed oligochaetes	Ruidisch, El-Matbouli and Hoffmann (1991)
Myxobolus portucalensis	*Anguilla anguilla*	Triactinomyxon	*Tubifex tubifex*	El-Mansy, Molnár and Székely (1998)
Myxobolus pseudodispar	*Rutilus rutilus*	Triactinomyxon	*Tubifex tubifex, Lumbriculus hoffmeisteri*	Székely, Molnár, Eszterbauer and Baska (1999)
Myxidium giardi	*Anguilla anguilla*	Aurantiactinomyxon	*Tubifex tubifex*	Benajiba and Marques (1993)
Sphaerospora renicola	*Cyprinus carpio*	Undetermined neoactinomyxum	Unknown, *Branchiura sowerbyi*	Grossheider and Körting (1993); Molnár, El-Mansy, Székely and Baska (1999b)
Sphaerospora truttae	*Salmo truta*	Echinactinomyxon	*Lumbriculus variegatus*	Özer and Wootten (2000)
Thelohanellus hovorkai	*Cyprinus carpio*	Aurantiactinomyxon	*Branchiura sowerbyi*	Yokoyama (1997); Székely, El-Mansy, Molnar and Baska (1998); Anderson, Canning, Schäfer, Yokoyama and Okamura (2000)
Thelohanellus nikolskii	*Cyprinus carpio*	Aurantiactinomyxon	*Branchiura sowerbyi*	Székely, El-Mansy, Molnár and Baska (1998)
Zschokkella nova	*Carassius carassius*	Siedleckiella	*Tubifex tubifex*	Uspenskaya (1995)
Zschokkella sp.	*Carassius auratus*	Echinactinomyxon	*Branchiura sowerbyi*	Yokoyama, Ogawa and Wakabayashi (1993)
Proliferative kidney disease	*Oncorhynchus mykiss*	*Tetracapsula bryosalmonae*	**Plumatella* sp., *Fredericella sultana*	Longshaw, Feist, Canning and Okamura (1999)

Phylogeny

As mentioned previously, due to their small size, shape and protistan behavior, myxosporeans have traditionally been grouped with the protists, although they are known to be multicellular. Interestingly, about a century ago Stolc (1899) claimed that myxozoans are not protists at all, but have multicellular spores and should be included in the Metazoa. This hypothesis seemed to go largely unnoticed at the time, but was, much later, reaffirmed in 1938 by Weill. Weill (1938) ventured a step further and suggested that they might belong to the cnidarians because of the similarity between the polar capsules and nematocysts (Kent *et al.* 2001). Furthermore, the coelozoic myxozoans showed such remarkable similarities to some parasitic cnidarians that Weill (1938) suggested a specific affinity with the narcomedusan, *Polypodium hydriforme*. Many morphological studies such as that of Grassé and Lavette (1978) have agreed that there are clear-cut metazoan features present in the myxozoans, such as separation of generative and somatic cells, the differentiation of the somatic cells and the occurrence of desmosome-like structures in the valve cells.

Although controversy regarding myxozoan phylogeny began many years ago, it is fortunate that molecular systematics has become a mainstream approach in taxonomic and phylogenetic studies (Kent *et al.* 2001), enabling scientists to make more concise conclusions about what were previously mere hypotheses. Unfortunately the use of these modern techniques does not exclude controversial results.

Initially, as sequences of the nuclear small 18S rDNA became readily available, Smothers, Von Dohlen, Smith and Spall (1994) showed that myxozoans grouped together with the Metazoa as a sister group to nematodes and not with the three cnidarian sequences as previously assumed (Kent *et al.* 2001).

Shortly after the results were published by Smothers *et al.* (1994), a rather provocative study was conducted by Siddall, Martin, Bridge, Desser and Cone (1995) who placed the Myxozoa within the Cnidaria, supported strongly by morphological similarities. Siddall *et al.* (1995) showed the myxozoans as a sister group to the narcomedusan fish parasite, *Polypodium hydriforme* (Kent *et al.* 2001). As mentioned previously, this hypothesis was also formulated much earlier by Weill (1938) who proposed a possible phylogenetic link with representatives of the Cnidaria based upon similarities of the polar filaments with

cnidarian nematocysts cells. Furthermore, myxozoan pansporoblast formation and larval endoparasitic forms of cnidarians such as *Polypodium hydriforme* display striking parallels (Schlegel, Lom, Stechmann, Bernhard, Leipe, Dyková and Sogin 1996). Electron microscopy has also revealed structural and morphological similarities between nematocysts and polar filaments (Lom and De Puytorac 1965) that are difficult to explain merely by convergent evolution. Siddall *et al.* (1995) proposed that the molecular data coupled with morphological evidence argue that the phylum Myxozoa be abandoned and be included in the clade of parasitic Cnidarians (Bartholomew 1998).

A third study conducted by Schlegel *et al.* (1996) obtained similar results to that of Smothers *et al.* (1994), placing the myxozoans as a sister group to the nematodes (Fig. 2.2). Neither Smothers *et al.* (1994) nor Schlegel *et al.* (1996), could decide whether the myxozoans are a sister group of all bilaterians, or if they are related to a particular bilaterian lineage, such as the nematodes. Both studies (Smothers *et al.* 1994; Schelgel *et al.* 1996) clearly showed that myxozoans are not specifically related to the Cnidaria as suggested by some other authors (Weill 1938; Siddall *et al.* 1995) as well as some ultrastructural studies (Lom 1990).

Other 18 rDNA studies (Cavalier-Smith, Allsopp, Chao, Boury-Esnault and Vacelet, 1996) including one Hox genes study (Anderson, Canning and Okamura 1998) have suggested that myxozoans are more closely allied with triploblast metazoans. Hox genes play important roles in development of body plans and have been described from a variety of metazoans. Anderson *et al.* (1998) reported on the presence of Hox class genes in myxozoans that are typical of triploblasts. According to Anderson *et al.* (1998), this finding further confirmed the phylogenetic affinity of myxozoans with the Bilateria and also revealed an extreme example of parasitic degeneracy (Kim, Kim and Cunningham 1999). Eventually, Okamura, Curry, Wood and Canning (2002) identified a strange organism from bryozoans, *Buddenbrockia plumatellae* Schröder, 1910, as a myxozoan, probably an ancestor of myxosporea, and verified the bilaterian origin of the Myxozoa.

Much research still has to be conducted before the true origins of these incredible animals are understood. Currently, the myxozoans have been moved to the animal kingdom in Cavalier-Smith's (1998) "Revised six-kingdom of life".

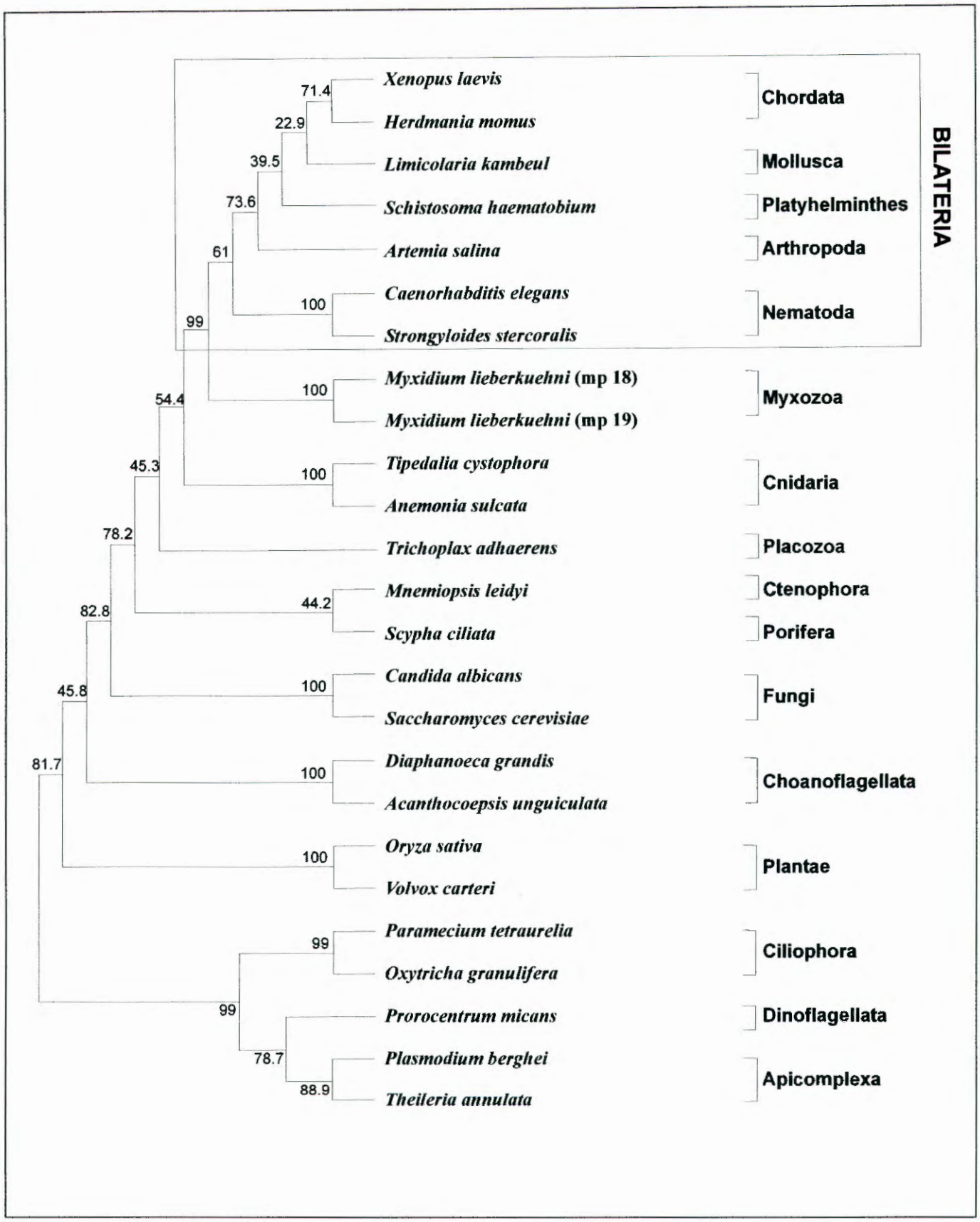


Figure 2.2. Consensus tree of maximum parsimony replicates showing myxozoans grouped together with the Metazoa as a sister group to the nematodes. Numbers indicate bootstrap values. Redrawn from Schlegel, Lom, Stechmann, Bernhard, Leipe, Dyková and Sogin (1996).

In this revision Cavalier-Smith (1998) removed myxozoans from the Protozoa and placed them within the Animalia (Fig. 2.3). Since it has not yet been established whether myxozoans are derived from Cnidaria or from other bilaterial animals, Cavalier-Smith (1998) has appropriately excluded them from both subkingdoms Radiata and Bilateria and ranked them as a third subkingdom of the Animalia. Cavalier-Smith (1998) further concluded that the great differences in phenotype between Myxozoa and both Radiata and Bilateria also justify this rank. Many years ago Lankester (1877) noted 'that it was very hard to disprove the idea that many of the Protozoa are not descended from Enterozoa by degeneration'. It appears that only the Myxozoa have actually done so (Cavalier-Smith 1998). Myxozoans now represent one of the 36 phyla in the animal kingdom and may be classified as follows (combination of Lom and Dyková 1992; Cavalier-Smith 1998 and Kent *et al.* 2001):

Empire: Eukaryota
Kingdom: Animalia
Subkingdom: Myxozoa Grassé, 1970 stat. nov. Cavalier-Smith, 1996 (unicellular non ciliate parasites with multicellular spores)
Phylum: Myxosporidia Bütschli, 1881 stat. nov. Grassé, 1970
Class: Malacosporea Canning, Curry, Feist, Longshaw and Okamura, 2000 (freshwater, with soft valves, parasites of bryozoans; one order, family and genus).
Order I: **Malacovalvulida Canning, Curry, Feist, Longshaw and Okamura, 2000**
Tetracapsuloides Canning, Okamura and Curry, 1996 (with four polar capsules)
Buddenbrockia plumatellae Schröder, 1910
Class: Myxosporea Bütschli, 1881
Order I: **Bivalvulida Shulman, 1959** (marine and freshwater, with two valves to spore)
Suborder I: **Variisporina Lom and Noble, 1984** (Marine and freshwater, mostly coelozoic). Includes *Ceratomyxa* Thélohan, 1892; *Chloromyxum* Mingazzini, 1890; *Hoferellus* Berg, 1898; *Myxidium* Bütschli, 1882; *Enteromyxum* Palenzuela, Redondo and Alvarez-Pellitero, 2002; *Myxobilatus Davis*, 1994; *Ortholinea* Lom and Noble, 1984; *Parvicapsula* Shulman, 19534; *Polysporoplasma* Sitja-Bobadilla and Alvarez-Pellitero, 1995; Sinuolinea Davis, 1917; *Sphaerospora* Thélohan, 1892; *Zshokkella* Auerbach, 1910
SuborderII: **Platysporina Kudo, 1919** (Marine and freshwater, mostly histozoic). Includes *Myxobolus* Bütschli, 1882; *Henneguya* Thélohan, 1892; and *Thelohanellus* Kudo, 1933.
SuborderIII: **Sphaeromyxina Lom and Noble, 1984** (Marine, with ribbon-like polar filaments in polar capsules at opposing end of spore). Includes *Sphaeromyxa* Thélohan, 1892.
Order II: **Multivalvulida Shulman, 1959** (marine, with more than two spore valves). Includes *Hexacapsula* Arai and Matsumoto, 1953; *Kudoa* Meglitsch, 1947; *Trilospora* Noble, 1939 and *Unicapsula* Davis, 1924.

Relationships amongst the myxozoans

Small subunit ribosomal DNA sequences from approximately 59 myxozoan species are available in GenBank. Kent *et al.* (2001) produced a single most parsimonious tree from the phylogenetic analysis of all the CLUSTAL aligned 18S rDNA data available for the myxozoans (Fig. 2.4). The results of this study indicate that only the genus *Kudoa* Meglitsch, 1947 is clearly monophyletic.

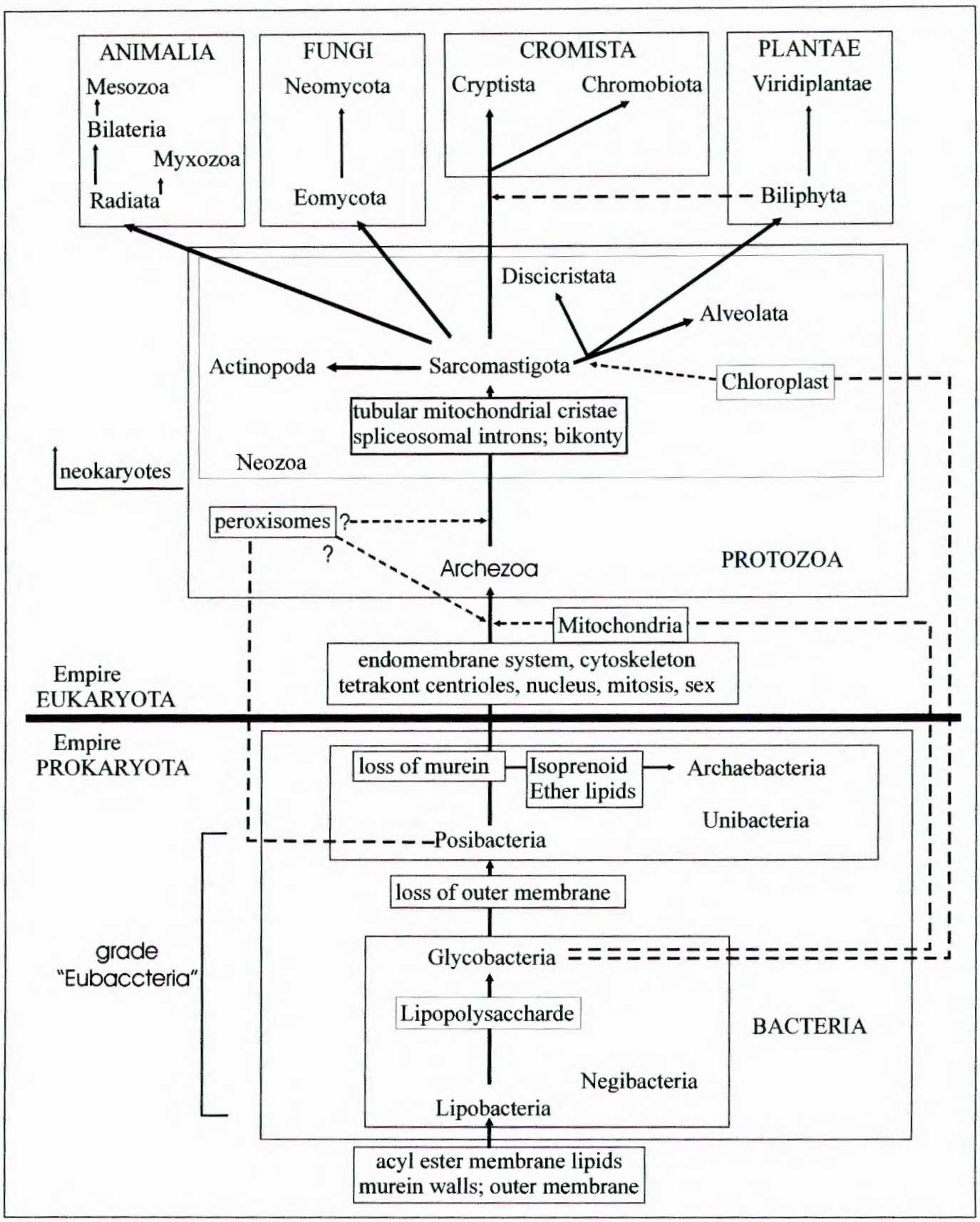


Figure 2.3. Postulated phylogenetic relationships between the six kingdoms (uppercase) and their subkingdoms. Infrakingdoms are also shown for the two basal paraphyletic kingdoms. The four major symbiogenetic events in the history of life are shown in dashed arrows. Myxozoans are placed together with the Animalia. Redrawn from Cavalier-Smith (1998).

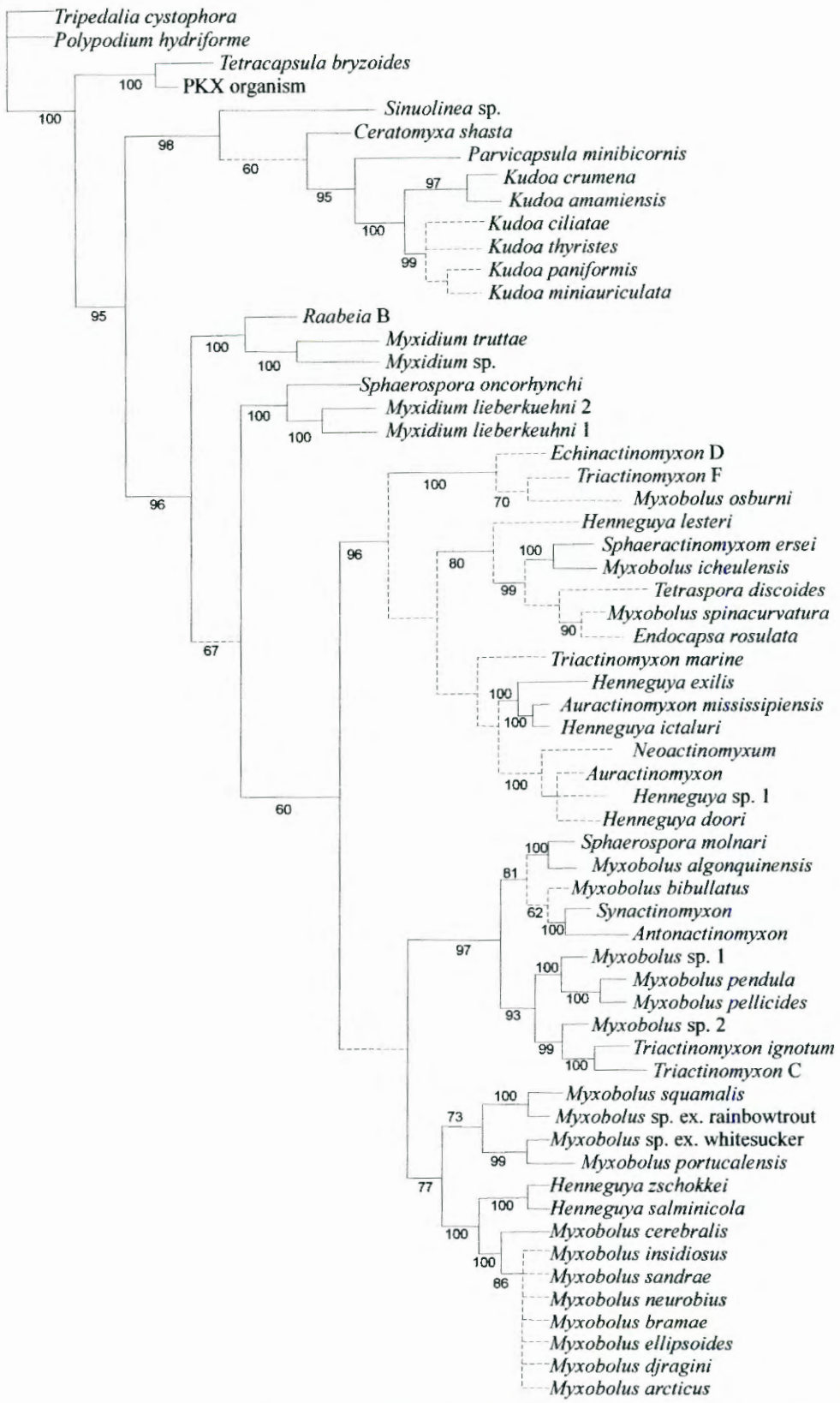


Figure 2.4. Single most parsimonious tree from phylogenetic analysis of all CLUSTAL aligned 18S rDNA data for myxozoans (length = 10.865, retention index = 64.5%). Solid lines indicate groupings that were also found in the most parsimonious tree found when hypervariable sites were excluded and that are also consistent with the trees found from distance-based neighbour joining methods. Branches with dotted lines indicate lack of stability in alignment, lack of stability where variable characters were included, or disagreement between parsimony and distance approaches. Numbers at nodes are parsimony jackknife support indices after 1 000 jackknife sampling replicates. Redrawn from Kent, Andree, Bartholomew, El-Matbouli, Desser, Devlin, Feist, Hedrick, Hoffmann, Khattra, Hallett, Lester, Longshaw, Palenzuela, Siddall and Xiao (2001).

Myxosporean development in the fish host (Kent** et al. **2001)

Myxosporean development in a fish host has only been fully described for *M. cerebralis* (Fig. 2. 5). Salmonid fish are exposed to waterborne *M. cerebralis* spores through contact with waterborne triactinomyxon spores or though ingestion of infected *Tubifex tubifex* (Wolf and Markiw 1984; El-Matbouli and Hoffmann 1989). As early as one-minute post-exposure, the waterborne triactinomyxon spores accumulate at the openings of the mucous cells over the entire epidermis, the buccal cavity, and the respiratory epithelial cells of the gills. The triactinomyxon spores extrude their polar filaments and inject them directly into the mucous cell openings or into surrounding epidermis cells to anchor the spores and allow the sporoplasm to penetrate into the epidermis.

Presporogonic/extrasporogonic phase (Fig. 2.5: 3-13): during the first 60 minutes following penetration, the sporoplasm migrates intercellularly in the epidermis and gill epithelium. The cell, enveloping the sporoplasm internal cells, disintegrates and each cell penetrates a host epidermal or gill epithelial cell. These cells then undergo endogenous cleavage, producing an inner secondary cell within an enveloping primary cell. Secondary cells proliferate through rapid, synchronous mitosis and the host cell nucleus is compressed between the large parasitic aggregate and the host cell plasmalemma (Daniels, Herman and Burke 1976; El-Matbouli, Hoffmann and Mandok 1995). The secondary cells then undergo endogenous divisions to produce new cell doublets with an enveloping cell and inner cell. These cells rupture the membrane of the original primary cell and enter the host cell cytoplasm. At this point, some cell doublets seem to be destroyed within the cytoplasm of the host cell. When cell doublets are free within the host cell cytoplasm, they pierce the host cell plasmalemma and enter the extracellullar space. The now extracellularly situated cell doublets either penetrate neighboring epithelial cells or migrate deeper into the dermis and subcutis layers and penetrate new host cells, where the cycle starts again.

Shortly after exposure, aggregates of cell doublets can be found intercellulary in the subcutis. These stages continue the proliferative cycle of secondary cell mitosis to form cell doublets. Around four days post-exposure, cells of *M. cerebralis* migrate intercellularly in nervous tissue, where proliferation of cell doublets continues as the parasite migrates through the central nervous system. From days 6-14 most parasitic stages can be found in the spinal cord and from days 16-24 most are found in the brain.

Sporogonic phase (Fig. 2.5: 13-16): at the site of sporulation a plasmodium develops. The primary cell grows and the nucleus divides to produce numerous internal vegetative nuclei. The enveloped cells divide to produce many cells termed generative cells. For each spore, valvogenic cells (which become the spore valves) enclose capsulogenic cells (which become the polar capsules) and a binucleate sporoplasm or two uni-nucleate sporoplasms. Myxospores are eventually released from the fish host and are infective to the annelids.

Actinosporean development within annelids

Schizogony (Fig. 2.5: 17-20): myxosporean spores released from the fish host are ingested by the annelid worms (eg. *Tubifex tubifex*). In the gut lumen of the worm, spores extrude the polar filaments by which they attach to the gut epithelium. The valves of the spore then open along the suture line, and the binucleate sporoplasm penetrates between the gut epithelial cells. Both nuclei of the sporoplasm undergo multiple division to produce multinucleate cells. These stages divide by plasmotomy to produce numerous uninucleate cells, which wander intercellularly through the gut epithelial cells of the worm. Some of these stages undergo further nuclear and cellular divisions, forming additional multinucleate and uninucleate cells. Others fuse to form binucleate stages.

Gametogeny (Fig. 2.5: 20-25): The nuclei in the binucleate stage divide to form four nuclei, which divide to form early pansporocysts with four cells, two enveloping somatic cells and two generative cells termed α and β. Three mitotic divisions of the two generative cells yield 19 diplogametocytes, which undergo one mitotic division to produce 16 haploid gametocytes and 19 polar bodies. Each gametocyte from the α line unites with one from the β line to produce eight zygotes. Based on the life cycle of *M. cerebralis*, this is the only phase in the life cycle in which sexual stages occur. Meanwhile the somatic cells divide twice to produce eight enveloping cells (El-Matbouli and Hoffmann 1998).

Sporogony (Fig. 2.5: 27-29): at the end of gametogamy, the eight zygotes in each pansporocyst are surrounded by eight somatic cells. Each zygote then undergoes two mitotic divisions to produce a four cell stage. Three cells are located peripherally and divide to form three capsulogenic and three valvogenic cells, while the fourth centrally located cell undergoes numerous mitotic divisions to form the sporoplasm of the

actinosporean spore with numerous internal cells. Subsequently the capsulogenic cells and the sporoplasm are enclosed within a shell composed of three valves. Behind the sporoplasm, the valvogenic cells extend infolded membranes that ultimately turn into the shell valves of the styles and the three projections of the triactinomyxon spore. This final stage with pansporocysts containing eight (or four with *Tetraspora*) folded actinosporeans begins to appear 90 days post exposure (El-Matbouli and Hoffmann 1998). Actinospores released from worms may remain viable for up to two weeks (Xiao and Desser 2000).

Hosts

Myxozoans were initially thought to be primarily parasites of fish, but as more research is conducted on this group it is becoming evident that they are more widespread than was previously thought. Although the majority of myxozoan species have been described from teleost fish hosts, they have been reported from trematodes, annelids, insects, bryozoans, octopus, elasmobranchs, amphibians, the brain of a mole and even in human faeces.

Trematodes, annelids and insects. Whilst examining a digenean worm collected from an estuarine fish in the Escatawpa River in Mississippi fish, Overstreet (1976) discovered *Fabespora vermicola* Overstreet, 1976, infecting the tegument and other tissues of the digenean. The occurrence of this infection was the first record of a myxozoan infecting a digenean. It was, however, not the first record of a myxosporean from an invertebrate. Kudo (1920) described a *Myxobolus* Bütschli, 1882 sp. from an annelid and *Chloromyxum diploxys* (Gurley 1893) Thélohan, 1895 from an insect.

Bryozoa. These lace animals are known myxozoan hosts and contain free floating sacs with developing and mature spores. Korotneff (1892) was the first to record the presence of myxozoans in bryozoans when he described *Myxidium bryozoides* Korotneff, 1892 in *Plumatella fungosa* (Canning, Curry, Feist, Longshaw and Okamura 2000).

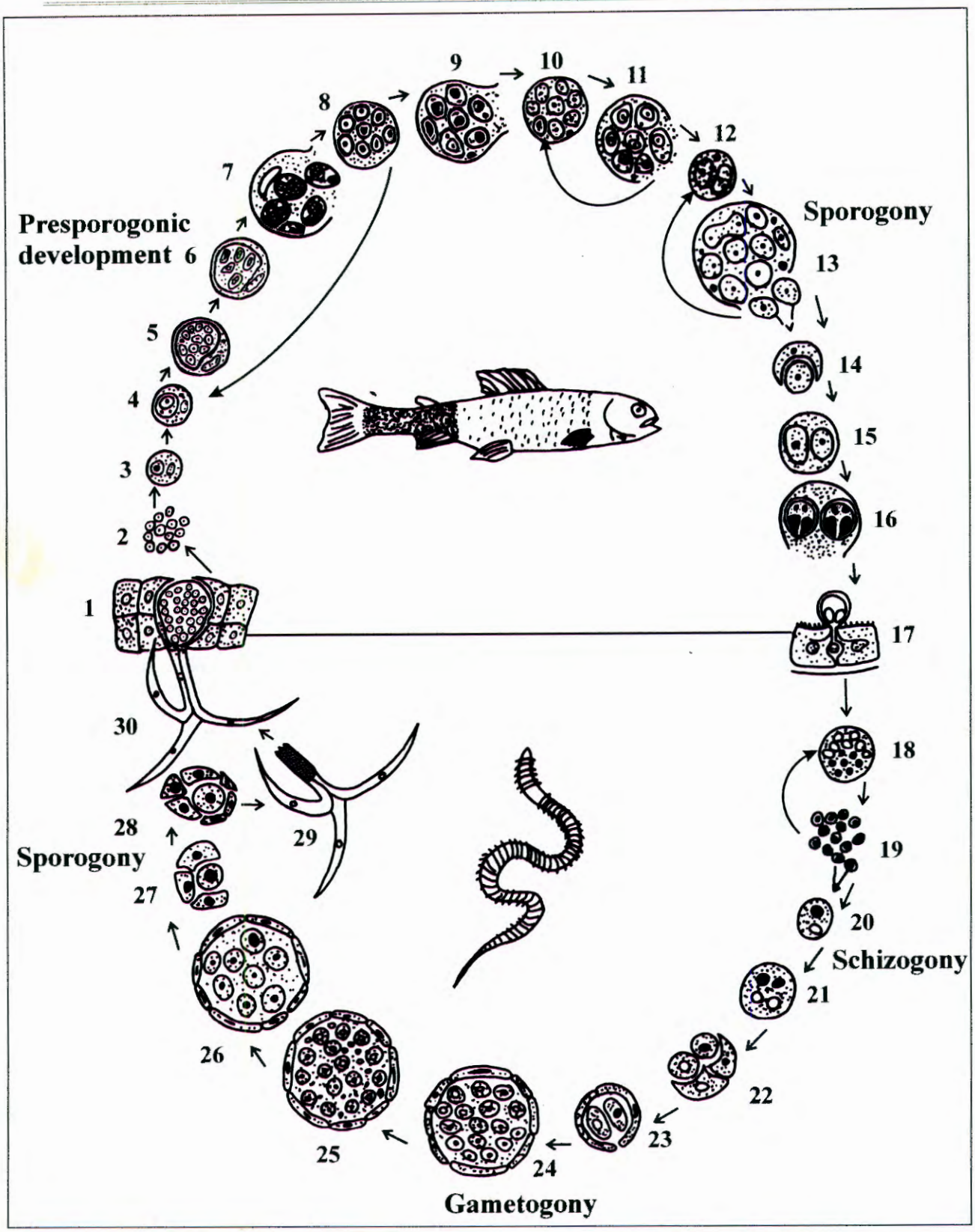


Figure 2.5. Diagram of the life cycle and development of the Myxozoa Grassé, 1970, based largely on the life cycle of *Myxobolus cerebralis* Höfer, 1903. **1-16**. Myxosporean development in the fish host. **17-30**. Actinosporean development in the annelid host. **1.** Actinospore attaches to the surface of the fish and releases sporoplasm into the fish. **2.** Sporoplasm internal cells divide by endogeny. **3-13.** Presporogonic or extrasporogonic vegetative replication. **14-16.** Sporulation with formation of multicellular spores within plasmodia. **17.** Fully-developed myxospores released from fish host and ingested by annelids. **18-20. Schizogony** in gut epithelium of the worm. The resulting binucleate cells have an alpa and beta nucleus, which develop into complementary gametes by the end of gamogony. **21-26. Gamogony**. Internal cells in pansporocysts undergo three mitotic and one meiotic divisions. **24-25.** Resulting gametes fuse to form a pansporocyst with eight zygotes. **27-29. Sporogony**. Multicellular spores are formed with three valves, three polar capsules and a sporoplasm. Inflated spores (**29**) are released with the worms faeces, float in the water, and contact the fish host to complete the life cycle. Redrawn from Kent, Andree, Bartholomew, El-Matbouli, Desser, Devlin, Feist, Hedrick, Hoffmann, Khattra, Hallett, Lester, Longshaw, Palenzuela, Siddall and Xiao (2001).

Two new species, *Tetracapsula bryozoides* Canning, Okamura and Curry, 1996 and *T. bryosalmonae* Canning, Curry, Feist, Longshaw and Okamura, 1999 have recently been described (Canning, Curry, Feist, Longshaw and Okamura 1999). The latter species was previously known as the organism causing Proliferative Kidney Disease (PKD) in salmonid fish (Canning *et al.* 2000). An entire new class and order were created to accommodate the myxozoan parasites of bryozoans (Canning *et al.* 2000).

Octopus. Recently, Yokoyama and Masuda (2001) discovered a myxosporean belonging to the genus *Kudoa* Meglitsch, 1947 infecting the North-Pacific giant octopus *Paroctopus dofleini*. The infected octopus exhibited muscle degeneration, or "post-mortem myoliquefication" in the arms. Infections such as this could have serious effects on the octopus aquaculture industry.

Elasmobranch fishes. Even mighty cartilaginous sharks are not free of myxosporean infections. Stoffregen and Anderson (1990) reported that numerous skeletal muscles of a black-tip reef shark, *Caracharhinus melanopterus*, that died at an urban zoological park in New York, USA, were infected with a myxozoan parasite from the genus *Unicapsula* Davis, 1924. Heupel and Bennett (1996) discovered an epaulette shark, *Hemiscyllium ocellatum*, infected by a myxosporean from the genus *Kudoa*, collected from Heron Island on the Great Barrier Reef.

Amphibia. Myxosporean infections in amphibians were initially recorded during the late 1800's (Ohlmacher 1893; Whitnery 1893; Gurley 1894; Thélohan 1895; Labbé 1899). Fletcher (1888) published the first report of a *Myxobolus* species infecting the golden swamp frog, *Hyla auria* in Sydney, Australia. Since then many papers have been published in this regard. As in the case of many animals, declining amphibian populations are a concern in many parts of the world. Pathological reports such as testicular myxosporidiasis (Browne, Scheltinga, Pomering and Mahony 2002) have been reported as posing a serious threat to natural amphibian populations.

Mole. Remarkably, Friedrich, Ingolic, Freitag, Kastberger, Hohmann, Skofitsch, Neumeister and Kepka (2000) described the first record of a putative myxozoan or paramyxean life cycle stage in the brain of the mole *Talpa europaea*. Due to the

vertebrate host and the parasitic cells showing the enveloped state this parasite was classified as belonging to the myxozoans.

Human. Three reports exist of myxosporean infections in human stool samples. McClelland, Murphy and Cone (1997) reported on two separate occasions that human stool samples were found to contain spores of *Henneguya salmonicola* Ward, 1919. A one-year-old boy taken to his physician because of acute non-bloody diarrhea showed the presence of, amongst others, *H. salmonicola*. These organisms were initially mistaken for human spermatozoa. The presence of spermatozoa in the stool samples was reported to the physician and a preliminary investigation into sexual abuse was begun. The child's illness was, however, resolved a week later and was thought to be of viral origin. The second patient was a 61-year-old male who presented occasional bouts of bloody diarrhea. Stool samples showed the presence of a variety of protozoans. A stool specimen subject to ova and parasite examination was found to contain spores of *H. salmonicola* in small numbers. The patient recovered without treatment and the cause of his illness was never determined.

Boreham, Hendrick, O'Donoghue and Stenzel (1998) reported on the presence of myxozoan spores in the fecal samples of three patients presenting abdominal pain and diarrhea. The spores were identical to those of a *Myxobolus* species previously described from the freshwater fish, *Plectroplites ambiguus*. All patients had recently eaten fish caught from local waters, and frozen fillets of these fish were infected with *M. plectroplites* plasmodia. The passage of spores unchanged through the alimentary tract suggests that they were merely incidental findings and unrelated to the clinical symptoms.

Thirdly, during a study of parasitic infections in human immunodeficiency virus (HIV)-positive patients, a parasite belonging to the myxozoans was identified in two patients (Moncada, López, Murcia, Nicholls, Léon, Guío and Corredor 2001). Only one of the patients was HIV positive. Spores relating to the genus *Myxobolus* were identified, but because the spores are highly resistant and probably not affected by the gastrointestinal fluids, it was difficult to establish whether the parasite developed in the human host, or whether it was acquired from a contaminated environment. The latter hypothesis was unlikely since the patient had been in prison for six months. On the other hand, because infection of fish in Columbia has been described only for a species of the genus

Henneguya Thélohan, 1892, even this hypothesis may be invalid. Besides the patient also had an infection of *Isospora belli*, a coccidian parasite which causes watery diarrhea and which was probably the cause of the illness. After treatment, however, the symptoms persisted and two months later the *Myxobolus* spores were still present in his fecal samples. The persistence of the spores indicates that this might not be an incidental finding, as in the previous two reports. The possible pathogenic role of these parasites, especially in immuno-suppressed patients must be elucidated in the future (Moncada *et al.* 2001).

Hyperparasitism

Pathological conditions affecting members of the Myxozoa have rarely been documented. Only three cases of micro-organisms that specifically infect myxosporeans have been recorded, all of them being microsporidians (Diamant and Paperna 1989) (Table 2.3).

Table 2.3. Microsporidian hyperparasites of myxozoans.

Myxosporean species	Fish host	Organ infected	Microsporidian hyperparasite	Locality	Reference
Leptotheca coris Stempell, 1990	*Coris julis*	Gall bladder	*Nosema marionis* Thélohan, 1892	Mediterranean	Stempell (1919)
Ortholinea polymorpha (Davis 1917)	*Opsanus tau*, *O. beta*	Urinary bladder	*Nosema notabilis* Kudo, 1939	Northwest Atlantic	Kudo (1944); Dyková and Lom (1999)
Ceratomyxa Thélohan, 1892 sp.	*Siganus argenteus*, *S. luridus*	Gall bladder	*Nosema ceratomyxae* Diamant and Paperna, 1985	Red Sea	Diamant and Paperna (1985)

Remarkably, these hyperparasites can exert pathogenic effects on the myxosporean hosts. Kudo (1944) reported that *Nosema notabilis* Kudo, 1939 was pathogenic to the myxosporean host. This was confirmed by Dyková and Lom (1999), who found that heavily infected plasmodia of *Ortholinea polymorpha* (Davis, 1917) revealed marked pathological signs. The most prominent of these were the reduction of surface projections and/or pinocytosis, inflated mitochondria with altered inner structures, affected vegetative nuclei, damage to generative cells and occurrence of various anomalous formations in the plasmodium cytoplasm. Diamant and Paperna (1989) recorded that *N. ceratomyxae* Diamant and Paperna, 1985 clearly affected the sporogenisis of the *Ceratomyxa* Thélohan, 1892 sp. host. According to Diamant and Paperna (1989) the *Ceratomyxa* sp. trophozoites harbouring *N. ceratomyxae* displayed various stages of degeneration. Thus, degenerative processes in the hyperparasitised *Ceratomyxa* sp. plasmodia and the

effective inhibition of the sporulation process would suggest that the development of the microsporidians interfere with the sporogenesis of the host (Diamant and Paperna 1989).

Pathogenicity

Myxosporeans and the fish hosts infected by them have a long evolutionary history and many of the host-parasite relationships have achieved a balance in which the parasite apparently causes little damage to the host (Bartholomew 1998). Like all parasitic organisms, however, myxosporeans do exert a certain pathogenic influence on the hosts. The degree of pathogenicity varies according to the parasites biology and ecology, state of development, host's nutrition, stress level as well as immunological system.

Although the majority of myxosporeans are not seriously pathogenic, a few have devastating influences on both freshwater and marine aquaculture and fisheries industries. Several notorious myxosporean species are well known in regions of the world where fishing industries form important components of the economy. Specific disease conditions are associated with certain genera. It has been determined that parasites belonging to the genera *Myxobolus*, *Henneguya*, *Thelohanellus* Kudo, 1933 and *Hoferellus* Berg, 1898 are usually considered amongst the most pathogenic (Gracia, Maíllo, Amigó and Salvadó 1997).

Since several myxosporean species have the potential to cause severe tissue destruction that may lead to the death of the hosts, these parasites pose a serious problem in fish husbandry (Schlegel *et al.* 1996). Probably the oldest known disease associated with myxozoans is salmonid "whirling disease" infecting trout in Europe and North America. Dr. Bruno Hofer of Munich University originally described whirling disease after investigations into serious losses of farm-reared rainbow trout in Germany in 1898 (Höfer 1903). Recently concerns about this disease in freshwater salmonids have once again appeared (Kent *et al.* 2001). The disease is caused by *Myxobolus cerebralis* infecting the spinal cartilage of juvenile salmonids resulting in the destruction of cartilage and associated tissues. Infected fish are recognised by external symptoms such as whirling in circles, a black tail, misshapen heads and spinal curvature (Hoffman 1970).

Another economically important disease caused by a malacosporean and also infecting salmonid culture in Europe and North America, is Proliferative Kidney Disease (PKD)

(Morris, Adams and Richards 2000). This disease causes hypertrophy of the trunk kidney in salmonids (Lom and Dyková 1992). It was recently discovered that the causative agent of PKD was a malacosporean. As mentioned, an entire new class and order of myxozoans was established to accommodate *Tetracapsula bryosalmonae*, which is responsible for the development of PKD.

The myxosporean *Ceratomyxa truttae* Legér, 1906 commonly infects the gall bladder of brown trout and other salmonids and results in a condition known as "jaundice of trout" and has caused severe epizootics in brood stocks, with heavy mortalities reported in aquaculture industries (Feist and Rintimäki 1994).

Enteromyxum leei is the most significant myxosporean infecting sea bream in the Mediterranean and has often been the cause of severe mortalities in cultured *Sparus aurata* in eastern Mediterranean waters (Diamant 1992). The parasite invades the intestinal tract of the fish resulting in severe chronic enteritis often causing emaciation and death, with up to 80% losses in some stocks (Kent *et al.* 2001).

Some species such as *Sphaerospora testicularis* Sitjà-Bobadilla and Alvarez-Pellitero, 1990 decrease the reproductive rate of sea bass by either destroying the germinative tissue or by feeding on the spermatozoa (Alvarez-Pellitero and Sitjà-Bobadilla 1993a). Infections in the reproductive organs of the fish may result in a decreased reproductive potential or even eventual parasitic castration.

Several marine myxosporeans are associated with enzymatic degradation of the hosts' musculature. When heavily infected fish are harvested and frozen, the flesh turns into a milky, gelatinous substance, rendering the fish unmarketable (Bartholomew 1998). A genus, which is notorious for causing post-mortem myoliquefaction, is the genus *Kudoa* that comprises more than 40 species affecting marine and estuarine fishes across the world. *Kudoa thyristes* (Gilchrist 1924) was originally described from the Cape Sea fish or "snoek" off the coast of South Africa by Gilchrist (1924). Fish infected with *K. thyristes* develope a condition identified locally as "pap-snoek", essentially referring to the milky or soft flesh exhibited by the infected fish. Today *K. thyristes* is known from somatic and cardiac musculature of wild and aquaculture-reared marine fishes worldwide, with severe infections resulting in the *soft flesh* condition (Moran and Kent 1999). The

marketability of the infected fish products decreases dramatically within days after they have been harvested. Losses result not only because of this occurrence, but also because of an adverse market perception toward the industry for supplying infected products (Moran and Kent 1999). *Kudoa thyristes* infections in pen reared Atlantic salmon are also recognised as a serious problem of aquaculture industries in Canada, the USA and Ireland (Moran and Kent 1999).

Octopus fisheries are economically important industries in Japan and are growing worldwide. As mentioned previously, a myxosporean infection resulting in the myoliquefaction of the flesh of harvested octopus was discovered by Yokoyama and Masuda (2001). Although the prevalence of myoliquefaction in the octopus industry is unknown, these infections hold potentially serious threats and should be recognised as an important emerging disease of octopus.

Emaciation disease has been a serious problem among cultured tiger puffer, *Takifugu rubribes* in Japan since 1996 (Tun, Ogawa and Wakabayashi 2002). Clinical signs of infections include sunken eyes, bony ridges on the head and a tapered body. Parasitological observations of the diseased fish revealed three myxosporeans attached to the surface of the intestine. These parasites were identified as belonging to the myxosporean genera *Myxidium* and *Leptotheca* Thélohan, 1895.

In many myxosporean infections it is difficult to detect a tissue response. Coelozoic species are generally innocuous and species developing in tissues (histozoic species) may be encapsulated in connective tissue. Little evidence of a humoral response has been demonstrated and it has been suggested that myxosporeans may mimic the host antigens, avoiding elicitation of an antibody response (McArthur and Sengupta 1982). Some species directly damage the hosts by causing pathological changes, some decrease fitness by reducing fecundity and others reduce the market value of the fish.

During the 1990's marine aquaculture expanded at a phenomenal rate, especially with net-pen culture of salmonids and seabream species (Kent *et al.* 2001). It is, however, difficult to assess the pathogenicity of myxosporeans and the economic losses they incur. This is particularly true in mariculture, partly due to the scarcity of parasitological studies on cultured marine fish. Nevertheless, with the development of marine aquaculture,

outbreaks of disease due to myxosporeans are being reported more frequently and it is possible that some species may, in future, become serious constraints for the mariculture industry (Alvarez-Pellitero and Sitjà-Bobadilla 1993a).

3. A Review on Fish-infecting African Myxosporeans

Myxosporean research in Africa dates back to the late 19th century (Gurley 1893). During the past 100 years the number of known myxosporean species recorded from freshwater, marine and estuarine fishes in Africa have grown tremendously. Most of the myxosporean research in Africa has been focused in just a few countries (Fig. 3.1) where the publications mostly dealt with species descriptions of myxosporeans infecting economically important fish hosts. Some pathological and faunistic studies were also conducted during this period.

Since myxosporean research in Africa has concentrated largely on the descriptions of new species, no research has been conducted on the life cycles and consequently on the intermediate actinosporean life cycle stages. This is possibly explained by the fact that only during the 1980s it was discovered that actinosporeans are alternating life forms of myxosporeans (Wolf and Markiw 1984). Investigations of parasites in animals that were previously considered to be insignificant invertebrates, was not a priority. This imbalance may change in the near future because of the recent advances in understanding myxosporean life cycles.

This chapter attempts to summarise the history of both freshwater and marine myxosporean research in Africa. Included are two tables (Tables 3.1 and 3.2) presenting all the known myxosporean species described or recorded from both freshwater and marine fishes on the African continent.

Freshwater myxosporean research in Africa

To date approximately a 100 myxosporean species have been described from freshwater fishes in Africa. The majority of research in Africa concentrated on species descriptions of myxosporeans infecting economically important freshwater fishes. This is most probably due to the fact that many of the African countries depend largely on fish as the main source of protein. In many African countries tilapia, in particular, represent the main food resource of a large proportion of the local populations. The world production of tilapia in fish farms was estimated at 800 000 tonnes in 1996 and its progression is one of the most important in aquaculture, simply because maintenance and reproduction of these fishes is relatively straight forward (Gbankoto *et al.* 2001a).

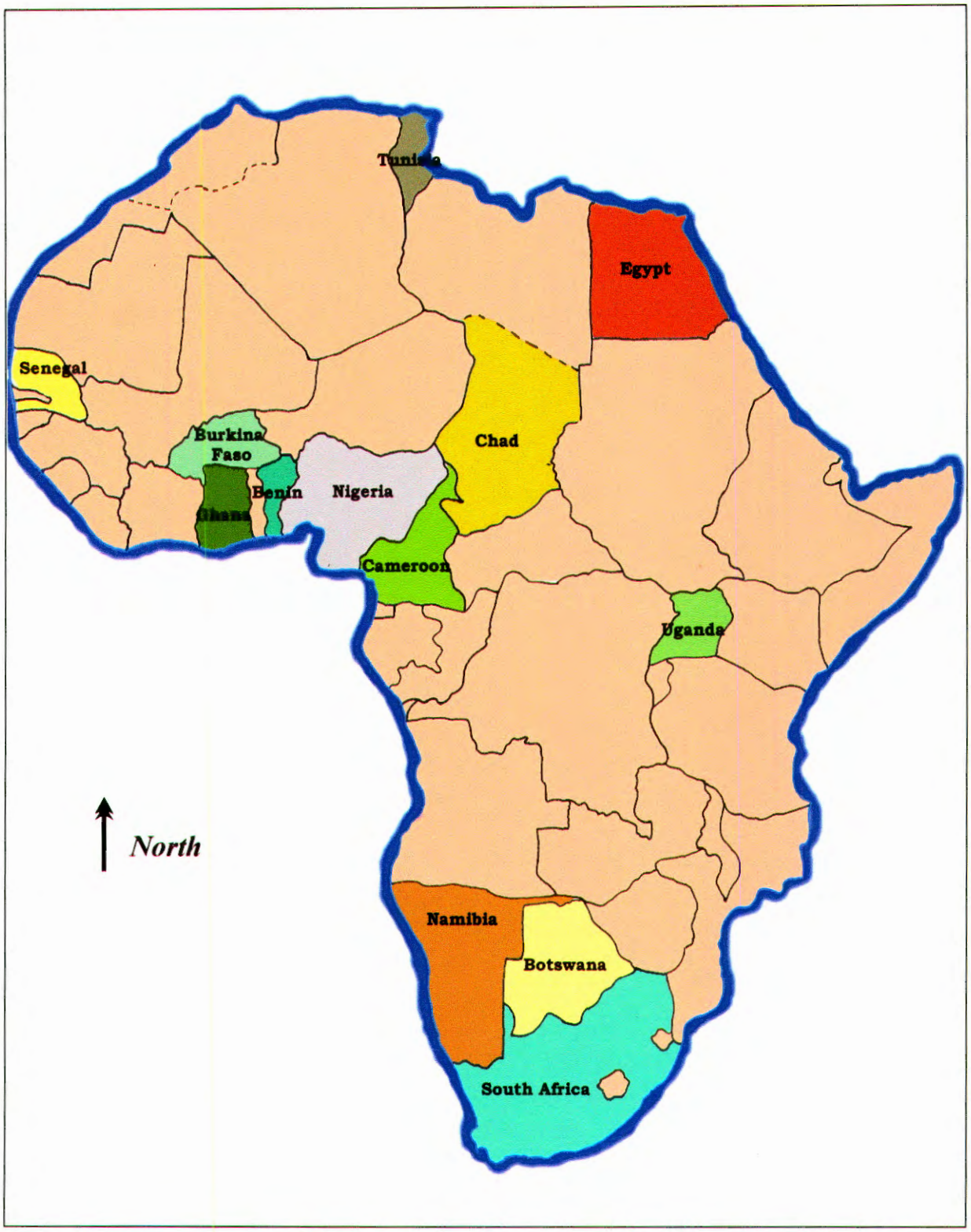


Figure 3.1. Map of Africa showing the isolated countries where myxosporean research has been conducted.

Despite the interest in cichlid rearing in Africa, little is known about their parasites in general (Fomena and Bouix 2000). In West Africa, fish farms are said to offer a solution to the problem of low fish catches in countries such as Benin and Côte d'Ivoire. In these regions tilapia species offer a real potential for fish farming and for the local economy (Gbankoto *et al.* 2001b). Consequently, studying the possible pathogens, in particular parasites such as myxosporeans, which hold the potential to seriously affect the aquaculture industry, has become essential in these countries. This might also explain the far greater volume of research conducted on freshwater myxosporean species in Africa. Another contributing factor is that a large percentage of the African countries are entirely landlocked, forcing them to be dependent on their freshwater ecosystems and fishes for survival.

Most early myxosporean research in Africa was confined to southern Africa, but as time passed, the picture changed entirely, with an abrupt end to myxosporean research occurring in southern Africa during the 1970's.

An early record from southern Africa is that of Fantham (1930) who described a *Myxobolus* species (Fig. 3.2) in barbel and carp collected from Brakpan and Florida in the Witwatersrand in South Africa. Thirty years later the next record of a freshwater myxosporean in Africa appeared. Baker (1963), working in Uganda on blood parasites of fishes, discovered a myxosporean infection in the internal organs of these fishes. A few years later Van Wyk (1968) recorded salmonid whirling disease in trout farms in the Cape Province in South Africa.

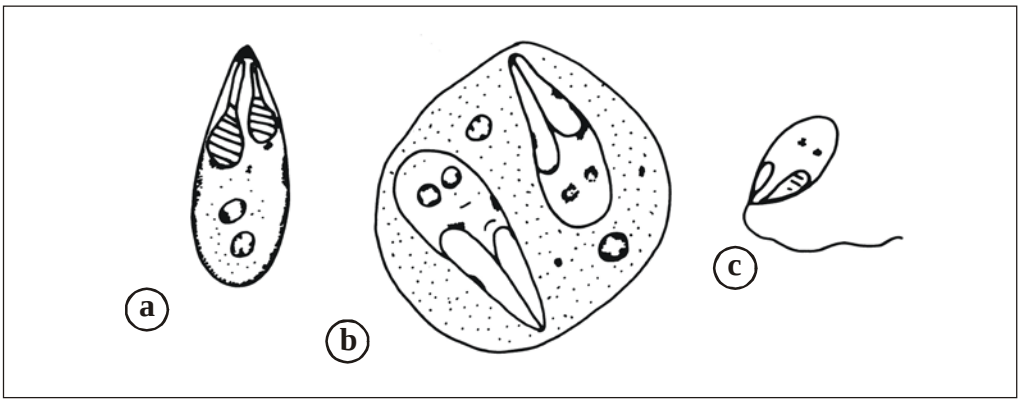


Figure 3.2. a-c. Diagrams of *Myxobolus ovoidalis* Fantham, 1930 spores recorded from barbel and carp collected from Brakpan and Florida on the Witwatersrand, South Africa. Magnification: a, b. × 800, c. × 350. Redrawn from Fantham (1930)

The onset of the 1970s gave rise to a sudden increase in myxosporean research in mostly Northern Hemisphere Africa, although one last record of a myxosporean from southern Africa appeared during that time. Peters (1971) recorded that what appeared to be eggs within the gill operculum of an African anabantid from the Okavango River, examined by Boulenger (1911), were actually myxosporean plasmodia.

Many papers describing new myxosporeans species from the continent appeared from the 1970s through to the 1990s. Eventually, Fomena and Bouix (1997) published a key to the myxosporeans infecting freshwater fishes in Africa. This valuable contribution provides a key, as well as sketches of all the known myxosporeans infecting African freshwater fishes. Several years later, Reed (2000) also conducted a review of all the known literature on myxosporeans infecting freshwater fishes in Africa published until mid 1999 as part of her M.Sc. dissertation. To avoid duplication of the literature review already conducted by Reed (2000), only a overview will be presented on freshwater myxosporean research in Africa conducted from the end of the previous decade, i.e. 1999 to 2002.

Literature review: 1999 to 2002

Numerous new species were described from the African continent during 1999. Ali (1999) described *Henneguya ghaffari* Ali, 1999 from the commercially important Nile perch, *Lates niloticus* in Egypt and also investigated the associated pathological changes in the infected organs of this fish. The infection resulted in hyperplasia of the interlamellar epithelial cells and atrophy of the respiratory lamellae at the cyst site. These fish were collected from Lake Wadi El-Raiyan, which at that time was a new man made lake with its main source of water being agricultural drainage. *Lates niloticus* was one of the well-established fish species in this lake that reached it through this new drainage system. Ali (1999) suggested that infections of *H. ghaffari* in the original habitat of *L. niloticus*, the River Nile, should be investigated, since the new habitat of these fish might favor infections by these parasites due to an "incomplete" ecosystem.

Three new myxosporean species were described from freshwater fishes in Chad by Kostoïngue, Fall, Faye and Toguebaye (1999). These authors described *Henneguya fusiformis* Kostoïngue, Fall, Faye and Toguebaye, 1999, *Thelohanellus citharini* Kostoïngue, Fall, Faye and Toguebaye, 1999 and *T. ndjamenaensis* Kostoïngue, Fall,

Faye and Toguebaye, 1999 from *Clarias anguillaris*, *Citharinus citharu*s and *Labeo parvus* respectively.

Negm-Eldin *et al.* (1999) described six new species from Egyptian freshwater fishes. The presence of myxosporean infections in these fishes was investigated due to the fact that myxosporean parasites of fish are recognised as being of extreme economic importance in Egypt. These authors felt that examination of the morphology and development of these parasites allowed for the specific identification of them. Furthermore, the determination of the life cycles would facilitate the treatment and prevention of infections in these valuable fish species.

The new millennium brought about a series of new myxosporean papers emerging from the continent. Fall, Fomena, Kostoïngue, Diebakate, Faye and Toguebaye (2000) examined cichlid fishes belonging to nine genera from Cameroon, Senegal and Chad. Their investigation revealed 19 myxosporean species, including descriptions of two new species namely *Myxobolus gandiolensis* Fall, Fomena, Kostoïngue, Diebakate, Faye and Toguebaye, 2000 from the kidneys of *Tilapia guineensis* and *Henneguya sarotherodoni* Fall, Fomena, Kostoïngue, Diebakate, Faye and Toguebaye, 2000 from the intestine of *Sarotherodon galileaus*. During a general study of myxosporean parasites of freshwater fishes in Cameroon, Fomena and Bouix (2000) described *Henneguya mbakaounensis* Fomena and Bouix, 2000 from *Lates niloticus* and *Myxobolus nouensis* Fomena and Bouix, 2000 from *Sarotherodon galilaeus* and *Tilapia mariae*.

In 2001, Kostoïngue, Diebakate, Faye and Toguebaye discovered four new myxosporean species of the genus *Henneguya* infecting the gill filaments of some freshwater fishes in the Chari and Logone Rivers in Chad. Gbankoto *et al.* (2001a) investigated the characteristics of the ovaries of tilapia species infected with *Myxobolus dahomeyensis* Siau, 1971 in Benin. Histological studies revealed that these infections resulted in the destruction of the oocytes and eventual castration of the host. Tilapia species are valued aquaculture species in Benin and infections such as these could affect the survival of host populations since they reduce the reproductive rate of fishes. During the same year, Gbankoto *et al.* (2001b) published another paper on the occurrence of myxosporean parasites in the gills of two tilapia species from Lake Nokoué in Benin and the effect on host size, sex and seasonal patterns of infection. This study was based on their previous

paper (Gbankoto *et al.* 2001a) that highlighted the impact those myxosporean infections had on the ovaries of these fish.

Most recently El-Mansy and Bashtar (2002) conducted histopathological and ultrastructural studies on *Henneguya suprabranchiae* Landsberg, 1987 infecting the suprabranchial organ of the sharptooth catfish, *Clarias gariepinus* in Egypt. They found that *H. suprabranchiae* was, in fact, a pathogenic species producing serious lesions in the cartilaginous tissues of the secondary respiratory organ of the catfishes, leading to respiratory disorders, loss of appetite and subsequently loss of weight.

Reed *et al.* (2002b) recorded seven myxosporean species, including descriptions of two new species, from the Okavango Delta, Botswana in southern Africa. This was the first paper on myxosporean infections of freshwater fishes to appear from southern Africa since the 1970s. Shortly after this, Reed *et al.* (2003a) recorded the myxosporean parasites of *C. gariepinus* in the Okavango Delta and included the description of two new species of each of *Henneguya* and *Myxobolus*.

There has been some concern regarding the validity of a few African *Henneguya* species. Ali (1999) mentioned that Fomena and Bouix (1997) included *Henneguya branchialis* Ashmawy, Abu-Elwafa, Imam and El-Otifi, 1989 as a species infecting *Clarias gariepinus*. According to Ali (1999), this species is a synonym of *H. suprabranchiae*, which was reported from the same host and infection sites in Israel. Ali (1999) further suggests that *Henneguya bopeleti* Fomena and Bouix, 1987 infecting the catfish *Chrysichthys nigrodigitatus*, is most likely the same species as *H. suprabranchiae*.

Table 3.1. Myxosporeans infecting freshwater fishes in Africa. Genera and species arranged alphabetically. Compiled from Fomena and Bouix (1997), Reed (2000) and additional literature. [Key: ≈ Possible synonyms of *H. suprabranchiae* Landsberg, 1987, # Synonym of *Clarias gariepinus* Burchell (1822)].

Myxosporean species	Fish species	Organ	Country	Reference
Genus *Chloromyxum* Mingazzini, 1890				
Chloromyxum birgii Fomena and Bouix, 1994	*Barbus aspilus, B. martorelli, Amphilius longirostris*	Gall bladder	Cameroon	Fomena and Bouix (1994)
Chloromyxum vanasi Ali, 1998	*Bagras bayad*	Gall bladder	Egypt	Ali (1998)
Genus *Henneguya* Thélohan, 1892				
Henneguya alestis Negm-Eldin, Govedich and Davies, 1999	*Alestes nurse*	Gills	Egypt	Negm-Eldin, Govedich and Davies (1999)
Henneguya auchenoglanii Kostoïngue, Diebakate, Faye and Toguebaye, 2001	*Auchenoglanis occidentalis*	Gills	Chad	Kostoïngue, Diebakate, Faye and Toguebaye (2001)
≈*Henneguya bopeleti* Fomena and Bouix, 1987	*Chrysichthys nigrodigitatus*	Gills	Nyong Basin (South Cameroon)	Fomena and Bouix (1987)
≈*Henneguya branchialis* Ashmawy, Abu-Elwafa, Imam and El-Otifi, 1989	*Clarias gariepinus*	Gills, intestine	Egypt	Ashmawy, Abu-Elwafa, Imam and El-Otifi (1989)
Henneguya camerounensis Fomena and Bouix, 1987	*Synodontis batesii, Eutropius multioeniatus*	Gills	Cameroon	Fomena and Bouix (1987)
Henneguya chrysichthyi Obiekezie and Enyenihi, 1988	*Chrysichthys nigrodigitatus*	Gills	Nigeria	Obiekezie and Enyenihi (1988)
Henneguya clariae Abolarin, 1971	*Clarias lazera* #	Gills	Nigeria	Abolarin (1971)
Henneguya ctenopomae Fomena and Bouix, 1996	*Ctenopoma nanum*	Gills	Cameroon	Fomena and Bouix (1996)
Henneguya cyprini Negm-Eldin, Govedich and Davies, 1999	*Cyprinus carpio*	Gills	Egypt	Negm-Eldin, Govedich and Davies (1999)
Henneguya fusiformis Kostoïngue, Fall, Faye and Toguebaye, 1999	*Clarias anguillaris*	Gills	Chad	Kostoïngue, Fall, Faye and Toguebaye (1999)
Henneguya ghaffari Ali, 1999	*Lates niloticus*	Intestine, pyloric caeca, gills	Egypt	Ali (1999)
Henneguya laterocapsulata Landsberg, 1987	*Clarias lazera #*	Body	Israel	Landsberg (1987)
Henneguya logonensis Kostoïngue, Diebakate, Faye and Toguebaye, 2001	*Citharinus citharus*	Gills	Chad	Kostoïngue, Diebakate, Faye and Toguebaye (2001)
Henneguya mailaoensis Kostoïngue, Diebakate, Faye and Toguebaye, 2001	*Mormyrus cashive*	Gills	Chad	Kostoïngue, Diebakate, Faye and Toguebaye (2001)
Henneguya malapteruri Fomena and Bouix, 1996	*Malapterurus electricus*	Skin, muscles	Cameroon	Fomena and Bouix (1996)
Henneguya massi Kostoïngue, Diebakate, Faye and Toguebaye, 2001	*Lates niloticus*	Gills	Chad	Kostoïngue, Diebakate, Faye and Toguebaye (2001)

Table 3.1 continued. Myxosporeans infecting freshwater fishes in Africa. Genera and species arranged alphabetically. Compiled from Fomena and Bouix (1997), Reed (2000) and additional literature. [Key: ≈ Possible synonyms of *H. suprabranchiae* Landsberg, 1987, # Synonym of *Clarias gariepinus* Burchell (1822)].

Myxosporean species	Fish species	Organ	Country	Reference
Henneguya mbakaouensis Fomena and Bouix, 2000	*Lates niloticus*	Gills	Cameroon	Fomena and Bouix (2000)
Henneguya mormyri Kostoïngue, Diebakate, Faye and Toguebaye, 2001	*Mormyrus cashive*	Gills	Chad	Kostoïngue, Diebakate, Faye and Toguebaye (2001)
Henneguya ntementis Fomena and Bouix, 1996	*Brienomyrrus brachyistus*	Kidneys, spleen, gall bladder wall	Cameroon	Fomena and Bouix (1996)
Henneguya nyongensis Fomena and Bouix, 1996	*Marcusenius moori*	Gills, muscles	Cameroon	Fomena and Bouix (1996)
Henneguya odzai Fomena and Bouix, 1996	*Marcusenius moori*	Gills	Cameroon	Fomena and Bouix (1996)
Henneguya samochimensis Reed, Basson and Van As, 2003	*Clarias gariepinus*	Gills	Botswana	Reed, Basson and Van As (2003a)
Henneguya sarotherodoni Fall, Fomena, Kostoïngue, Diebakate, Faye and Toguebaye, 2000	*Sarotherodon galilaeus*	Intestine	Central Africa	Fall, Fomena, Kostoïngue, Diebakate, Faye and Toguebaye (2000)
Henneguya suprabranchiae Landsberg, 1987	*Clarias lazera #*	Suprabranchial organ	Israel	Landsberg (1987)
Genus *Kudoa* Meglitsch, 1947				
Kudoa eleotrisi Siau, 1971	*Eleotris kribensis*	Gills	Benin	Siau (1971)
Genus *Myxidium* Bütschli, 1882				
Myxidium birgi Fomena and Bouix, 1986	*Aphyosemion splendopleure*	Gall bladder	Cameroon	Fomena and Bouix (1986)
Myxidium bouixi Siau, 1971	*Synodontis ansorgii*	Gall bladder	Benin	Siau (1971)
Myxidium brienomyri Fomena and Bouix, 1986	*Brienomyrus brachyistus*	Gall bladder	Cameroon	Fomena and Bouix (1986)
Myxidium camerounensis Fomena and Bouix, 1986	*Neolebias ansorgei*	Gall bladder	Cameroon	Fomena and Bouix (1986)
Myxidium distichodi Kostoïngue, Faye and Toguebaye, 1998	*Distichodus engycephalus*	Gall bladder	Chad	Kostoïngue, Faye and Toguebaye (1998)
Myxidium latesi Kostoïngue, Faye and Toguebaye, 1998	*Lates niloticus*	Gall bladder	Chad	Kostoïngue, Faye and Toguebaye (1998)
Myxidium mendehei Fomena and Bouix, 1994	*Barbus guirali, B. martorelli*	Kidneys	Cameroon	Fomena and Bouix (1994)
Myxidium nyongensis Fomena and Bouix, 1986	*Barbus aspilus, B. jae, B. guirali, B. martorelli, B. camptacanthus*	Gall bladder	Cameroon	Fomena and Bouix (1986)
Myxidium petrocephali Fomena and Bouix, 1986	*Petrocephalus simus*	Gall bladder	Cameroon	Fomena and Bouix (1986)
Myxidium schalli Ghaffer, Shahawi and Naas, 1995	*Synodontis schall*	Gall bladder	Egypt	Ghaffar, El-Shahawi and Naas (1995)
Myxidium schilba Ali, Sakran and Abdel-Baki, 1999	*Schilbe mystus*	Gall bladder	Egypt	Ali, Sakran and Abdel-Baki (1999)
Myxidium shamama Ali, Sakran and Abdel-Baki, 1999	*Labeo niloticus*	Kidney	Egypt	Ali, Sakran and Abdel-Baki (1999)
Myxidium Bütschli, 1882 sp.	*Malapterurus electricus*	Gall bladder	Egypt	Ali, Sakran and Abdel-Baki (1999)

Table 3.1 continued. Myxosporeans infecting freshwater fishes in Africa. Genera and species arranged alphabetically. Compiled from Fomena and Bouix (1997), Reed (2000) and additional literature. [Key: ≈ Possible synonyms of *H. suprabranchiae* Landsberg, 1987, # Synonym of *Clarias gariepinus* Burchell (1822)].

Myxosporean species	Fish species	Organ	Country	Reference
Genus *Myxobilatus* Davis, 1944				
Myxobilatus accessobranchialis Obiekezie and Okaeme, 1987	*Heterobranchus bidorsalis*	Accessory breathing organ	Nigeria	Obiekezie and Okaeme (1987)
Myxobilatus synodontis Siau, 1971	*Synodontis ansorgii*	Gills	Benin	Siau (1971)
Genus *Myxobolus* Bütschli, 1882				
Myxobolus africanus Fomena, Bouix and Birgi, 1985	*Hepsetus odoe*	Gills	Cameroon	Fomena, Bouix and Birgi (1985)
Myxobolus agolus Landsberg, 1985	*Oreochromis aureus*×*O. niloticus, O. niloticus vulcani*	Kidneys, spleen	Israel	Landsberg (1985)
Myxobolus amieti Fomena, Bouix and Birgi, 1985	*Ctenopoma nanum*	Gills, eyes, muscles	Cameroon	Fomena, Bouix and Birgi (1985)
Myxobolus bagri Negm-Eldin, Govedich and Davies, 1999	*Bagrus bayad*	Gills	Egypt	Negm-Eldin, Govedich and Davies (1999)
Myxobolus beninensis Sakiti, Blanc, Marqués and Bouix, 1991	*Sarotherodon melanotheron*	Gills	Benin	Sakiti, Blanc, Marqués and Bouix (1991)
Myxobolus bilongi Fomena, Marqués, Bouix and Njiné, 1994	*Labeo* sp.	Gills, fins	Cameroon	Fomena, Marqués, Bouix and Njiné (1994)
Myxobolus brachysporus (Baker, 1963)	*Tilapia esculenta, T. variabilis*	Spleen	Lake Victoria (Uganda)	Baker (1963)
Myxobolus burkinei Kabré, Sakiti, Marqués and Sawadogo, 1995	*Labeo coubie*	Gills, fins	Burkina Faso	Kabré, Sakiti, Marqués and Sawadogo (1995)
Myxobolus camerounensis Fomena, Marqués and Bouix, 1993	*Oreochromis niloticus*	Gills, eyes, muscles	Cameroon	Fomena, Marqués and Bouix (1993)
Myxobolus chariensis Kostoïngue, Faye and Toguebaye, 1998	*Brycinus macrolepidotis*	Gills	Chad	Kostoïngue, Faye and Toguebaye (1998)
Myxobolus chrysichtyi Negm-Eldin, Govedich and Davies, 1999	*Chrysichthys auratus*	Gils	Egypt	Negm-Eldin, Govedich and Davies (1999)
Myxobolus citharinopsi Kostoïngue, Faye and Toguebaye, 1998	*Citharinops distichoides*	Gills	Chad	Kostoïngue, Faye and Toguebaye (1998)
Myxobolus clarii Mandour, Galal and Abed, 1993	*Clarias lazera*	Testis	Egypt	Mandour, Galal and Abed (1993)
Myxobolus comoei Kabré, Sakiti, Marqués and Sawadago, 1995	*Clarias angullaris*	Gills	Burkina Faso	Kabré, Sakiti, Marqués and Sawadago (1995)
Myxobolus dahomeyensis Siau, 1971	*Synodontis ansorgii*	Ovaries	Benin	Siau (1971)
Myxobolus distichodi Kostoïngue and Toguebaye, 1994	*Distichodus engycephalus*	Gills, liver, intestine	Chad	Kostoïngue and Toguebaye (1994)
Myxobolus dossoui Sakiti, Blanc, Marqués and Bouix, 1991	*Tilapia zillii, Hemichromis fasciatus, Oreochromis mosambica* × *O. niloticus*	Gills	Benin	Sakiti, Blanc, Marqués and Bouix (1991)
Myxobolus equatorialis Landsberg, 1985	*Oreochromis aureus* × *O. niloticus*	Spleen	Israel	Landsberg (1985)
Myxobolus etsatsaensis Reed, Basson and Van As, 2002	*Barbus thamalakanensis*	Gills	Botswana	Reed, Basson and Van As (2002b)

Table 3.1 continued. Myxosporeans infecting freshwater fishes in Africa. Genera and species arranged alphabetically. Compiled from Fomena and Bouix (1997), Reed (2000) and additional literature. [Key: ≈ Possible synonyms of *H. suprabranchiae* Landsberg, 1987, # Synonym of *Clarias gariepinus* Burchell (1822)].

Myxosporean species	Fish species	Organ	Country	Reference
Myxobolus exiguus Thélohan, 1895	*Abramis brama,Chondrostoma nasus, Mugil capito*	Gills, various organs	Tunisia	Thélohan (1895)
Myxobolus fotoi Fomena, Marqués and Bouix, 1993	*Oreochromis niloticus*	Gills	Cameroon	Fomena, Marqués and Bouix (1993)
Myxobolus galileaus Landsberg, 1985	*Sarotherodon galilaeus*	Kidneys, spleen	Israel	Landsberg (1985)
Myxobolus gariepinus Reed, Basson and Van As, 2003	*Clarias gariepinus*	Ovaries	Botswana	Reed, Basson and Van As (2003a)
Myxobolus gandiolensis Fall, Fomena, Kostoïngue, Diebakate, Faye and Toguebaye, 2000	*Tilapia guinensis*	Kidneys	Senegal	Fall, Fomena, Kostoïngue, Diebakate, Faye and Toguebaye (2000)
Myxobolus heterosporus (Baker, 1963)	*Tilapia esculenta, T. variabilis, Oreochromis niloticus*	Liver, kidneys, spleen	Uganda	Baker (1963)
Myxobolus homeosporus Baker, 1963	*Tilapia esculenta, T. variabilis*	Muscles	Lake Victoria (Uganda)	Baker (1963)
Myxobolus hydrocyni Kostoïngue and Toguebaye, 1994	*Hydrocynis forskali*	Gills	Chad	Kostoïngue and Toguebaye (1994)
Myxobolus israelensis Landsberg, 1985	*Oreochromis niloticus* × *O. aureus, Sarotherodon galilaeus, O. niloticus vulcani*	Kidneys, spleen	Israel	Landsberg (1985)
Myxobolus kainjiae Paperna, 1973	*Haplochromis niloticus, H. elegans*	Ovaries	Uganda	Paperna (1973)
Myxobolus kriebiensis Fomena and Bouix, 1994	*Brycinus longipinnis*	Skin, eyes, kidneys	Cameroon	Fomena and Bouix (1994)
Myxobolus lates Negm-Eldin, Govedich and Davies, 1999	*Lates niloicus*	Gills	Egypt	Negm-Eldin, Govedich and Davies (1999)
Myxobolus mailaoensis Kostoïngue, Faye and Toguebaye, 1998	*Synodontis gambiensis*	Kidneys	Chad	Kostoïngue, Faye and Toguebaye (1998)
Myxobolus maraensis Kostoïngue, Faye and Toguebaye, 1998	*Citharinus citharinus*	Gills	Chad	Kostoïngue, Faye and Toguebaye (1998)
Myxobolus ndjamenaensis Kostoïngue, Faye and Toguebaye, 1998	*Citharinus citharinus*	Kidneys	Chad	Kostoïngue, Faye and Toguebaye (1998)
Myxobolus nilei Faisal and Shalaby, 1987	*Oreochromis niloticus*	Gills, skin, eyes, kidneys, pancreas	Egypt	Faisal and Shalaby (1987)
Myxobolus niloticus Fahmy, Mandour and El-Naffar, 1971	*Labeo niloticus*	Fins	Egypt	Fahmy, Mandour and El-Naffar (1971)
Myxobolus njinei Fomena, Bouix and Birgi, 1985	*Barbus campthacanthus, B. guirali, B. batesii, B. martorelli*	Gills	Cameroon	Fomena, Bouix and Birgi (1985)
Myxobolus nkolyaensis Fomena and Bouix, 1994	*Barbus jae*	Gills	Cameroon	Fomena and Bouix (1994)

Table 3.1 continued. Myxosporeans infecting freshwater fishes in Africa. Genera and species arranged alphabetically. Compiled from Fomena and Bouix (1997), Reed (2000) and additional literature. [Key: ≈ Possible synonyms of *H. suprabranchiae* Landsberg, 1987, # Synonym of *Clarias gariepinus* Burchell (1822)].

Myxosporean species	Fish species	Organ	Country	Reference
Myxobolus nokoueensis Sakiti, Blanc, Marqués and Bouix, 1991	*Sarotherodon melanotheron*	Gills	Cameroon	Sakiti, Blanc, Marqués and Bouix (1991)
Myxobolus nouensis Fomena and Bouix, 2000	*Saratherodon galilaeus, Tilapia mariae*	Kidney, spleen	Cameroon	Fomena and Bouix (2000)
Myxobolus nyongana Fomena, Bouix and Birgi, 1985	*Barbus aspilus, B. jae, B. campthacanthus, B. guirali, B. martorelli*	Gills	Nyong Basin (Cameroon)	Fomena, Bouix and Birgi (1985)
Myxobolus oloi Fomena and Bouix, 1994	*Barbus aspilus, B. guirali, B. camptacanthus*	Gills, kidneys, heart	Cameroon	Fomena and Bouix (1994)
Myxobolus paludinosus Reed, Basson and Van As, 2002	*Barbus paludinosus*	Gills	Botswana	Reed, Basson and Van As (2002b)
Myxobolus polycentropsi Fomena, Bouix and Birgi, 1985	*Polycentropsis abbreviata*	Gills	Cameroon	Fomena, Bouix and Birgi (1985)
Myxobolus sarigi Landsberg, 1985	*Oreochromis niloticus* × *O. aureus, Sarotherodon galilaeus, O. niloticus*	Kidneys, spleen	Israel	Landsberg (1985)
Myxobolus sarotherodoni Sakiti, Blanc, Marqués and Bouix, 1991	*Sarotherodon melanotheron*	Gills	Benin	Sakiti, Blanc, Marqués and Bouix (1991)
Myxobolus stenosus Paperna, 1973	*Synodontis schall*	Gills	Uganda	Paperna (1973)
Myxobolus synodonti Fomena, Bouix and Birgi, 1985	*Synodontis batesii*	Stomach wall	Cameroon	Fomena, Bouix and Birgi (1985)
Myxobolus synodontis Negm-Eldin, Govedich and Davies, 1999	*Synodontis schall*	Gills	Egypt	Negm-Eldin, Govedich and Davies (1999)
Myxobolus tilapiae Abolarin, 1974	*Tilapia zillii, Oreochromis niloticus, Sarotherodin galilaeus*	Gills, fins	Nigeria	Abolarin (1974)
Myxobolus zillii Sakiti, Blanc Marqués and Bouix, 1991	*Tilapia zillii*	Gills	Benin	Sakiti, Blanc, Marqués and Bouix (1991)
Genus *Sphaerospora* Thélohan, 1892				
Sphaerospora melenensis Fomena, Marqués and Bouix, 1993	*Oreochromis niloticus*	Kidneys	Cameroon	Fomena, Marqués and Bouix (1993)
Sphaerospora sangmelimaensis Fomena and Bouix, 1994	*Petrocephalis simus, Brienomyrus brachyistus, Hepsetus odoe*	Kidneys	Cameroon	Fomena and Bouix (1994)
Sphaerospora tilapiae Fomena, Marqués and Bouix, 1993	*Oreochromis niloticus*	Kidneys, spleen	Cameroon	Fomena, Marqués and Bouix (1993)
Genus *Thelohanellus* Kudo, 1933				
Thelohanellus assambai Fomena, Marqués, Bouix and Njiné, 1994	*Labeo* sp	Gills, fins	Cameroon	Fomena, Marqués, Bouix, and Njiné (1994)
Thelohanellus citharini Kostoïngue, Fall, Faye and Toguebaye, 1999	*Citharinus citharinus*	Heart	Chad	Kostoïngue, Fall, Faye and Toguebaye (1999)

Table 3.1 continued. Myxosporeans infecting freshwater fishes in Africa. Genera and species arranged alphabetically. Compiled from Fomena and Bouix (1997), Reed (2000) and additional literature. [Key: ≈ Possible synonyms of *H. suprabranchiae* Landsberg, 1987, # Synonym of *Clarias gariepinus* Burchell (1822)].

Myxosporean species	Fish species	Organ	Country	Reference
Thelohanellus ndjamenaensis Kostoïngue, Fall, Faye and Toguebaye, 1999	*Labeo parvus*	Gills	Chad	Kostoïngue, Fall, Faye and Toguebaye (1999)
Thelohanellus niloticus, (Gurley, 1893)	*Labeo niloticus*	Skin	Egypt	Gurley (1893)
Thelohanellus sanageansis Fomena, Marqués, Bouix and Njiné,1994	*Labeo* sp.	Gills, fins	Cameroon	Fomena, Marqués, Bouix and Njiné (1994)
Thelohanellus valeti Fomena and Bouix, 1987	*Barbus aspilus, B. jae*	Operculum, stomach wall	Cameroon	Fomena and Bouix (1987)
Genus *Unicauda* Davis, 1944				
Unicauda strongylura (Gurley, 1893), [syn. *Henneguya strongylura* (Gurley, 1893) Labbé,1899]	*Synodontis schall*	Unknown	Egypt	Gurley (1893)

Marine myxosporean research in Africa

Research on marine myxosporeans in Africa is very scanty with only 52 species known from the entire extent of the African coastline (Table 3.4). Most species have been described from Senegal, with just a few others from Tunisia, Namibia and South Africa.

The earliest records of marine myxosporean research in Africa date back to the early 1900s. During those years myxosporean research was concentrated in southern Africa and several papers were published from the South African coastline. H.B. Fantham published a series of papers in the *South African Journal of Science* on myxosporeans from the Cape south coast (Fantham 1919; 1930). Fantham (1919) recorded several myxosporeans from the bile of a number of intertidal fish hosts (Table 3.2). He also briefly discussed a paper by Gilchrist (1918) regarding a possible microsporidian from the muscles of the "snoek", off the Cape coast, which apparently resulted in so-called soft or "pappy" specimens. Fantham (1919) mentioned that he had seen preparations of the parasite and that he noted evidence of a cyst wall around groups of four "spore-like bodies" as mentioned by Gilchrist (1918). Dr. Fantham then suggested that the soft-flesh phenomenon is similar to one described by Fantham and Porter (1914) from the Australian barracoutta, caused by a *Chloromyxum* Mingazzini, 1890 species. He continued to mention that the "snoek" and the barracoutta are the same or closely related fish species and that the parasite was possibly a myxosporean species from the genus *Chloromyxum*, rather than a microsporidian.

Table 3.2. Myxosporean species observed along the Cape South Coast of South Africa by Fantham (1919). Key: n.p.- Not provided.

Myxosporean	Spore length	Host	Organ	Location
Fantham (1919)				
Myxidium Bütschli, 1882 sp.	15µm-20µm	*Clinus taurus, Dentex argyrozona*	Bile	St. James Bay, Kalk Bay
Myxidium sp.	n.p.	*Canthurus blochii, Clinus cottoides*	Bile, blood?	St. James Bay, Kalk Bay
Hofferellus Berg, 1898 sp.	n.p	*Dentex argyrozona*	Kidney	False Bay
Lentospora Plehn, 1905 sp.	n.p.	*D. argyrozona, D. rupestris*	Gills, blood	False Bay
Leptotheca Thélohan, 1895 sp.	6µm long x 18µm broad	*C. superciliosus, C. taurus, C. cottoides, D. argyrozona*	Bile	False Bay

Taking into consideration the comments made by Fatham (1919), Gilchrist (1924) then described *Chloromyxum thyristes* Gilchrist, 1924 infecting the muscles of Cape Sea fish, or "snoek" and reported the flesh of the fishes infected with this myxosporean, becoming soft and liquid. This species has subsequently been placed in the genus *Kudoa* and is now known as *Kudoa thyristes*.

Fantham (1930) presented a continuation of the series of his findings. In this paper he actually described a number of species (Table 3.3) (Fig. 3.3). Unfortunately his species descriptions do not contain sufficient descriptive information and illustrative drawings. This prevents separation of the species described by him from other similar species and his species must therefore be considered *nomina nuda* or invalid.

Table 3.3. Summary of myxosporean species described by Fantham (1930). Key: n.p.- Not provided.

Myxosporean	Fig. 3.3	Spore measurements (µm)	Host	Organ	Location
Fantham (1930)					
Leptotheca obovalis Fantham, 1930	a, b	30-60 x 4-12	*Blennius cornutus*	Bile	St James Bay
	n.p.	16-17 x 5-7	*Lepidopus caudatus*	Bile	Table Bay
	n.p.	n.p.	*Clinus taurus*	Bile	Kalk Bay
Leptotheca Thélohan, 1895 sp.	n.p.	17 x 19	*Dentex argyrozona*	Bile	False Bay
Myxidium contortum Fantham, 1930	c, d	21-24 x 5-8	*Blennius cornutus*	Bile	False Bay
Myxidium pagelli Fantham, 1930	e	22-28 x 9-11.5	*Lithognathus lithognathus*	Bile	Cape Town fish market (Table Bay)

Table 3.3. Continued. Myxosporean species described by Fantham (1930). Key: n.p.- Not provided.

Myxosporean	Fig. 3.3	Spore measurements (µm)	Host	Organ	Location
Myxidium parvoviforme Fantham, 1930	f	8-10 x 5.5-7	*Sciaena hololepidota*	Bile	Kalk Bay
Sphaeromyxa arcuata Fantham, 1930	g	22-27 x 6-8	*Dentex argyrozona*	Bile	Kalk Bay
Sphaeromyxa curvula Fantham, 1930	h	19-22 x 4-6	*Caranthus blochii*	Bile	St. James Bay
Sphaerospora subelegans Fantham, 1930	n.p.	9 -13 in diameter	*Merrluccius capensis*	Bile	Table Bay

Fantham (1930) noted that most of the spores of myxosporeans collected from South African intertidal fish appeared to be larger than similar species infecting European marine fish, possibly indicating that myxosporeans show zoogeographical differentiation, as is the case with Metazoa.

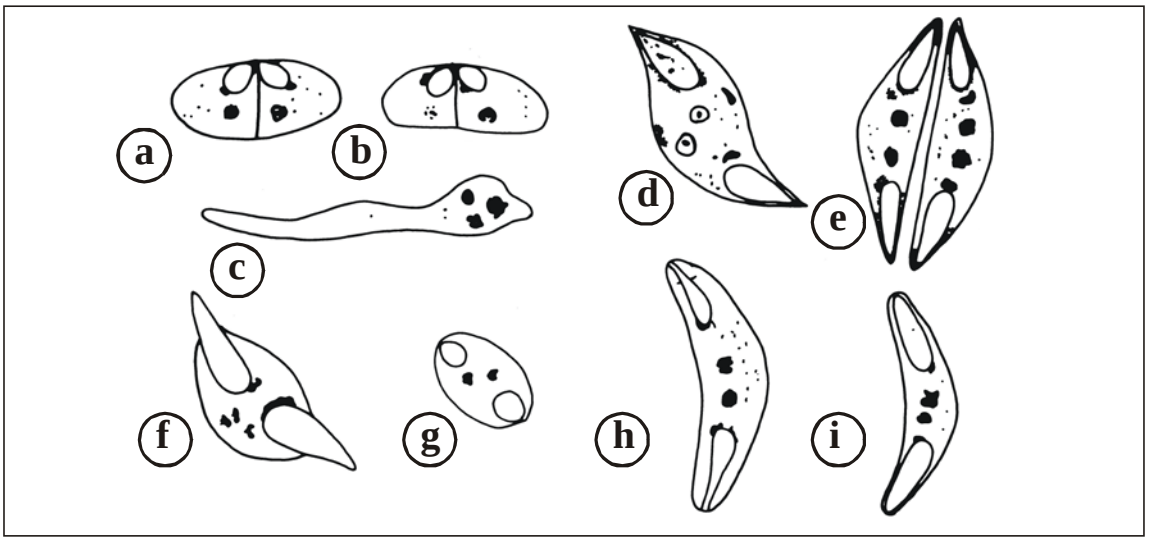


Figure 3.3. Line drawings of myxosporean species described by Fantham (1930). **a-c.** Spores and trophozoites of *Leptotheca obovalis* Fantham, 1930. **d,e.** Spores of *Myxidium contortum* Fantham, 1930. **f.** Spores of *Myxidium contortum* Fantham, 1930. **g.** Spore of *Myxidium parvoviforme* Fantham, 1930. **h.** Spore of *Sphaeromyxa arcuata* Fantham, 1930. **i**. Spore of *Sphaeromyxa curvula* Fantham, 1930. Magnification: × 800. Redrawn from Fantham (1930).

In 1947, Davies and Beyers, two scientists from the Low Temperature Research Laboratory in Cape Town, published a paper on a protozoan disease of some South African trawled fish and a possible routine detection of this disease using fluorescence. Investigations into problems of "mealiness" of cooked flesh of Cape John Dory (*Zeus capensis*) and milky spots in fillets of stockfish (*Merluccius capensis*) revealed that the abnormalities were as a result of heavy infections of the muscle fibre by a protozoan

parasite. The parasite was identified as the one described by Gilchrist in 1924. Approximately 25% of the John Dory catches were extremely emaciated and so milky that they could not be filleted. The stockfish catches showed no visible signs of infection until after they were smoked, developing milky spots embedded in the flesh. These milky spots, when pressed, oozed disintegrated flesh, packed full of the characteristic spores of the parasite. It was discovered that the infected muscle fibres fluoresced under ultra-violet light, filtered through Wood's glass, enabling them to survey large samples of the catch for the distribution of infection within the tissues, the intensity of infection and, the number of fish infected. Approximately 76% of the John Dory catch was infected compared to 70% of the stockfish catch.

Dubina and Isakov (1976) described two new species, *Myxidium giganteum* Dubina and Isakov, 1976 and *Ceratomyxa schulmani* Dubina and Isakov, 1976 from the gall bladder of deep sea *Alepocephalus australis* off the coast of South Africa. A number of years later Schulman, Kovaleva and Dubina (1979) described a further eight new species of myxosporeans belonging to two genera, namely *Pallistus* Schulman, Kovaleva and Dubina, 1979 and *Alatospora* Schulman, Kovaleva and Dubina, 1979 from the gall bladders of marine fish from the Atlantic coast of Africa.

After these initial papers prior to the 1980s, an abrupt end to southern African myxosporean research occurred and approximately 15 years passed before a sudden explosion of myxosporean species from West Africa appeared, mostly from the Senegalese coast.

The first paper to appear after the void was that of Bahri, Marqués, Coste, Bouix and Hassine (1995) who reported the presence of a cutaneous myxosporean in *Mugil cephalus* from Tunisia. Many of the mullet caught by fishermen in the past in Tunisia were rejected because of their unpleasant appearance, which was as a result of a *Myxobolus exiguus* (Thélohan, 1895) infection (Siau 1978). Mullets represent one of the most important resources in Tunisian lagoons, consequently prompting this investigation into myxosporidiases. The exact extent of the disease could not be determined since only caught fish could be considered and the percentage of diseased fish eliminated by predators and by natural selection remained unknown.

Most of the research on marine myxosporeans in Africa has been conducted by scientists in Senegal. In their first publication Kpatcha, Diebakate and Toguebaye (1996a) examined 1630 fishes from 37 families and 51 genera caught off the coast of Senegal. They subsequently described nine myxosporean species, of which five were new species. Kpatcha, Diebakate, Faye and Toguebaye (1996b) described a further seven species from Senegal, of which six from the genus *Ceratomyxa* from gall bladders of marine fishes were new.

In Tunisia, Bahri, Hassine and Marqués (1996) reported a *Henneguya* species infecting the gills of wild gilthead bream, *Sparus aurata*. This species of sea bream has become an important cultured fish species in the Mediterranean and as a result the authors decided to start an inventory of myxosporean parasite fauna infecting wild and cultured sea bream from the Tunisian coast and fish farms. Whilst in search of the highly pathogenic *Myxidium leei*, the authors discovered a *Henneguya* species on the gills of the bream, with a relatively low prevalence of 4%. According to Bahri *et al.* (1996) cultured sea bream in Tunisia are not parasitised by *M. leei* and the *Henneguya* species on the gills of the fish was only noted on the wild *S. aurata*. The results indicated that the infections probably resulted from aquaculture conditions, the origin of the fish, or were due to the development of pathogenic forms associated with the fish.

Also in Tunisia, Bahri and Marqués (1996) described four species of myxosporeans from the genus *Myxobolus* from *Mugil cephalus* in Ichkeul lagoon, including *Myxobolus bizerti* Bahri and Marqués, 1996 and *M. ichkeulensis* Bahri and Marqués, 1996 (Table 3.4). Following the Bahri and Marqués (1996) paper, Fall, Kpatcha, Diebakate, Faye and Toguebaye (1997) published a similar report on myxosporeans from the genus *Myxobolus* infecting *M. cephalus* in Senegal. In this paper they described five species, of which three were considered new species.

In Senegal once again, Faye, Kpatcha, Fall and Toguebaye (1997) investigated the parasites of four commercially important fish hosts. Results revealed four species of myxosporeans infecting the hearts of the hosts. Three species were identified as being from the genus *Henneguya* and one species was recognised as a member of the genus *Myxobolus* (Table 3.4). These authors noted that the infections might render the heart dysfunctional due to the high numbers of cysts present in the heart muscle. In the same

year Kpatcha, Faye, Diebakate, Fall and Toguebaye (1997) described a further eight new *Henneguya* species from marine fish caught off the coast of Senegal.

Still in Senegal, Kpatcha, Diebakate, Faye and Toguebaye (1999) described *Kudoa boopsi* Kpatcha, Diebakate, Faye and Toguebaye, 1999 from the gills of *Boops boops*. This description was only the second in the world of a *Kudoa* species infecting the gills of a host, most others having been found within the muscles. During the same year, Faye, Kpatcha, Diebakate, Fall and Toguebaye (1999) reported further gill infections of myxosporean parasites in fish from the coast of Senegal. Three species were identified and one was described as a new species. In the same year, Diebakate, Fall, Faye and Toguebaye (1999) described *Unicapsula marquesi* Diebakate, Fall, Faye and Toguebaye, 1999 from the gills of *Polydactylus quadrifilis* caught off the Senegalese coast. This was the first record of this genus in Africa.

Eventually a paper appeared from southern Africa, marking the revival of myxosporean research in the region. Ali (2000) described *Ortholinea basma* Ali, 2000 from the gall bladder of the agile klipfish *Clinus agilis*, collected from the tidal pools at Port Nolloth in South Africa. This was the first research to be conducted on South African marine myxosporeans since the early 1970s. This description was also the first record of this genus infecting marine fishes in Africa.

Table 3.4. Myxosporeans infecting marine fishes in Africa. Genera and species arranged alphabetically.

Myxosporean species	Fish species	Organ	Country	Reference
Genus *Alatospora* Shulman, Kovaleva and Dubina, 1979				
Alatospora africana Shulman, Kovaleva and Dubina, 1979	*Callanthias ruber*	Gall bladder	Atlantic coast of Africa	Shulman, Kovaleva and Dubina (1979)
Alatospora dracoidea Shulman, Kovaleva and Dubina, 1979	*Chlorophthalmus agassisi*	Gall bladder	Atlantic coast of Africa	Shulman, Kovaleva and Dubina (1979)
Alatospora contrariocapsularia Shulman, Kovaleva and Dubina, 1979	*Macrorhamphosus gracilis*	Gall bladder	Atlantic coast of Africa	Shulman, Kovaleva and Dubina (1979)
Alatospora parvicapsula Shulman, Kovaleva and Dubina, 1979	*Aulopus cadenati*	Gall bladder	Atlantic coast of Africa	Shulman, Kovaleva and Dubina (1979)
Alatospora samaroidea Shulman, Kovaleva and Dubina, 1979	*Chlorophthalmus atlanticus*	Gall bladder	Atlantic coast of Africa	Shulman, Kovaleva and Dubina (1979)
Alatospora sp.	*Xenodermychthys socialis*	Gall bladder	Atlantic coast of Africa	Shulman, Kovaleva and Dubina (1979)
Genus *Bibteria* Kovaleva, Zubchenko and Krasin, 1983				
Bibteria admiranda Kovaljova, Zubchenko and Krasin, 1983	*Spondyiliosoma cantharus*	Kidney	Senegal	Kpatcha, Diebakate and Toguebaye (1996a)
Genus *Ceratomyxa* Thélohan, 1892				
Ceratomyxa acanthuri Kpatcha, Diebakate, Faye and Toguebaye, 1996	*Acanthurus monroviae*	Gall bladder	Senegal	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Ceratomyxa australis Gaevskaya and Kovaleva, 1979	*Trachurus trachurus capensis*	Gall bladder	Namibia	Gaevskaya and Kovaleva (1979)
Ceratomyxa fistulariae Kpatcha, Diebakate, Faye and Toguebaye, 1996	*Fistularia petimba*	Gall bladder	Senegal	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Ceratomyxa lagocephali Kpatcha, Diebakate, Faye and Toguebaye, 1996	*Lagocephalus laevigatus*	Gall bladder	Senegal	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Ceratomyxa shulmani Dubina and Isakov, 1976	*Alepocephalus australis*	Gall bladder	South Africa	Dubina and Isakov (1976)
Ceratomyxa syacii Kpatcha, Diebakate, Faye and Toguebaye, 1996	*Syacium micrurum*	Gall bladder	Senegal	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Ceratomyxa trachinocephali Kpatcha, Diebakate, Faye and Toguebaye, 1996	*Trachinocephalus myops*	Gall bladder	Senegal	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Ceratomyxa trichuiri Kpatcha, Diebakate, Faye and Toguebaye, 1996	*Trichiurus lepturus*	Gall bladder	Senegal	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Ceratomyxa truncata Thélohan, 1895	*Sardinella maderensis, S. aurita*	Gall bladder	Senegal	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Genus *Davisia* Laird, 1953				
Davisia donecae Gaevskaya and Kovaleva, 1979	*Trachurus trachurus capensis*	Gall bladder	Namibia	Gaevskaya and Kovaleva (1979)
Genus *Henneguya* Thélohan, 1892				
Henneguya brachydeuteri Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	*Brachydeuterus auritus*	Heart	Senegal	Kpatcha, Faye, Diebakate, Fall and Toguebaye (1997)
Henneguya joalensis Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	*Cephalopholis taeniops*	Kidney	Senegal	Kpatcha, Faye, Diebakate, Fall and Toguebaye (1997)

Table 3.4. continued. Myxosporeans infecting marine fishes in Africa.

Myxosporean species	Fish species	Organ	Country	Reference
Henneguya kayarensis Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	*Galeoides decadactylus*	Liver	Senegal	Kpatcha, Faye, Diebakate, Fall and Toguebaye (1997)
Henneguya lutjani Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	*Lutjanus agennes*	Gills	Senegal	Kpatcha, Faye, Diebakate, Fall and Toguebaye (1997)
Henneguya mbourensis Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	*Dentex canariensis*	Kidney	Senegal	Kpatcha, Faye, Diebakate, Fall and Toguebaye (1997)
Henneguya ouakamensis Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	*Mugil cephalus*	Gills and heart	Senegal	Kpatcha, Faye, Diebakate, Fall and Toguebaye (1997)
Henneguya priacanthi Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	*Pricanthus arenatus*	Gills	Senegal	Kpatcha, Faye, Diebakate, Fall and Toguebaye (1997)
Henneguya yoffensis Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	*Sparus caeruleostictus*	Gills and Heart	Senegal	Kpatcha, Faye, Diebakate, Fall and Toguebaye (1997)
Henneguya sp.	*Sparus aurata*	Gills	Tunisia	Bahri, Hassine and Marqués (1996)
Henneguya sp. 1	*Brachideuterus auritus*	Heart	Senegal	Faye, Kpatcha, Fall and Toguebaye (1997)
Henneguya sp. 2	*Sparus caeruleosticus*	Heart	Senegal	Faye, Kpatcha, Fall and Toguebaye (1997)
Henneguya sp. 3	*Mugil cephalus*	Heart	Senegal	Faye, Kpatcha, Fall and Toguebaye (1997)
Genus *Kudoa* Meglitsh, 1947				
Kudoa boopsi Kpatcha, Diebakate, Faye and Toguebaye, 1999	*Boops boops*	Gills	Senegal	Kpatcha, Diebakate, Faye and Toguebaye (1999)
Kudoa thyristes (Gilchrist, 1924)	*Thyristes atun, Merluccius capensis*	Muscles	South Africa	Gilchrist (1924)
Genus *Leptotheca* Thélohan, 1895				
Leptotheca elongata Thélohan, 1895	*Merluccius senegalensis*	Gall bladder	Senegal	Kpatcha, Diebakate and Toguebaye (1996a)
Leptotheca lutjani Kpatcha, Diebakate and Toguebaye, 1996	*Lujanus fulgens*	Kidneys	Senegal	Kpatcha, Diebakate and Toguebaye (1996a)
Leptotheca pegusae Kpatcha, Diebakate and Toguebaye, 1996	*Pegusa lascaris*	Gall bladder	Senegal	Kpatcha, Diebakate and Toguebaye (1996a)
Genus *Myxidium* Bütschli, 1882				
Myxidium abudefdufi Kpatcha, Diebakate and Toguebaye, 1996	*Abudefduf marginatus*	Gall bladder	Senegal	Kpatcha, Diebakate and Toguebaye (1996a)
Myxidium elopsi Kpatcha, Diebakate and Toguebaye, 1996	*Elops senegalensis*	Intestine	Senegal	Kpatcha, Diebakate and Toguebaye (1996a)
Myxidium giganteum Doflein, 1898	*Raja miraletus*	Gall bladder	Senegal	Kpatcha, Diebakate and Toguebaye (1996a)
Myxidium gigantissimum Dubina and Isakov, 1976	*Alepocephalus australis*	Gall bladder	South Africa	Dubina and Isakov (1976)
Genus *Myxobolus* Bütschli, 1882				
Myxobolus bizerti Bahri and Marqués, 1996	*Mugil cephalus*	Gills	Tunisia	Bahri and Marques (1996)

Table 3.4. continued. Myxosporeans infecting marine fishes in Africa.

Myxosporean species	Fish species	Organ	Country	Reference
Myxobolus episquamalis Egusa, Maeno and Sorimachi, 1990 (possible junior synomym of *M. exiguus*)	*M. cephalus*	Scales	Tunisia	Bahri and Marqués (1996)
Myxobolus exiguus Thélohan, 1985	*M. cephalus*	Scales, fins	Tunisia	Bahri, Marqués, Coste, Bouix and Hassine (1995)
	M. cephalus	Gills	Senegal	Fall, Kpatcha, Diebakate, Faye and Toguebaye (1997)
Myxobolus goreensis Fall, Kpatcha, Diebakate and Toguebaye, 1997	*M. cephalus*	Gills	Senegal	Fall, Kpatcha, Diebakate, Faye and Toguebaye (1997)
Myxobolus hannensis Fall, Kpatcha, Diebakate and Toguebaye, 1997	*Mugil cephalus*	Gill arches	Senegal	Fall, Kpatcha, Diebakate, Faye and Toguebaye (1997)
Myxobolus hani Faye, Kpatcha, Diebakate, Fall and Toguebaye, 1999	*Mugil curema*	Gill arches	Senegal	Faye, Kpatcha, Diebakate, Fall and Toguebaye (1999)
Myxobolus ichkeulensis Bahri and Marqués, 1996	*Mugil cephalus*	Gill arches	Tunisia	Bahri and Marqués (1996)
Myxobolus mugilis Negm-Eldin, Govedich and Davies, 1999	*Mugil cephalus*	Gills	Egypt	Negm-Eldin, Govedich and Davies (1999)
Myxobolus mülleri Bütschli, 1882	*Mugil cephalus*	Gills	Senegal	Fall, Kpatcha, Diebakate, Faye and Toguebaye (1997)
Myxobolus raibauti Fall, Kpatcha, Diebakate and Toguebaye, 1997	*Mugil cephalus*	Skin	Senegal	Fall, Kpatcha, Diebakate, Faye and Toguebaye (1997)
Myxobolus spinacurvatura Maeno, Sorimachi, Ogawa and Egusa, 1990	*Mugil cephalus*	Intestine, gall bladder	Tunisia	Bahri and Marqués (1996)
Genus *Ortholinea* Shulman, 1962				
Ortholinea basma Ali, 2000	*Clinus agilis*	Urinary bladder	South Africa	Ali (2000)
Genus *Palliatus* Kovaleva and Dubina, 1979				
Palliatus mirabilis Shulman, Kovaleva and Dubina, 1979	*Xenodermychthys socialis*	Gall bladder	Atlantic coast of Africa	Shulman, Kovaleva and Dubina (1979)
Palliatus grandis Shulman, Kovaleva and Dubina, 1979	*Alepocephalus australis*	Gall bladder	Atlantic coast of Africa	Shulman, Kovaleva and Dubina (1979)
Palliatus indecorus Shulman, Kovaleva and Dubina, 1979	*Alepocephalus rostratus*	Gall bladder	Atlantic coast of Africa	Shulman, Kovaleva and Dubina (1979)
Genus *Sphaeromyxa* Thélohan, 1892				
Sphaeromyxa balbiani Thélohan, 1892	*Abudefduf marginatus, Sardinella maderensis*	Gall bladder	Senegal	Kpatcha, Diebakate and Toguebaye (1996a)
Genus *Unicapsula* Davis, 1924				
Unicapsula marquesi Diebakate, Fall, Faye and Toguebaye, 1999	*Polydactylus quadrifilis*	Gills	Senegal	Diebakate, Fall, Faye and Toguebaye (1999)
Genus *Zschokkella* Auerbach, 1910				
Zschokkella mugilidae Kpatcha, Diebakate and Toguebaye, 1996	*Mugil capurii*	Gall bladder	Senegal	Kpatcha, Diebakate and Toguebaye (1996a)

4. Materials and Methods

Materials and methods associated with the collection of both marine and freshwater myxosporeans are very similar. The most notable difference lies in the initial sampling of the marine and freshwater fish hosts. Throughout this chapter any differences between freshwater and marine sampling will be pointed out. All other methods should be accepted as being exactly the same for both habitats.

Collection of fish hosts

Fieldwork for the sampling of ***freshwater fish-infecting myxosporeans*** was conducted at various sampling sites in the Okavango River and Delta, Botswana from 1997 to 2001 (Fig. 4.1). The great extent of the Okavango Delta provides an incredible diversity of habitats for different fish species (Fig. 4.2a). Table 4.1 provides a list of sampling sites and the type of habitats they represent. These sites were allocated specific names for the purposes of the study and hence, these names will not necessarily be found on a general map of the Okavango River and Delta. The different environments sampled include:

Mainstream (Fig. 4.2b) – This is a perennial channel that flows constantly.
Channels (Fig. 4.2c) – These include permanently flowing channels that connect various parts of the mainstream with each other, or connect lagoon environments with the mainstream.
Lagoons (Fig. 4.2d) – These are natural lagoons formed by drifting papyrus occasionally creating vast areas isolated from the strong flowing currents of the mainstream.
Floodplains (Fig. 4.2e) – These are shallow areas seasonally inundating grasslands that create a breeding ground for many juvenile fishes.
Backwaters (Fig. 4.2f) – Backwater environments are formed in areas after the annual floods have subsided and isolated pockets of water are left adjacent to the mainstream channel due to the elevated riverbank in certain areas.

Fishes were collected from mainstream and lagoon environments using a series of gill nets ranging in mesh size from 50 mm to 150 mm (Fig. 4.3a). The gill nets were strategically placed in specific areas in the late afternoons and left overnight. Early the next morning the nets were lifted from the water and the fish, which were mostly still alive, collected.

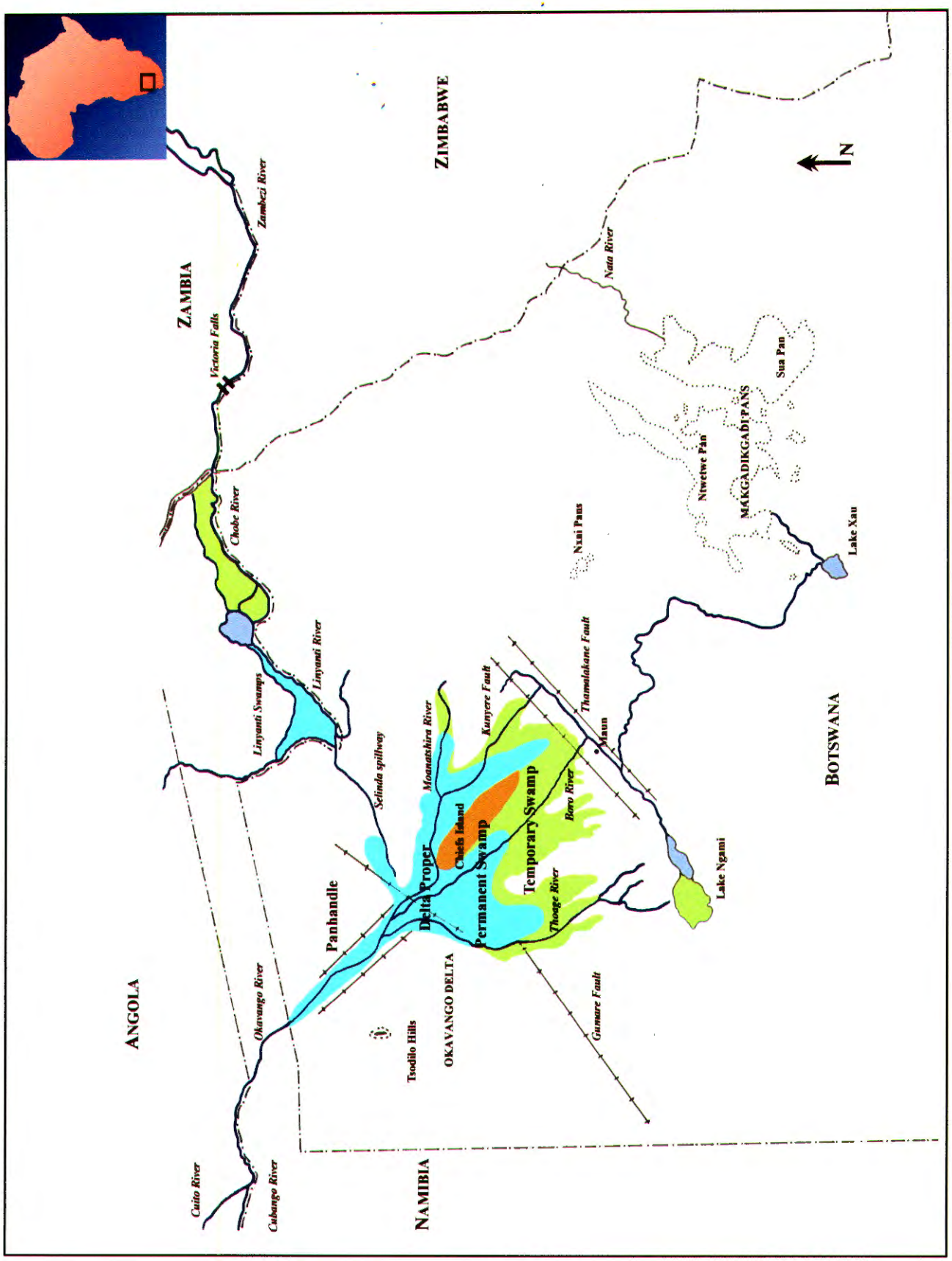


Figure 4.1. Map of the Okavango River and Delta in Botswana illustrating the rivers, Panhandle, Permanent Swamp and Temporary Swamp where sampling took place. Redrawn from Ross (2003).

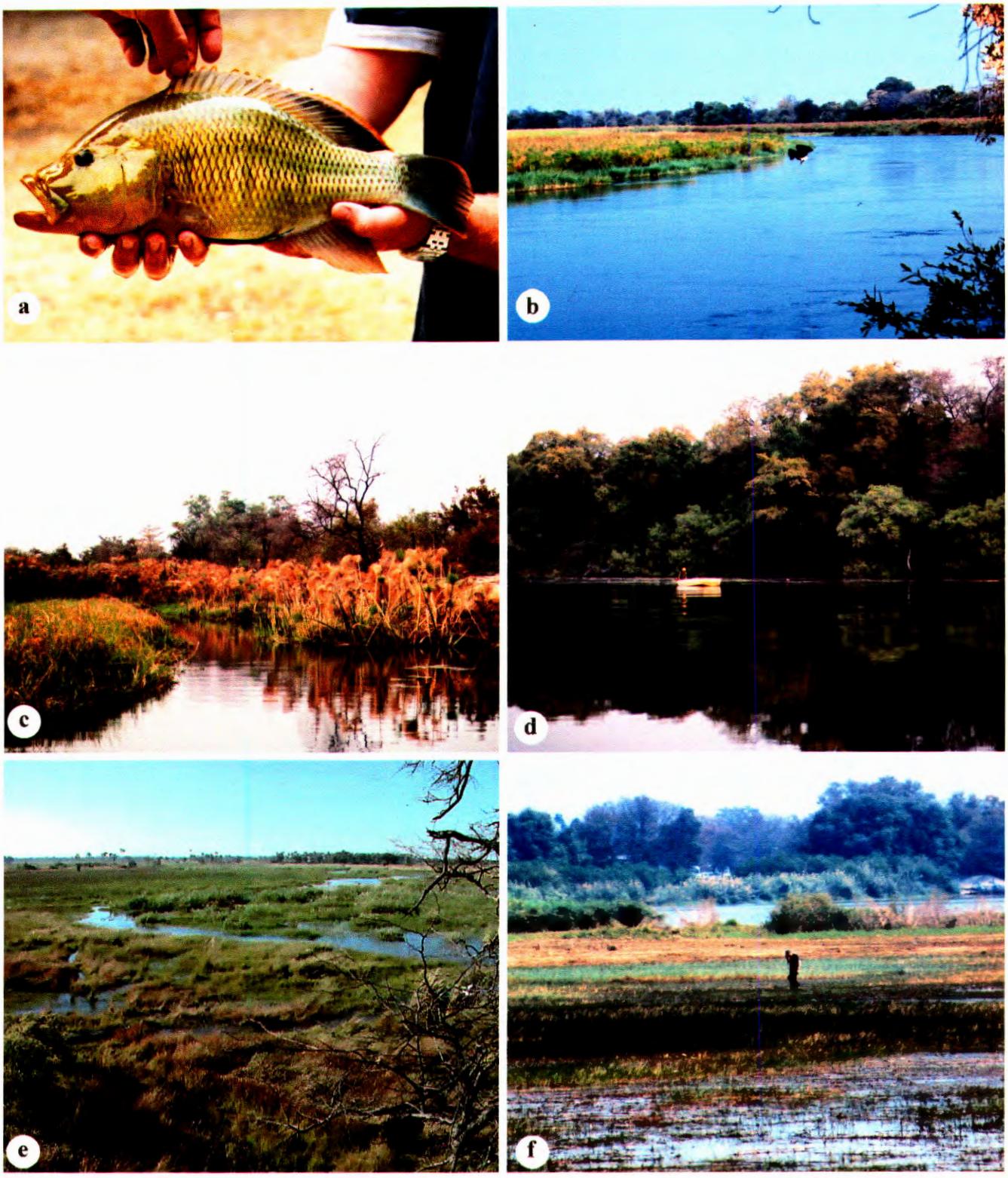


Figure 4.2. **a.** Photograph of *Serranochromis robustus* (Günther, 1864) the "Nembwe", one of the many species of fish found in the Okavango River and Delta, Botswana. **b-f.** Different habitat types sampled in the Okavango River and Delta, Botswana. **b.** Okavango mainstream. **c.** Channel environment. **d.** Lagoon environment. **e.** Floodplain environment. **f.** Backwater environment.

Site name	Habitat type	Reach
Boro River (Moremi)	Mainstream	Delta Proper
Crocodile lagoon	Lagoon	Panhandle
Drodsky's mainstream	Mainstream	Panhandle
Duba lagoon	Lagoon	Delta Proper
Estasta mainstream	Mainstream	Panhandle
Guma lagoon	Lagoon	Panhandle
Guma floodplains	Floodplain	Panhandle
Kalatog channel	Channel	Panhandle
Kotze farm	Off mainstream	Panhandle
Lechwe island	Permanent swamp	Delta Proper
Leopard island	Channel	Delta Proper
Makwena	Lagoon	Delta Proper
Mohembo backwaters	Backwater	Panhandle
Mohembo floodplains	Floodplain	Panhandle
Mokoro lagoon	Lagoon	Panhandle
Nkoga mainstream	Mainstream	Panhandle
Nxamaseri	Backwater	Panhandle
Nxameseri fish farm	Backwater	Panhandle
Nxaraga camp	Permanent swamp	Delta Proper
Nxabega permanent swamp	Permanent swamp	Delta Proper
Nxabega temporary swamp	Temporary swamp	Delta Proper
Observation island	Channel in permanent swamp	Delta Proper
Pepere lagoon	Lagoon	Panhandle
Picnic lagoon	Lagoon	Delta Proper
Samochima lagoon	Lagoon	Panhandle
Seronga backwaters	Backwater	Panhandle
Shakawe backwaters	Backwater	Panhandle
Shakawe mainstream	Mainstream	Panhandle
Thamalakane river (Maun)	Temporary swamp	Delta Proper
Thebe lagoon	Lagoon	Panhandle
Thoage lagoon	Lagoon	Delta Proper
Tim's channel	Channel off mainstream	Panhandle
Upper Thoage island	Mainstream	Panhandle
Xaro backwaters	Backwater	Panhandle
Xaro mainstream	Mainstream	Panhandle

Smaller fish species were collected from floodplains and backwaters as well as the fringes of mainstream environments using hand nets (Fig. 4.3b), scoop nets, cast nets (Fig. 4.3c) and seine nets (Fig. 4.3d). Larger predatory fishes were collected from the mainstream and lagoon environments during the evenings using conventional rod and line methods (Fig. 4.3e). All fishes collected were taken back to a mobile field laboratory where they were kept alive in aerated aquaria (Fig. 4.3f). Fish species were identified using Skelton's (1993, 2001): "*A complete guide to the freshwater fishes of southern Africa*".

Figure 4.3. Different fish sampling methods used in the Okavango River and Delta, Botswana. **a.** Gill nets. **b.** Hand nets. **c.** Scoop nets. **d.** Cast nets. **e.** Rod and line. **f-i.** Mobile field laboratory at Shakawe Fishing Camp, where fishes were dissected (**g**), fish organs examined for myxosporean infections (**h**) and samples preserved.

south coast, South Africa. These sampling sites were situated at the De Hoop and De Mond Nature Reserves and at Jeffrey's Bay (Fig. 4.4).

Most fishes were collected from the De Hoop Nature Reserve (Fig. 4.5a), which is situated near the southern most tip of Africa. Small intertidal fish species were collected from intertidal rock pools using small hand nets and hand lines (Fig. 4.5b), while larger intertidal fishes were collected using mostly hand lines and occasionally cast nets. Some other larger surf zone fishes were collected by means of rod and line through the aid of officials from the Western Cape Nature Conservation Board (Figs. 4.5c, d). Adjacent to the De Hoop Nature Reserve lies the De Mond Nature Reserve (Fig. 4.5e) where estuarine fishes were collected from the Heuningsnes Estuary using mostly cast nets and seine nets (Fig. 4.5f). The live fish collected from both the De Hoop and De Mond Nature Reserves were transported back to temporary field laboratories set up at either the Potberg or Koppie Alleen (Figs. 4.5g, h) Environmental Education Centers in the De Hoop Nature Reserve. The live fish were transferred to aerated aquaria at these field laboratories where they were held until examination for parasitic infections. Intertidal fish collected from rock pools at Jeffrey's Bay were caught using mostly hand lines and small hand nets. Temporary field laboratories were also set up at Jeffrey's Bay, where the fishes were kept in aerated aquaria until they were examined for parasitic infections. The fishes collected at all three localities were identified using Smith and Heemstra (1986), Branch, Griffiths, Branch and Beckley (1994) and Van Der Elst (1995).

Examination of fish hosts

All fishes collected were measured in millimeters (mm) from the tip of the snout to the tips of the caudal fin. Recorded measurements of the fishes collected are illustrated in the tables of results in Chapters 5 and 6 as follows:

Average (minimum – maximum)

If fewer than five individuals of a certain species were examined, their lengths have all been recorded, for example 23, 56, 43, 44. The authors of fish species names have only been included for those fishes examined for the purpose of this study and have been omitted from any fish species names referred to from general literature. The same applies to any myxozoan species referred to from general literature.

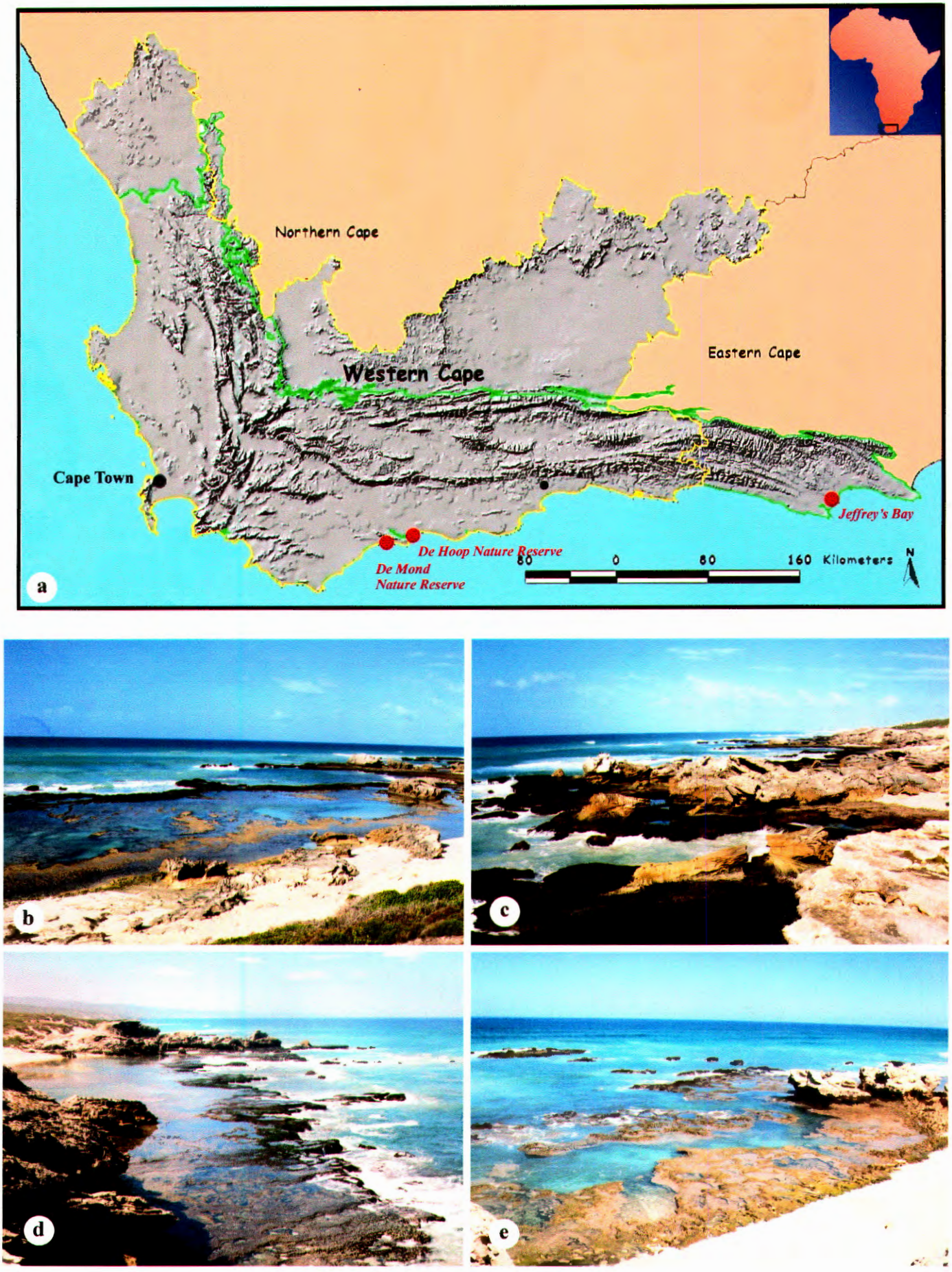


Figure 4.4. **a.** Map of the western Cape, South Africa, illustrating the collection localities where sampling took place along the Cape south coast of South Africa. **b-e.** Photographs of intertidal pools at De Hoop Nature Reserve where fishes were collected.

Figure 4.5. a . Intertidal rock pools at De Hoop Nature Reserve. **b.** Collecting intertidal fishes using hand nets. **c, d.** Officials from the Western Cape Nature Conservation Board collecting fishes using rod and line methods. **f.** The Heuningsnes River Estuary at De Mond Nature Reserve. **f.** Collecting estuarine fishes using a cast net at De Mond Nature Reserve. **g.** Koppie Alleen Environmental Education Centre. **h.** Field laboratory at De Hoop Nature Reserve.

larger fish species were anesthetized using benzocaine before they were subject to further examination. Gill arches were individually dissected using sharp scissors and pinsettes. The body cavity was cut open ventrally from the anus to between pectoral fins to display the internal organs. Once dissected, the gills, gill arch and buccal cavities and other internal organs were examined using both a dissection and compound microscope (see Figs. 4.3g, h, i).

In the case of detecting a possible myxosporean infection, a squash preparation of the tissue or organ concerned was made. To prepare a squash preparation, a piece of tissue, approximately 5mm^3, was crushed between a microscope coverslip and glass slide. This temporary preparation was viewed between 10X – 100X magnification, using a compound light microscope in order to determine the presence of any myxosporean spores.

Preservation of myxosporean spores

The standard techniques when working with myxosporeans requires the observation of live spores, but due to the isolated sampling localities at both the Okavango River and Delta, Botswana and the southern Cape coast, South Africa mature myxosporean spores found were mostly fixed in 10% buffered neutral formalin. This enabled transport of the spores back to the laboratory in the Department of Zoology and Entomology at the University of the Free State, Bloemfontein. The extended fieldtrips to the Okavango took place for up to two months at a time and required a 4000km round trip. This made attempts to transport live myxosporean spores impossible.

Permanent preparations of freshwater myxosporeans from the Okavango Delta, were made by impregnating the spores with silver nitrate. To prepare these slides, organs containing a myxosporean infection with mature spores were smeared across a microscope slide, to sufficiently separate the spores. The slide was left to air dry and subsequently placed in a 2% silver nitrate solution for approximately 10 minutes. The slide was removed from the silver nitrate solution, rinsed in distilled water and placed on a white background in direct sunlight for 30 minutes to impregnate. Once impregnated and dry, the slides were mounted with coverslips using Eukitt or Canada Balsam mounting media. This method of impregnating the spores with silver nitrate proved to be useful for viewing the number of coils per polar filament.

The surveys conducted along the Cape south coast never extended longer than two weeks and only involved a 2000 km round trip. Therefore, in the case of gall bladder myxosporean infections of intertidal fishes collected along the Southern Cape coast of South Africa, live spores were transported back to the laboratory of the Department of Zoology and Entomology at the University of the Free State, Bloemfontein. This was achieved using small haematocrit tubes that were sealed at each end. The samples were kept refrigerated at all times to prevent bacterial infections.

The contents of some myxosporean-infected gall bladders from intertidal fish hosts collected from the Southern Cape coast were stained with Giemsa in attempts to preserve them. These smears were fixed in absolute methanol for 10 minutes and stained with Giemsa's stain (diluted 9:1 with a phosphate buffer of pH 7) for another 10 minutes.

Measurement of spores

All of the spores were measured according to the guidelines provided by Lom and Arthur (1989) (Fig. 4.6). Measurement of live spores is required when working with myxosporeans. This was, however, not always possible. Subsequently it is stated in the text of species descriptions whether the spore measurements were obtained from live or fixed samples.

According to Lom and Arthur (1989) for spores with polar capsules situated at one end, that is, at the anterior end or apex, the length is the distance from the apex to the posterior or opposite end. In Bipolaria, the length is the distance between the opposite ends of the spore. Spore width is measured perpendicular to the length, in the plane of the suture. Minimum and maximum values of spore measurements are provided in micrometers (μm), followed in parentheses by the arithmetic mean and standard deviation.

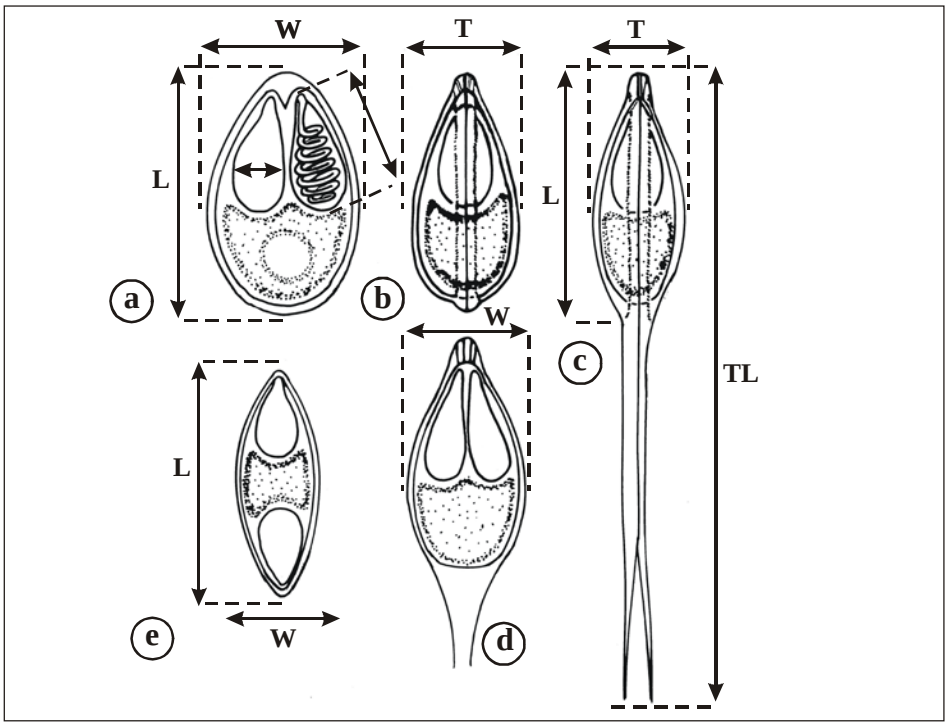


Figure 4.6. Diagram illustrating the measurement of myxosporean spores as stipulated by Lom and Arthur (1989). **a, b.** *Myxobolus* Bütschli, 1882 in frontal (a), and sutural (b) or side (b). **c, d**. *Henneguya* Thélohan, 1892 in frontal and side view. **e**. *Myxidium* Bütschli, 1882 in frontal view. Measurement of the polar capsules is indicated in (a). **L**-length of the spores, **T**-thickness of spore, **W**-width of spore. In spores with caudal appendages such as *Henneguya*, **TL**-total length of spore. Redrawn and simplified from Lom and Arthur (1989).

Preparation of material

Photo microscopy

Live and formalin-fixed spores were photographed using a Zeiss Axiophot microscope with differential interference contrast on a layer of 0.5% non-nutrient agar at a magnification of 63X using oil immersion at the laboratory in the Department of Zoology and Entomology at the University of the Free State, Bloemfontein.

Histology

Tissue samples, approximately 1cm³, of all the fish organs were fixed using Davidson's Solution for the purpose of histological sectioning. Tissue samples collected were initially processed at the Department of Anatomical Pathology, Faculty of Medicine, University of the Free State, Bloemfontein, South Africa. Subsequently processing was conducted at the Institute of Parasitology, Ceske Budejovice, Czech Republic by Prof. Iva Dyková. Much of the histological processing also took place at the histology laboratory of Kingston University, Kingston-upon-Thames, London, UK. The methods used at the

various institutes were all standard procedures, so for the purpose of this study, the method used at Kingston University will be described.

Small tissue samples of $1cm^3$ were pre-fixed in a solution of acetic acid (1):(9) Davidson's Solution (Table 4.2) for 24 hours. The samples were transferred to stock solution of Davidson's Solution.

Table. 4.2. The components of Davidson's Solution

Chemical	Proportion
96% Ethanol (EtOH)	3 parts
40% Formaldehyde conc.	2 parts
Glycerol	1 part
Water (Tap/ Sea /Distilled)	3 parts

Fixed tissue samples were processed for wax imbedding using a Shandon Elliot Processor. This process involved removing the tissue samples from the stock of Davidson's stock solution and washing it four times with 70% Industrial Methylated Spirits (IMS). The samples were then dehydrated through a series of IMS concentrations (Table 4.3). Once fully dehydrated, the tissue samples were transferred to a clearing solution of Histoclear (National Diagnostics) for a total time of 4 hours and subsequently transferred to melted wax solution for another four hours (Table 4.3).

Table 4.3. Steps in the dehydration and embedding of tissue samples into wax.

Step	Duration
70% IMS	2 hours
80% IMS	2 hours
95% IMS	2 hours
100% IMS	2 hours
100% IMS	2 hours
Histoclear	2 hours
Histoclear	2 hours
Wax	2 hours
Wax	2 hours

The tissue samples were embedded in wax moulds using a Shannon Histocentre and sections were made at 5 to 6 µm thick using a Shannon Hypercut Microtome. The sections were stretched on a water bath and mounted on glass microscope slides and left to dry on a drying rack.

Haematoxylin and Eosin staining

Prior to staining, the sections were transferred to a 50^0C oven for a period of 24 hours. Sections were then stained using Haematoxylin and Eosin. The protocol for this method is illustrated in Table 4.4.

Table 4.4. Procedure for Haematoxylin and Eosin staining.

Procedure	Duration
Dewax in Histoclear	7 minutes
Hydrate through alcohol series (100%, 95%, 70%, tap water)	2 minutes at a time
Stain in Erlich's Haematoxylin	10 minutes
Blue in tap water	Rinse
Differentiate in acid alcohol	Dip
Re-blue in tap water	5 minutes
Dehydrate to 70% Ethanol	2 minutes
Counterstain in alcoholic eosin	3 minutes
Dehydrate through 95%, 100% ethanol	2 minutes
Clear in Histoclear	5 minutes
Mount on microscope slide using a coverslip and Histomount	

Masson's Trichome Staining

Some sections were also stained using Masson's Trichome. This stain demonstrates the presence of significant connective tissue growth amongst other things. The procedure for this is illustrated in Table 4.5.

Table 4.5. Procedure for Masson's Trichome staining.

Procedure	Duration
Histoclear	5 minutes
Absolute alcohol	2 minutes
90% alcohol	1 minute
70% alcohol	1 minute
Distilled water	Rinse
Weigerts iron haematoxylin	5 minutes
Wash in running tap water	15 minutes
1% ponceau 2R in 1% acetic acid	Dip
Distilled water	Rinse
Differentiate in 1% phosphomolybdic acid	4 minutes
Distilled water	Rinse
Counterstain in 2% aniline blue	2 minutes
Distilled water	Rinse
Wash well in acetic acid	1 minute, blot excess
Absolute alcohol	5 minutes
Histoclear	5 minutes
Mount on microscope slide using a coverslip and Histomount	

Reference material

All reference material, in the form of spores, fixed in 10% buffered neutral formalin, have been deposited in the parasite collection of the Department of Zoology and Entomology, University of the Free State, Bloemfontein, South Africa where it has been allocated a reference number. Type material will be deposited in the collection of the National Museum, Bloemfontein (South Africa) where it will be allocated a NMBP number indicating its place in the National Museum, Bloemfonteins' Parasite collection.

Scanning Electron Microscopy (SEM)

Myxosporean spores fixed in 10 % buffered neutral formalin for the purpose of scanning electron microscopy were prepared on two different media. The spores were initially filtered onto 0.5µm Nucleopore filters, before dehydration. The background of the images was, however, spoiled due to the visibility of the pores in the filter itself. The spores were then adhered to small coverslips by means of Polylysin adhesive (Sigma). This method provided a more uniform background and was done as follows: a drop of undiluted Polylysin was applied to a clean coverslip and given a few moments to dry. A drop of spores was placed on the surface of the coverslip containing the Polylysin and allowed to settle to the surface of the coverslip for 5 minutes.

Once attached to the adhesive medium on the coverslip, the spores were first rinsed in tap water and then dehydrated through a series of ethanol concentrations (30%, 50%, 70%, 80%, 90%, and 96% - 10 minutes each and twice in 100% for 10 minutes each time). The spores were critically point dried in a Biorad Critical Point Dryer, coated with gold in an EMScope SC500 sputter coater and viewed using a Jeol Winsem JSM 6400 at 5 or 10kV.

Transmission electron microscopy (TEM)

Some spore samples were prepared for transmission electron microscopy at the Department of Anatomical Pathology, Faculty of Medicine, University of the Free State, The Institute of Parasitology, Ceske Budejovice, Czech Republic as well as in the Electron Microscope Unit of Kingston University, Kingston-upon-Thames, London, United Kingdom. The method applied at Kingston University was as follows:

Tissues containing sporogonic plasmodia were primarily fixed in 2.5% cacodylate buffered glutaraldehyde, stored in a holding buffer and post-fixed with 1% OsO_4. The

osmium tetroxide solution was removed from tissue samples and replaced with 30% ethanol for approximately 15 minutes. The 30% ethanol was then replaced with fresh 30% ethanol and left for 1 hour and subsequent dehydration continued using a series of IMS concentrations (50%, 70%, 90%) for 15 minutes each. The samples were rinsed in 100% IMS thrice for 15 minutes at a time.

Once the series of dehydration steps had been completed, the samples were placed in propylene oxide (an intermediary-clearing agent) for 15 minutes. This step was repeated three times. The next step involved infiltration of tissues with the embedding agent. The samples were placed in a 3:1 solution of Epoxy Resin mixture (3) and Propylene oxide (1) and were left over night. New resin was mixed the next morning and the tissues transferred to this after which they were placed in the beam capsules and left overnight. This time was sufficient for polymerisation of the blocks.

Semi-thin sections were cut at 2-3µm using a LKB III Ultramicrotome. The sections were stained with 1 % toluidine blue in 1 % borax and viewed under a compound microscope in order to determine the region that needed to be sectioned. Ultra-thin sections were cut at 40 – 70nm and placed on copper grids, dried on filter paper and stored. The copper grids containing the sections were stained using the following method:

Six drops of 5% uranyl acetate in alcohol were placed onto a dental wax surface on the interior of a Petri dish with a lid. The grids were inverted and placed on the drops of stain for 20 minutes and removed and rinsed under a stream of running distilled water. Excess water was removed from the grids by using a small piece of filter paper.

A second Petri dish was prepared containing dental wax and a few pellets of pure sodium hydroxide. Approximately 6 drops of Reynolds' lead citrate were placed on the wax. The grids were once again inverted onto the drops of lead citrate and left for approximately 5 minutes, after which they were removed and washed under a stream of 0.02M sodium hydroxide solution followed by a wash in a stream of distilled water. These grids containing the sections were dried using small pieces of filter paper and stored in grid boxes until viewed using a Philips 301 transmission electron microscope at 60 kV.

5. Diversity of fish-infecting Myxosporeans in the Okavango River and Delta, Botswana

The Okavango Delta is situated in northwestern Botswana in the middle of the Kalahari Desert (Fig. 5.1a). This vast swampland forms part of the Kalahari Basin, which is a large internal drainage system that terminates in the Makgadikgadi Pans. The Delta itself occurs where the Okavango River flows into a collapsed section of the Earth's crust, this being the southern most extension of the East African Rift Valley System. The collapse has taken place between several sets of fault lines, the Gomare Fault in the north and the Kunyere and Thamalakane Faults in the south (see Fig. 4.1, Chapter 4). This area is still prone to earthquakes, indicating that the subsistence is still taking place (Ellery and Ellery 1997).

The Okavango River, which rises in the Benguela Plateau in the Angolan Highlands, is the third largest river in southern Africa and the largest in the world that does not flow into the sea (Balfour 1996). It originates as two tributaries, the Cuito and the Cubango that eventually join to form the mighty Okavango (see Fig. 4.1, Chapter 4). Soon after crossing the Namibian border at Mohembo (Fig. 5.1b), the river meanders its way through the Panhandle (Fig. 5.1c), which is a narrow strip of wetland approximately 100 kilometers long. In the Panhandle, the river itself is more than a kilometer wide at some places and flows alternately through acres of papyrus floating on its own root systems or beneath towering wild fig and ebony trees that offer shade on the high river banks (Balfour 1996) (Figs. 5.1d, e). Once the river flows over the Gomare fault, it spreads out and takes on the appearance of a delta, splitting into a web of channels and islands (Bailey 1998) (Fig. 5.1f).

The entire Okavango Delta is a dynamic ecosystem that is driven by an annual flood, which takes about six months to flow the distance of around 250 km as the crow flies from Mohembo to Maun in the south. It can be divided into two distinct parts. The permanent or perennial delta, which retains water all year round and the seasonal delta, which, apart from its main channels, is grassland area for most of the year, until the annual flood inundates the region to transform it briefly to a lush wetland (Bailey 1998). The annual floods increase the drainage area of the Okavango Delta from 6000 to 8000

km² during the dry season to approximately 16 000 km² during the flood season (Ross 2003).

In Botswana there are more than 25 000 people living near the Okavango Delta itself, who are all heavily dependant on the water and other natural resources such as the abundant fish populations. The fishes in the Okavango Delta thus represent an incredibly valuable natural resource for the people living in and around the area (Figs. 5.1g, h, i). The Okavango River and Delta contain distinct fish communities that are separated from each other by the physical characteristics of the many different habitats in which they co-evolved (Merron 1991) (see Fig. 4.2, Chapter 4). The fish population of the Okavango Delta comprises 68 species of which 23 are endemic to the Okavango and upper Zambezi River system (Skelton 2001). To date the Okavango has not been exposed to any introductions or translocations of fishes (Basson and Van As 2002).

This chapter presents an expansion and continuation of the research conducted by Reed (2000) and aims to report on all myxosporean parasites found infecting fishes in the Okavango River and Delta from the period 1997 to 2001. The results and other information from Reed (2000) are summarised in this chapter to ensure a complete overview of the distribution records and infestation levels of all the myxosporean species collected from 1997 to 2001. Information collected in 1997, 2000 and 2001 is presented in this thesis for the first time. Also included are some additional data from 1998 and 1999 that did not form part of Reed (2000).

Following this brief introduction will be a review of myxosporean research conducted to date in the Okavango River and Delta, Botswana. This will be followed by the results of the present study, which includes the description of two new myxosporean species. Following the species descriptions will be a section discussing miscellaneous myxosporean species recorded from 1997-2001, even if they were merely observations or if insufficient material made complete species descriptions impossible.

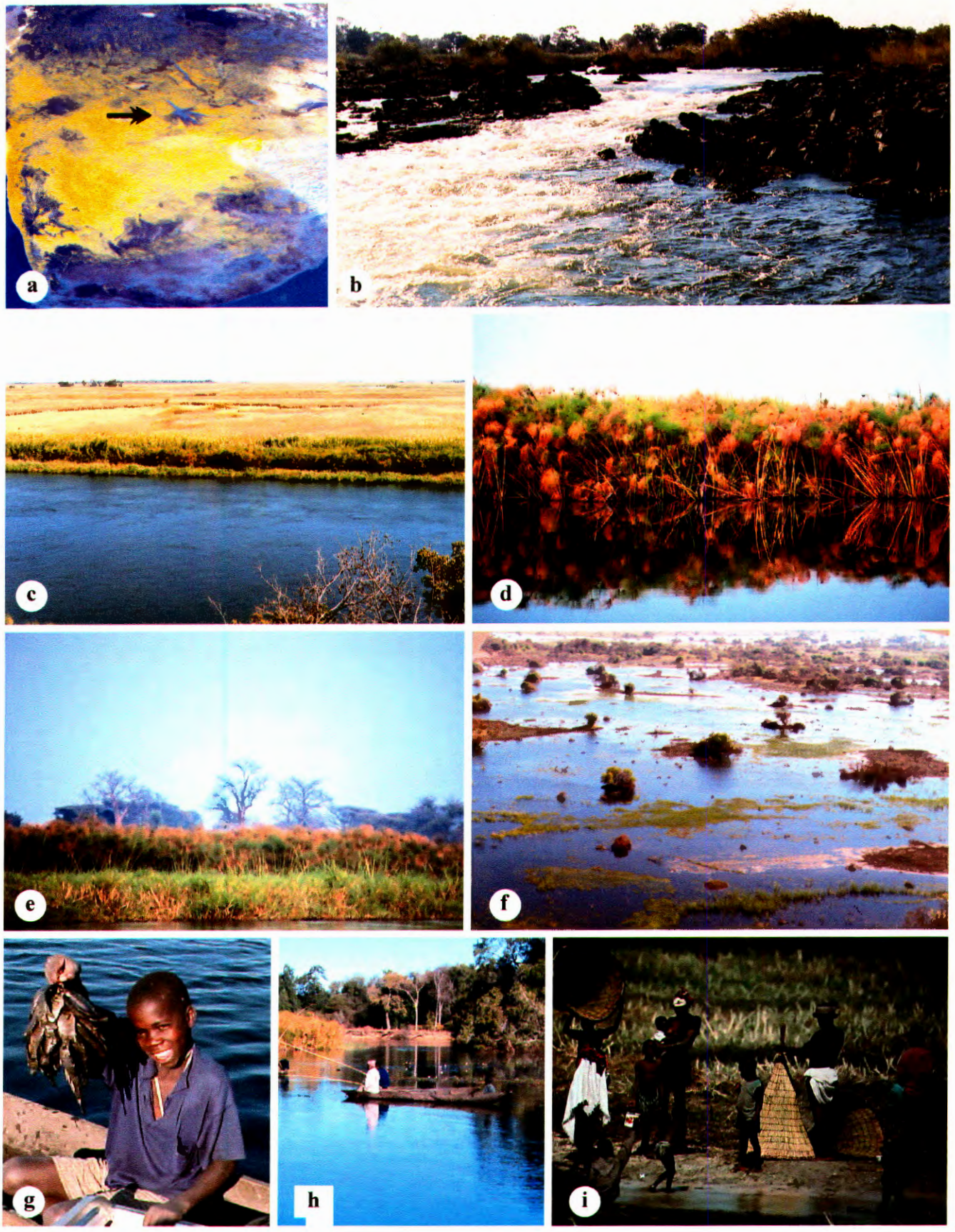


Figure 5.1. **a.** Okavango River and Delta (arrow), Botswana from space (NORAD satellite image, CSIR). **b.** Okavango River at Mohembo. **c.** View of the Panhandle showing the mainstream and floating papyrus. **d.** Floating beds of papyrus. **e.** Okavango River bank in the Panhandle. **f.** Aerial view of the Okavango Delta, after passing over the Gomare Fault. **g-i.** Local fishermen and women.

The chapter will be concluded with a discussion of the results obtained to date. This will include discussion of the prevalence and infestation data of all the Okavango fishes found infected with myxosporeans from 1997 to 2001 and will also include some discussion on the biodiversity, host specificity, pathology and distribution of these Okavango myxosporeans.

Review

The very first results of myxosporean research conducted in the Okavango River and Delta were presented in Reed (2000). The results of this dissertation were based on surveys conducted in the Okavango during June and July 1998 and 1999. During that time, a total of 275 fishes belonging to 31 species from nine different families were examined for myxosporean parasites. Five myxosporeans from the genus *Henneguya* were collected from four different fish hosts of which only one was identified as a known species, *Henneguya branchialis*. As mentioned in Chapter 3, this species has subsequently been recognised as a synonym of *H. suprabranchiae*. A comprehensive morphological description of the four unknown species was also provided in the dissertation. Furthermore, eight myxosporeans from the genus *Myxobolus* were found infecting nine different fish hosts, of which four were identified as known species and described. Once again, detailed descriptions of the four unknown species were provided in the dissertation. It was also found that some fish species showed very high gill infections of these parasites, which might have caused some form of respiratory deficiency. The results obtained from this MSc. study provided new insight into the occurrence of myxosporeans in Botswana and also re-initiated the study of these fish parasites in southern Africa.

Subsequent to Reed (2000) two consecutive papers were published on the results of this dissertation (see Appendix I). Reed *et al.* (2002b) recorded the presence of seven myxosporeans from the genus *Myxobolus* infecting the Okavango fishes. Two species, namely *M. etsatsaensis* Reed, Basson and Van As, 2002 and *M. paludinosus* Reed, Basson and Van As, 2002 infecting the gills of *Barbus thamalakanensis* Fowler, 1953 and *B. paludinosus* respectively, were the first new myxosporean species to be described from the Okavango River and Delta. In the second paper, Reed *et al.* (2003a) described the myxosporeans found infecting the sharptooth catfish, *Clarias gariepinus*. In this paper *Henneguya suprabranchiae* was recorded for the first time in southern Africa.

Henneguya samochimensis Reed, Basson and Van As, 2003 and *Myxobolus gariepinus* Reed, Basson and Van As, 2003 were described as new species from the gills and ovaries, respectively, of *C. gariepinus*.

A third paper has been prepared for publication (Reed, Basson and Van As, in prep.). In this paper, two new species of the genus *Henneguya* from the Okavango Delta are described. *Henneguya macrolepidotus* and *H. xarensis* are described from the gills of *Marcusenius macrolepidotus* (Peters, 1852) and *Schilbe intermedius* Rüppell 1832, respectively. Therefore, to date, twelve myxosporean species have been recorded from fishes in the Okavango Delta in Botswana, six of which were originally described from Okavango fishes (Table 5.1).

Table 5.1. Fish-infecting myxosporeans from the Okavango Delta in Botswana.

Myxosporean	Host	Organ	Reference
Henneguya macrolepidotus Reed, Basson and Van As (in prep)	*Marcusenius macrolepidotus* (Peters, 1852)	Gills	Reed, Basson and Van As (in prep)
Henneguya samochimensis Reed, Basson and Van As, 2003	*Clarias gariepinus* (Burchell, 1822)	Gills	Reed, Basson and Van As (2003a)
Henneguya suprabranchiae Landsberg, 1987	*Clarias gariepinus* (Burchell, 1822)	Gills	Reed, Basson and Van As (2003a)
Henneguya xarensis Reed, Basson and Van As (in prep)	*Schilbe intermedius* Rüppell, 1832	Gills	Reed, Basson and Van As (in prep)
Myxobolus africanus Fomena, Bouix and Birgi, 1985	*Hepsetus odoe* (Bloch, 1749)	Gills, fins	Reed, Basson and Van As (2002b)
Myxobolus camerounensis Fomena, Marques and Bouix, 1993	*Oreochromis andersonii* (Castelnau, 1861); *Tilapia ruweti* (Poll and Thys van den Audenaerde, 1965)	Gill arch, buccal cavity	Reed, Basson and Van As (2002b)
Myxobolus etsatstaensis Reed, Basson and Van As, 2002	*Barbus thamalakanensis* Fowler, 1953	Gills	Reed, Basson and Van As (2002b)
Myxobolus gariepinus Reed, Basson and Van As, 2003	*Clarias gariepinus* (Burchell, 1822)	Ovaries	Reed, Basson and Van As (2003a)
Myxobolus hydrocyni Kostoïngue and Toguebaye, 1994	*Hydrocynus vittatus* (Castelnau, 1861)	Gill operculum and gill arch	Reed, Basson and Van As (2002b)
Myxobolus nyongana (Fomena, Bouix and Birgi, 1985)	*Barbus poechii* Steindachner, 1911	Gills	Reed, Basson and Van As (2002b)
Myxobolus paludinosus Reed, Basson and Van As, 2002	*Barbus paludinosus* Peters, 1852	Gills	Reed, Basson and Van As (2002b)
Myxobolus cf. *tilapiae* Abolarin, 1971	*Tilapia rendalli* (Boulenger, 1896)	Buccal cavity	Reed, Basson and Van As (2002b)

Results

During the course of several field trips to the Okavango River and Delta from 1997 to 2001 a total of 2858 fishes representing 14 families and 65 species were examined for all parasites, including myxosporeans. Results revealed the presence of 29 different fish-infecting myxosporean species collected from 26 fish species during this period (Table 5.2). The results represented here include all records of any myxosporean infections observed from 1997 to 2001. Also included are the results of 275 fishes representing 31 species from nine families that were examined by Reed (2000) during 1998 and 1999.

Table 5.2. Results of fishes examined for myxosporean infections during 1997, June/July 1998, 1999 and 2000 and August 2001 from the Okavango River and Delta, in Botswana. [Key: **Inf**- Number of hosts infected; **L**-Collection localities; **M**-Myxosporean species; **N**- Total number of fish examined; **O**-Organs of fish hosts infected; **P**- Prevalence (%); **S**- Mean size and size range of fish hosts (mm); **Y** –Years sampled; × - not infected].

Fish host	N	S	Inf	P (%)	O	M	Y	L
Mormyridae								
Mormyrus lacerda Castelnau, 1861	24	320 (105-420)	3	13	Gills	*Henneguya* sp. A	1997, 2000, 2001	Samochima lagoon
Marcusenius macrolepidotis (Peters, 1852)	103	177 (60-276	31	30	Gills	*Henneguya macrolepidotus* sp. n..	1997 - 2001	Duba lagoon, Guma lagoon, Mokoro lagoon Samochima lagoon, Thoage lagoon, Tim's channel
Petrocephalus catostoma (Günther, 1866)	39	50 (30-100)	×	×	×	×	×	×
Pollimyrus castelnaui (Boulenger, 1911)	28	48 (31-62)	×	×	×	×	×	×
Cyprinidae								
Barbus afrovernayi Nichols and Boulton, 1927	92	32 (19-56)	8	9	Gills, skin	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)	1999-2001	Etsatsa mainstream, Nxameseri, Shakawe backwaters, Tim's channel
Barbus barnardi Jubb, 1965	82	31 (20-47)	10	12	Gills, skin	*Myxobolus nongana* (Fomena, Bouix and Birgi, 1985)	1997, 1999, 2000, 2001	Little Duba, Mohembo floodplains, Observation Island, Picnic lagoon, Seronga backwaters, Shakawe backwaters, Tim's channel
Barbus bifrenatus Fowler, 1935	31	35 (20-51)	×	×	×	×	×	×
Barbus eutaenia Boulenger, 1904	7	52 (38-62)	×	×	×	×	×	×
Barbus fasciolatus Günther, 1868	26	36 (20-48)	×	×	×	×	×	×
Barbus haasianus David, 1936	59	26 (17-38)	1	2	Gills, skin	*Myxobolus* sp. 1	2001	Nxameseri
Barbus miolepis Boulenger, 1902	43	53 (20-75)	1	2	Gills	*Myxobolus* sp. 2	2000	Shakawe backwaters
Barbus multilineatus Worthington, 1933	48	28 (21-35)	3	5	Gills	*Myxobolus etsatsaensis* Reed, Basson and Van As, 2002	1999	Etsatsa mainstream
			5	9	Gills, skin	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)	1999, 2001	Etsatsa mainstream, Tim's channel
Barbus paludinosus Peters, 1852	81	46 (24-101)	5	6	Gills	*Myxobolus etsatsaensis* Reed, Basson and Van As, 2002	1999	Etsatsa mainstream, Lechwe island, Little Duba
			9	16	Gills	*Myxobolus paludinosus* Reed, Basson and Van As, 2002	1999, 2001	Etsatsa mainstream, Lechwe island, Shakawe backwaters, Little Duba, Upper Thoage
			1	2	Gills	*Myxobolus* sp. 3		Little Duba
Barbus poechii Steindachner, 1911	51	61 (22-117)	8	15	Gills	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)	1997, 1998, 1999, 2001	Drodsky's backwaters, Etsatsa mainstream, Shakawe backwaters, Xaro mainstream
Barbus radiatus Peters, 1853	44	30 (21-55)	2	5	Gills, skin	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)	2001	Mohembo floodplains, Tim's channel
Barbus thamalakanensis Fowler, 1953	13	28 (20-55)	4	31	Gills	*Myxobolus etsatsaensis* Reed, Basson and Van As, 2002	1998, 1999	Etsatsa mainstream, Nxabega, Pepere backwaters
Barbus unitaeniatus Güther, 1866	1	35	1	100	Skin	*Myxobolus* sp. 4	2000	Boro River
Coptostomabarbus wittei David and Poll, 1937	11	24 (18-32)	1	9	Skin	*Myxobolus* sp. 5	2000	Shakawe backwaters
Labeo lunatus Jubb, 1963	2	270, 323	×	×	×	×	×	×
Mesobola brevianalis (Boulenger, 1908)	1	43	×	×	×	×	×	×
Characidae								
Brycinus lateralis (Boulenger, 1900)	82	87 (40-127)	×	×	×	×	×	×

Table 5.2 continued. Results of fishes examined for myxosporean infections during 1997, June/July 1998, 1999 and 2000 and August 2001 from the Okavango River and Delta, in Botswana. [Key: **Inf**- Number of hosts infected; **L**-Collection localities; **M**-Myxosporean species; **N**- Total number of fish examined; **O**-Organs of fish hosts infected; **P**- Prevalence (%); **S**- Mean size and size range of fish hosts (mm); **Y** –Years sampled; × - not infected].

Fish host	N	S	Inf	P (%)	O	M	Y	L
Hydrocynus vittatus (Castelnau, 1861)	51	320 (100-740)	11	22	Gills	*Myxobolus hydrocyni* Kostoïngue and Toguebaye, 1994	1998 - 2001	Duba lagoon, Mokoro lagoon, Samochima lagoon, Xaro mainstream
Micralestes acutidens (Peters, 1852)	47	49 (13-80)	×	×	×	×	×	×
Rhabdalestes maunensis (Fowler, 1935)	88	43 (26-76)	2	2	Gills, skin	*Myxobolus* sp. 6	2001	Samochima lagoon, Shakawe backwaters
Hepsetidae								
Hepsetus odoe (Bloch, 1794)	95	281 (135-395)	11	12	Gills, skin, fins	*Myxobolus africanus* Fomena, Bouix and Birgi, 1985	1998, 2000	Guma lagoon, Nxaraga, Samochima lagoon
Distichodontidae								
Hemigrammocharax machadoi Poll, 1967	24	27 (23-30)	×	×	×	×	×	×
Hemigrammocharax multifasciatus Boulenger, 1923	27	30 (20-42)	×	×	×	×	×	×
Claroteidae								
Parauchenoglanis ngamensis (Boulenger, 1911)	1	185	×	×	×	×	×	×
Schilbeidae								
Schilbe intermedius Rüppell, 1832	211	192 (32-342)	74	35	Gills	*Henneguya xarensis* sp. n.	1997 - 2001	Duba lagoon, Guma lagoon, Mokoro lagoon, Nxaraga, Pepere lagoon, Picnic lagoon, Samochima lagoon, Upper Thoage
Amphiliidae								
Leptoglanis sp.	12	26 (22-32)	×	×	×	×	×	×
Clariidae								
Clarias gariepinus (Burchell, 1822)	45	465 (40-955)	5	9	Gills	*Henneguya samochimensis* Reed, Basson and Van As, 2003	1998 - 2001	Duba lagoon, Mokoro lagoon, Nxabega permanent swamp, Nxaraga, Tim's channel
			2	4	Acces-sory breathing organ	*Henneguya suprabranchiae* Landsberg, 1987	1999, 2001	Duba lagoon, Mokoro lagoon
			4	7	Ovaries	*Myxobolus gariepinus* Reed, Basson and Van As, 2003	1999, 2001	Duba lagoon, Mokoro lagoon
Clarias stappersii Boulenger, 1915	14	105 (40-485	1	7	Acces-sory breathing organ	*Henneguya suprabranchiae*	2001	Mokoro lagoon
			1	7	Skin	*Myxobolus* sp. 7	2001	Tim's channel
Clarias theodorae Weber, 1897	27	115 (23-237)	1	4	Skin	*Myxobolus* sp. 7	2000	Samochima lagoon
Mochokidae								
Synodontis leopardinus Pellegrin, 1914	1	150	×	×	×	×	×	×
Synodontis macrostigma Boulenger, 1911	4	105, 107, 140, 160	×	×	×	×	×	×
Synodontis macrostoma Skelton and White, 1990	10	48 (38-57)	×	×	×	×	×	×
Synodontis nigromaculatus Boulenger, 1905	48	197 (35-280)	×	×	×	×	×	×
Synodontis thamalakanensis	5	40, 130, 162, 180, 220	×	×	×	×	×	×

Table 5.2 continued. Results of fishes examined for myxosporean infections during 1997, June/July 1998, 1999 and 2000 and August 2001 from the Okavango River and Delta, in Botswana. [Key: **Inf**- Number of hosts infected; **L**-Collection localities; **M**-Myxosporean species; **N**- Total number of fish examined; **O**-Organs of fish hosts infected; **P**- Prevalence (%); **S**- Mean size and size range of fish hosts (mm); **Y** –Years sampled; × - not infected].

Fish host	N	S	Inf	P (%)	O	M	Y	L
Synodontis vanderwaali Skelton and White, 1990	9	183 (160-215)	×	×	×	×	×	×
Synodontis woosnami Boulenger, 1911	14	186 (150-210)	×	×	×	×	×	×
Poeciliidae								
Aplocheilichthys hutereaui (Boulenger, 1913)	241	24 (14-46)	×	×	×	×	×	×
Aplocheilichthys johnstoni (Günther, 1893)	67	30 (16-46)	×	×	×	×	×	×
Aplocheilichthys katangae (Boulenger, 1912)	45	27 (15-70)	×	×	×	×	×	×
Cichlidae								
Oreochromis andersonii (Castelnau, 1861)	82	160 (45-430)	8	10	Gills, skin, buccal cavity	*Myxobolus camerounensis* Fomena, Marques and Bouix, 1993	1998	Mohembo backwaters, Nxameseri, Xaro mainstream
Oreochromis macrochir (Boulenger, 1912)	17	134 (20-329)	1	6	Gills	*Myxobolus camerounensis* Fomena, Marques and Bouix, 1993	2001	Samochima lagoon
Pharyngochromis acuticeps (Steindagner, 1866)	30	89 (24-155)	×	×	×	×	×	×
Pseudocrenilabrus philander (Weber, 1897)	351	29 (14-111)	14	4	Skin	*Myxobolus* sp. 8	1997, 2000, 2001	Boro River, Crocodile island, Mohembo floodplains, Shakawe backwaters, Tim's channel
Sargochromis carlottae (Boulenger, 1905)	18	142 (80-245)	×	×	×	×	×	×
Sargochromis codringtonii (Boulenger, 1908)	5	90, 101, 125, 302, 540	×	×	×	×	×	×
Sargochromis giardi (Pellegrin, 1903)	7	160 (15-340)	×	×	×	×	×	×
Sargochromis greenwoodi (Bell-Cross, 1975)	17	230 (41-450)	×	×	×	×	×	×
Sargochromis mortimeri (Bell-Cross, 1975)	1	60	×	×	×	×	×	×
Serranochromis altus Winemiller and Kelso-winemiller, 1990	3	210, 220, 205	×	×	×	×	×	×
Serranochromis angusticeps (Boulenger, 1907)	23	258 (68-440)	×	×	×	×	×	×
Serranochromis longimanus (Boulenger, 1911)	2	70, 67	×	×	×	×	×	×
Serranochromis macrocephalus (Boulenger, 1899)	16	252 (100-350)	×	×	×	×	×	×
Serranochromis robustus jallae (Günther, 1864)	21	306 (200-410)	×	×	×	×	×	×
Serranochromis thumbergi (Castelnau, 1861)	8	140 (85-270)	×	×	×	×	×	×
Tilapia rendalli (Boulenger, 1896)	71	110 (34-293)	1	1	Gills, skin	*Henneguya* sp. 1	2001	Shakawe backwaters
			5	7	Buccal cavity	*Myxobolus* cf. *tilapiae* Abolarin, 1974	1998, 2001	Shakawe backwaters, Thebe lagoon, Xaro mainstream
Tilapia ruweti (Poll and Thys van den Audenaerde, 1965)	13	55 (18-100)	1	8	Gills	*Myxobolus camerounensis* Fomena, Marques and Bouix, 1993	1999	Etsatsa mainstream
			4	30	Gills	*Myxobolus* sp. 9	1998	Pepere lagoon
Tilapia sparrmanii Smith, 1840	148	59 (15-190)	3	2	Gills	*Myxobolus* sp. A	1998, 2000,	Boro River, Pepere backwaters, Shakawe backwaters

Table 5.2 continued. Results of fishes examined for myxosporean infections during 1997, June/July 1998, 1999 and 2000 and August 2001 from the Okavango River and Delta, in Botswana. [Key: **Inf**- Number of hosts infected; **L**-Collection localities; **M**-Myxosporean species; **N**- Total number of fish examined; **O**-Organs of fish hosts infected; **P**- Prevalence (%); **S**- Mean size and size range of fish hosts (mm); **Y** –Years sampled; × - not infected].

Fish host	N	S	Inf	P (%)	O	M	Y	L
Anabantidae								
Ctenopoma multispine Peters, 1844	21	54 (19-93)	1	5	Gills	*Myxobolus* sp. 10	1998	Guma lagoon
			1	5	Gills	*Myxobolus* sp. 11	1998	Pepere lagoon
			1	5	Gills	*Henneguya* sp. 2	1999	Upper Thoage
Microctenopomae intermedium (Pellegrin, 1920)	33	32 (18-50)	1	3	Gills	*Henneguya* sp. 3	1998	Pepere backwaters
Mastacembelidae								
Aethiomastacembelus frenatus (Boulenger, 1901)	13	67 (16-160)	×	×	×	×	×	×
Aethiomastacembelus vanderwaali (Skelton, 1976)	4	22, 70, 87, 115	×	×	×	×	×	×

Species descriptions

Two new myxosporean species, from the genera *Henneguya* and *Myxobolus* were collected from the gills of *Mormyrus larcerda* Castelnau, 1861 and from underneath the scales of *Tilapia sparrmanii* Smith, 1840, respectively.

Henneguya sp. A

(Figs. 5.2a, d, f, g)

Host: *Mormyrus lacerda* Castelnau, 1861

Site of infection: Gills

Locality: Samochima Lagoon, Okavango Panhandle, Botswana

Total prevalence: 13% (3/24)

Reference material: Deposited in the Aquatic Parasitology Research Group, Department of Zoology and Entomology, University of the Free State, Bloemfonteins' Parasite Collection.

***Description of vegetative stages*:** Many tiny rounded to sub-spherical sporogonic plasmodia were found infecting the primary gill lamellae. They were whitish in colour and measured less than 0.5 mm in diameter.

***Description of spores (based on 20 formalin fixed spores)*:** Mature spores are ovoid in valvular view with the anterior end being rounded and tapering to a blunt point. Two smooth shell valves adhere along a narrow, smooth sutural edge (Fig. 5.2a). The total length of the spores is 32.0 – 36.0 (34.2 ± 1.28) µm, with the spore body measuring 10.0

– 12.0 (11.3 ± 0.6) µm long × 5.0 – 6.0 (5.4 ± 0.4) µm wide. Two filiform and narrow caudal appendages extend from the spore body measuring 21.0 – 24.0 (24.2 ± 0.5) µm in length. Two pyriform-shaped polar capsules are situated in the anterior of the spore extending to at least one third of the spore body, measuring 3.5 – 5.0 (4.3 ± 0.4) µm long × 1.5 – 2.0 (1.8 ± 0.2) µm wide (Figs. 5.2a, d, f, g). Each polar capsule contains a polar filament with 3 – 4 filaments turns.

***Remarks*:** *Henneguya* sp. A does not conform to the description of any known *Henneguya* species. *Henneguya* species in Africa infecting similar hosts include *H. odzai* Fomena and Bouix, 1996, *H. macrolepidotus* Reed, Basson and Van As (in prep.), *H. mormyri* Kostoingue, Diebakate, Faye and Toguebaye, 2001 and *Henneguya nyongensis* Fomena and Boux, 1996. Compared with *H. odzai* described from the gills of *Mormyrus moori* in Cameroon by Fomena and Bouix (1996), *Henneguya* sp. A has a distinctly more pointed anterior, while that of *H. odzai* is almost entirely round. *Henneguya* sp. A differs significantly from *H. macrolepidotus* described from the gills of *Marcusenius macrolepidotus* in Botswana by Reed *et al.* (in prep.) since the spores of *H. macrolepidotus* are very elongated and have a much broader spore body. The spores of *H. mormyri*, described from the gills of *Mormyrus cashive* by Kostoïngue *et al.* (2001), are very similar to those of *Henneguya* sp. A, but the spore body of *H. mormyri* is much more pointed anteriorly with a shorter spore body.

***Myxobolus* sp. A**

(Figs. 5.2b, c, e, h)

Host: *Tilapia sparrmanii* Smith, 1840

Site of infection: Epidermis underneath the scales

Locality: Boro River, Pepere Backwaters, Shakawe, Okavango River and Delta, Botswana.

Total prevalence: 2 % (3/148)

Reference material: Deposited in the Aquatic Parasitology Research Group, Department of Zoology and Entomology, University of the Free State, Bloemfonteins' Parasite Collection.

***Description of vegetative stages*:** Many rounded to sub-spherical sporogonic plasmodia were found in the epidermis underneath the scales. They were whitish in colour and measured approximately 0.5 mm – 3 mm in diameter.

***Description of spores (based on 20 formalin fixed spores)*:** Mature spores are sub-spherical in valvular view with two smooth shell-valves joining along well-defined, narrow, smooth-edged sutural ridge (Fig. 5.2b). The spore dimensions are 10.0 – 13.0 (12.0 ± 0.5) µm long × 10.0 – 11.5 (10.7 ± 0.6) µm wide. A small intercapsular process is visible between the converging anterior polar capsules. Two pyriform-shaped polar capsules are situated in the anterior of the spore extending to past the mid-length of the spore, measuring 5.5 – 7.0 (6.2 ± 0.6) µm long × 3.5 – 5.0 (4.1 ± 0.3) µm wide (Figs. 5.2b, c, e, h). Each polar capsule contains a polar filament with 7 – 8 filaments turns. No mucous envelope or obvious iodinophilous vacuole is visible.

***Remarks*:** *Myxobolus* sp. A does not conform to the description of any of the known *Myxobolus* species. Several *Myxobolus* species have been described from *Tilapia* hosts in Africa (see Chapter 3). *Myxobolus* sp. A is similar to *M. brachysporus* (Baker, 1963) described from the spleen of *Tilapia esculenta* and *T. variabilis* in Lake Victoria by Baker (1963). Although they are similar in shape, the spores of *M. brachysporus* are broader than they are wide and appear generally more compressed than the almost spherical spores of *Myxobolus* sp. A. *Myxobolus* sp. A has a similar almost spherical spore shape and dimensions to that of *M. doussoui* Sakiti, Blanc, Marqués and Bouix, 1991 described from the gills of *Tilapia zilli* in Benin by Sakiti, Blanc, Marqués and Bouix (1991). The major difference between the two species is that *M. doussoui* has two unequally sized polar capsules compared to the two equally sized polar capsules of *Myxobolus* sp. A. *Myxobolus* sp. A strongly resembles *M. nilei* (Faisal and Shalaby, 1987) described from *Oreochromis niloticus* in Egypt by Faisal and Shalaby (1987). The spores of *M. nilei* are, however, much narrower and have much larger polar capsules than those of *Myxobolus* sp. A.

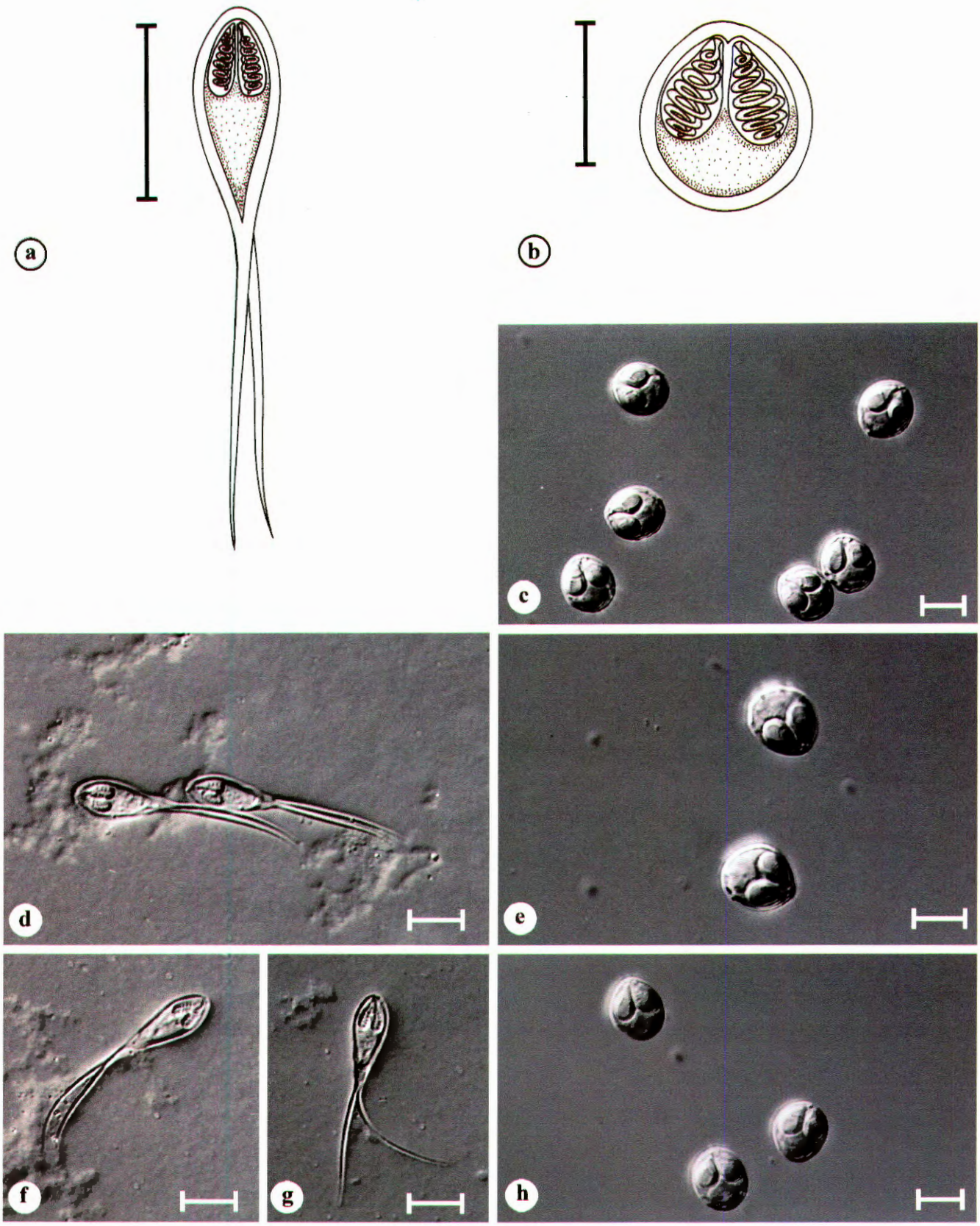


Figure 5.2. Line drawings (**a, b**) and light micrographs of formalin fixed spores (**c-h**) of *Henneguya* Thélohan, 1892 sp. A. (**a, d, f, g**) from the gills of *Mormyrus lacerda* Castelnau, 1861 and *Myxobolus* Bütschli, 1882 sp. A. (**b, c, e, h**) from underneath the scales of *Tilapia sparrmanii* Smith, 1840, both collected from the Okavango River and Delta, Botswana. Scale bars 10μm.

Miscellaneous Okavango myxosporeans

Several records of myxosporean species were recorded from silver nitrate impregnated material or live observations, all of which did not provide sufficient material for complete species descriptions. It is important to note the presence of these infections for the purpose of future research and to ensure that material is gathered to complete these species descriptions.

***Henneguya* sp. 1**

Host: Tilapia rendalli (Boulenger, 1896).

Site of infection: Buccal cavity.

Localities: Mohembo Floodplains, Shakawe Backwaters, Thebe Lagoon, Xaro, Okavango River and Delta, Botswana.

Total prevalence: 1.4% (1/71).

Remarks: Henneguya sp. 1 was recorded from the buccal cavity of *Tilapia rendalli* (Boulenger, 1896) in Reed (2000) and described as *Henneguya* sp. B. This species has not been seen since and currently there is insufficient material to complete the description. The spores, as described by Reed (2000) have a rounded spore body that is extended by two very short and stout caudal appendages (Fig. 5.3a). The polar capsules contain polar filaments with approximately six coils.

***Henneguya* sp. 2**

Host: Ctenopomae multispine Peters, 1844.

Site of infection: Gills.

Localities: Upper Thoage, Okavango River and Delta, Botswana.

Total prevalence: 5% (1/21).

Remarks: Henneguya sp. 2 was recorded from the gills of *Ctenopomae multispine* Peters, 1844. The spores of this species have an elongated and oblong spore body, which is extended by two short caudal appendages. The polar capsules are also slender, ovoid and narrow (Fig. 5.3b).

***Henneguya* sp. 3**

Host: Microctenopomae intermedium (Pellegrin, 1920).

Site of infection: Gills.

Localities: Pepere Backwaters, Okavango River and Delta, Botswana.

Total prevalence: 3% (1/33).

Remarks: Henneguya sp. 3 was recorded from the gills of *Microctenopomae intermedium* (Pellegrin, 1920). The spores of this species have characteristically ovoid to elongated spore bodies and two short and thin caudal appendages (Fig. 5.3c).

***Myxobolus* sp. 1**

Host: Barbus haasianus David, 1936.

Site of infection: Gills and skin.

Localities: Nxameseri, Okavango River and Delta, Botswana.

Total prevalence: 2% (1/60).

Remarks: Myxobolus sp. 1 was recorded from the gills and skin of a single *Barbus haasianus* David, 1936. This infection was merely a visual observation in the field and no material of this species was collected.

***Myxobolus* sp. 2**

Host: Barbus miolepis Boulenger, 1902.

Site of infection: Gills.

Localities: Shakawe Backwaters, Okavango River and Delta, Botswana.

Total prevalence: 2% (1/43).

Remarks: Myxobolus sp. 2 was recorded from a histological section through the gills of *Barbus miolepis* Boulenger, 1902. This section shows a small plasmodium packed full of spores from the genus *Myxobolus* (Fig. 5.8a).

***Myxobolus* sp. 3**

Host: Barbus paludinosus Peters, 1852.

Site of infection: Gills.

Localities: Little Duba, Okavango River and Delta, Botswana.

Total prevalence: 1.2% (1/81).

Remarks: Myxobolus sp. 3 was recorded from the gills of *Barbus paludinosus*. The spores of this species are large and pyriform in shape with two large pyriform-shaped polar capsules situated in the anterior end of the spore (Fig. 5.3d).

***Myxobolus* sp. 4**

Host: Barbus unitaeniatus Günther, 1866.

Site of infection: Skin.

Localities: Boro River, Okavango River and Delta, Botswana.

Total prevalence: 100% (1/1).

Remarks: Myxobolus sp. 4 was recorded from the skin smear of a single *Barbus unitaeniatus* Günther, 1866. No material of this species was collected.

***Myxobolus* sp. 5**

Host: Coptostomabarbus wittei David and Poll, 1937.

Site of infection: Gills.

Localities: Shakawe Backwaters, Okavango River and Delta, Botswana.

Total prevalence: 9% (1/11).

Remarks: Myxobolus sp. 5 was recorded on several occasions from the gills of *Coptostomabarbus wittei* David and Poll, 1937. No material of this species was collected.

***Myxobolus* sp. 6**

Host: Rhabdalestes maunensis (Fowler, 1935).

Site of infection: Gills and skin.

Localities: Shakawe Backwaters, Okavango River and Delta, Botswana.

Total prevalence: 2.2% (2/88).

Remarks: Myxobolus sp. 6 is another unidentified *Myxobolus* species that was recorded from the gills and skin of *Rhabdalestes maunensis* (Fowler, 1935). These records were merely noted and no material of this species was collected.

***Myxobolus* sp. 7**

Host: Clarias stappersii Boulenger, 1915 and *C. theodorae* Weber, 1897.

Site of infection: Skin.

Localities: Shakawe Backwaters, Okavango River and Delta, Botswana.

Total prevalence: 7% (1/15) for *C. stappersii* and 4% (1/27) for *C. theodorae*.

Remarks: Myxobolus sp. 7 was recorded from the skin of *Clarias stappersii* Boulenger, 1915 and *C. theodorae* Weber, 1897. The spores of this species are ovoid in shape with

two pyriform shaped polar capsules situated within the anterior end of the spores (Fig. 5.3e).

***Myxobolus* sp. 8**

Host: Pseudocrenilabrus philander (Weber, 1897).

Site of infection: Skin.

Localities: Mohembo Floodplains, Okavango River and Delta, Botswana.

Total prevalence: 4% (14/351).

Remarks: Myxobolus sp. 8 was recorded from the skin of *Pseudocrenilabrus philander* (Weber, 1897). The spores of this myxosporean are broadly rounded with two rounded polar capsules situated in the anterior of the spore (Fig. 5.3f).

***Myxobolus* sp. 9**

Host: Tilapia ruweti (Poll and Thys van den Audenaerde, 1965).

Site of infection: Gills.

Localities: Pepere Lagoon, Okavango River and Delta, Botswana.

Total prevalence: 30% (4/13).

Remarks: Myxobolus sp. 9 was recorded from the gills of *Tilapia ruweti* (Poll and Thys van den Audenaerde, 1965). The spores of this *Myxobolus* species are almost spherical and small, approximately 10 µm in length (Fig. 5.3g). Two pyriform shaped polar capsules are situated in the anterior end of the spores with four to five coils per polar filament.

***Myxobolus* sp. 10**

Host: Ctenopomae multispine Peters, 1844.

Site of infection: Gills.

Localities: Guma Floodplains, Okavango River and Delta, Botswana.

Total prevalence: 5% (1/21).

Remarks: Myxobolus sp. 10 was recorded from the gills of *Ctenopomae multispine*. The spores of this species have sharply pointed anterior ends with elongated and thin polar capsules (Fig. 5.3h).

***Myxobolus* sp. 11**

Host: Ctenopomae multispine Peters, 1844.

Site of infection: Gills.

Localities: Pepere Backwaters, Okavango River and Delta, Botswana.

Total prevalence: 5% (1/21).

Remarks: Myxobolus sp. 11 was also recorded from *C. multispine*. The spores of this myxosporean species are ovoid in shape with narrow elongated polar capsules in the anterior ends of the spores (Figs. 5.3i, j).

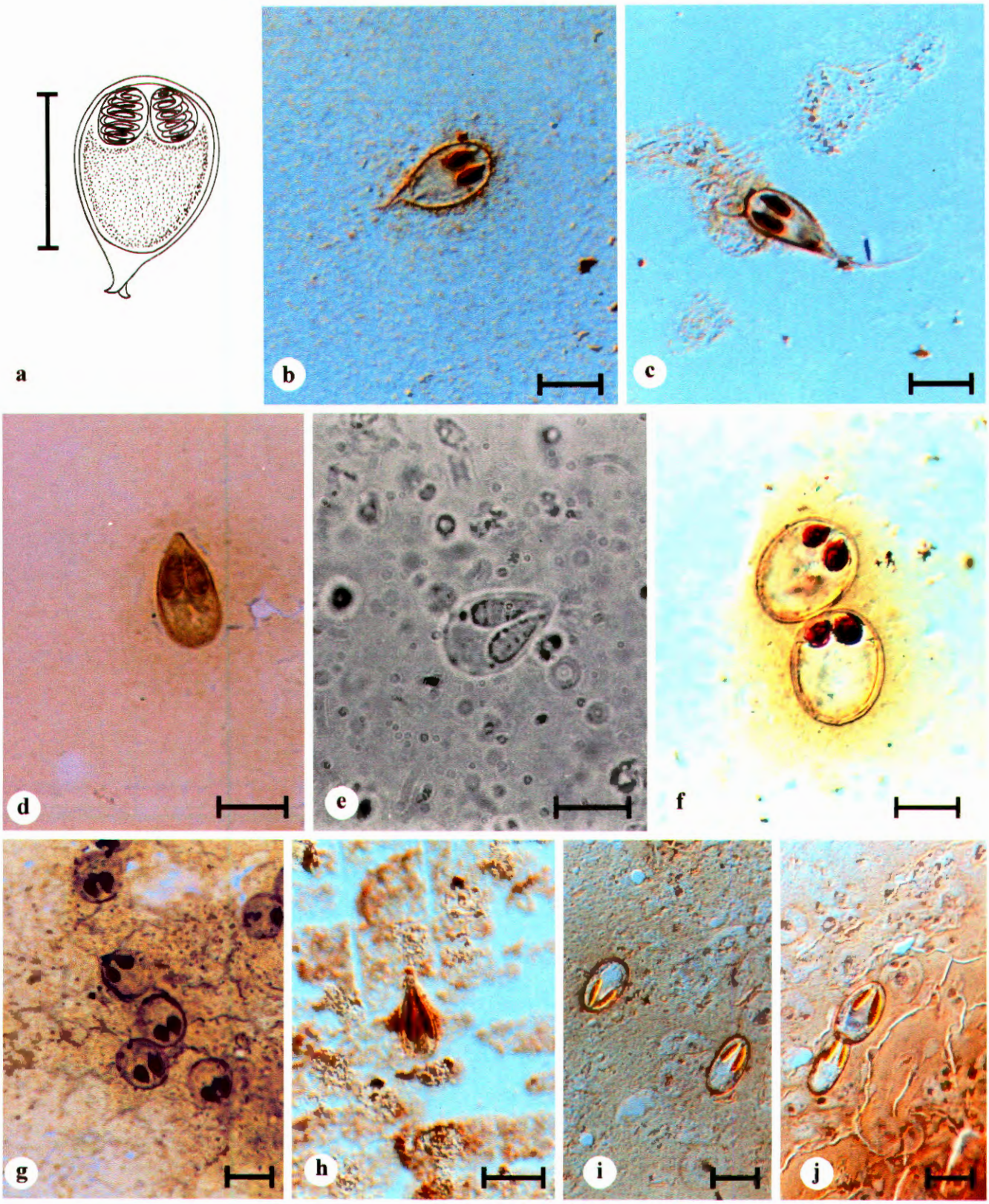


Figure 5.3. Line drawing (**a**) and light micrographs of silver impregnated (**b-d, f-j**) and live (**e**) spores of miscellaneous myxosporeans from the Okavango River and Delta, Botswana. **a.** *Henneguya* Thélohan, 1892 sp. 1. from the buccal cavity of *Tilapia rendalli* (Boulenger, 1896) [Redrawn from Reed (2000)]. **b**. *Henneguya* sp. 2 from the gills of *Ctenopomae multispine* Peters, 1844. **c**. *Henneguya* sp. 3 from the gills of *Microctenopomae intermedium* (Pellegrin, 1920). **d**. *Myxobolus* Bütschli, 1882 sp. 3 from the gills of *Barbus paludinosus* Peters, 1852. **e**. *Myxobolus* sp. 7 from the skin of *Clarias stappersii* Boulenger, 1915. **f.** *Myxobolus* sp. 8 from the gills of *Pseudocrenilabrus philander* (Weber, 1897). **g**. *Myxobolus* sp. 9 from the gills of *Tilapia ruweti* (Poll and Thys van den Aedeunaerde, 1965). **h**. *Myxobolus* sp. 10 from the gills of *Ctenopomae multispine* Peters, 1844. **i, j**. *Myxobolus* sp.11 from the gills of *C. multispine*. Scale bars 10µm.

Discussion

The data collected by examining 2858 fish hosts in the Okavango River and Delta has revealed the existence of 29 different myxosporean species infecting 26 different fish hosts. This large data set allows for the opportunity to examine relationships between the myxosporeans and their fish hosts. The specific results and relationships will be discussed below in order of fish families and will include a summary of distribution and infection prevalences for each of the myxosporeans associated with the fish species.

Family Mormyridae

The family Mormyridae represents a unique group of fishes with soft bodies and a snout that is often extended into a proboscis. Mormyrids are unique fishes and have a relatively large brain, comparable, relative to body weight, to that of humans, and, furthermore, they can also send and receive weak electrical currents (Skelton 2001). The family includes 18 genera and 200 species distributed throughout tropical Africa, including the Nile (Skelton 2001). Six mormyrid species are known from the Okavango Delta in Botswana. In Africa six myxosporeans have been described from mormyrid hosts in Chad and Cameroon (Table 5.3). Of these, four were described from the genus *Henneguya* and one each from the genera *Myxidium* and *Sphaerospora* Thélohan, 1892 respectively. All the *Henneguya* species described from mormyrid hosts in Africa are morphologically similar and have spores with a characteristically rounded anterior and extended spore body (see Chapter 7).

Table 5.3. Myxosporeans infecting mormyrid hosts in Africa.

Host	Myxosporean	Organ	Country	Reference
Henneguya mailaoensis Kostoïngue, Diebakate, Faye and Toguebaye, 2001	*Mormyrus cashive*	Gills	Chad	Kostoïngue, Diebakate, Faye and Toguebaye (2001)
Henneguya mormyri Kostoïngue, Diebakate, Faye and Toguebaye, 2001	*Mormyrus cashive*	Gills	Chad	Kostoïngue, Diebakate, Faye and Toguebaye (2001)
Henneguya nyongensis Fomena and Bouix, 1996	*Marcusenius moori*	Gills, muscles	Cameroon	Fomena and Bouix (1996)
Henneguya odzai Fomena and Bouix, 1996	*Marcusenius moori*	Gills	Cameroon	Fomena and Bouix (1996)
Myxidium petrocephali Fomena and Bouix, 1986	*Petrocephalus simus*	Gall bladder	Cameroon	Fomena and Bouix (1986)
Sphaerospora sangmelimaensis Fomena and Bouix, 1994	*Petrocephalis simus*	Kidneys	Cameroon	Fomena and Bouix (1994)

Of the six mormyrids species known from the Okavango Delta in Botswana, four were collected and examined for myxosporean parasites. The gills of *Mormyrus lacerda* Castelnau, 1861 and *Marcusenius macrolepidotus* were infected with *Henneguya* sp. A and *H. macrolepidotus* respectively (Table 5.2).

Mormyrus lacerda Castelnau, 1861 (Fig. 5.9a)

The western bottlenose, *Mormyrus lacerda* is a relatively large species, (up to 500 mm in length), distributed throughout the Cunene, Okavango, upper Zambezi and Kafue systems of southern Africa (Skelton 2001). This species is found in quiet river channels, deep pools and floodplain lagoons amongst the aquatic vegetation feeding largely on insect larvae, shrimps, oligochaetes, small snails and small fish (Skelton 2001). It is an important angling and subsistence species.

A total of 24 *M. lacerda* individuals were collected from various localities in the Okavango River and Delta and examined for myxosporean parasites from 1997 to 2002 (Table 5.2). The gills of three of the 24 fish examined were infected with *Henneguya* sp. A and showed an overall prevalence of 13% (Table 5.2). All three infected individuals collected in 1997, 2000 and 2001 were sampled in Samochima lagoon in the Panhandle region of the Okavango (Table 5.4). It is possible that the infection is localised to that specific area since many more individual *M. lacerda* were collected at other localities, but none was infected with *Henneguya* sp. A. The infection prevalence in each case was relatively high, even though only one or two individuals were collected from Samochima each year, at least 50% of the sample was always infected.

Table 5.4. *Mormyrus larceda* Castelnau, 1961 examined for myxosporean parasites from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1997								
Samochima lagoon	1	1	0	105	1	100	Gills	*Henneguya* sp. A
1998								
Xaro	3	3	0	250, 367, 302	×	×	×	×
Nxabega permanent swamp	8	8	0	320 (300-340)	×	×	×	×
1999								
Thoage lagoon	1	1	0	386	×	×	×	×
2000								
Samochima lagoon	2	2	0	250, 350	1	50	Gills	*Henneguya* sp. A

Table 5.4 continued. *Mormyrus larceda* Castelnau, 1961 examined for myxosporean parasites from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
Tim's channel	6	6	0	355 (310-410)	×	×	×	×
2001								
Nxameseri lagoon	1	1	0	357	×	×	×	×
Samochima lagoon	2	2	0	200, 420	1	50	Gills	*Henneguya* sp. A
Total	**24**	**24**	**0**	**320 (105-420)**	**3**	**13**	n.a.	n.a.

Marcusenius macrolepidotus (Peters, 1852) (Fig. 5.9b)

The bulldog, *Marcusenius macrolepidotis*, is one of the more widespread mormyrid species and reaches an average of 300 mm in length. This species is found in the Cunene, Okavango and Zambezi systems in southern Africa and in the eastern coastal rivers and lakes from Tanzania south to Umhlatuzi in Natal (Skelton 2001). It is usually found in well-vegetated, muddy-bottomed marginal habitats of rivers and floodplains where it preys on especially midge and mayfly larvae and pupae. A total of 103 *M. macrolepidotus* individuals were caught from various localities in the Okavango River and Delta from 1997 to 2001 and examined for the presence of myxosporean infections (Table 5.2). The gills of 31 *M. macrolepidotus* individuals were infected with *Henneguya macrolepidotus* giving an overall infection prevalence of 30% (Table 5.5).

Table 5.5. *Marcusenius macrolepidotus* (Peters, 1852) examined from 1997 to 2002 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1997								
Samochima lagoon	13	13	0	105 (69-143)	3	23	Gills	*Henneguya macrolepidotus* Reed, Basson and Van As (in prep)
1998								
Guma lagoon	22	22	0	180 (161-215)	2	9	Gills	*Henneguya macrolepidotus* Reed, Basson and Van As (in prep)
Pepere backwaters	3	3	0	60, 180, 200	×	×	×	×
Samochima lagoon	34	24	10	189 (112-250)	8	24	Gills	*Henneguya macrolepidotus* Reed, Basson and Van As (in prep)
Thebe lagoon	1	1	0	223	×	×	×	×

Table 5.5 continued. *Marcusenius macrolepidotus* (Peters, 1852) examined from 1997 to 2002 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1999								
Duba lagoon	15	0	15	190 (150-210)	15	100	Gills	*Henneguya macrolepidotus* Reed, Basson and Van As (in prep)
Thoage lagoon	1	1	0	276	1	100	Gills	*Henneguya macrolepidotus* Reed, Basson and Van As (in prep)
2000								
Tim's channel	8	8	0	178 (165-190)	1	13	Gills	*Henneguya macrolepidotus* Reed, Basson and Van As (in prep)
2001								
Crocodile lagoon	1	1	0	260	×	×	×	×
Mokoro lagoon	1	1	0	206	1	100	Gills	*Henneguya macrolepidotus* Reed, Basson and Van As (in prep).
Picnic lagoon	1	1	0	22	×	×	×	×
Samochima lagoon	3	3	0	180, 180, 200	×	×	×	×
Total	**103**	**78**	**25**	**177 (60-276)**	**31**	**30**	n.a.	n.a.

Henneguya macrolepidotus was collected from various lagoons throughout the Okavango. The highest infection prevalence was recorded in 1999 where 15/15 (100%) of the individual *M. macrolepidotus* collected from Duba lagoon were infected with *H. macrolepidotus*. This infection prevalence was notable since most of the other comparable sample sizes collected from Samochima lagoon in 1997 (3/13 or 23%) and 1998 (8/34 or 24%) had a much lower infection prevalence (Reed 2000).

Samochima lagoon is situated just off the fast flowing mainstream. Oxygen values are low in and around these mainstream channels during the receding water phase, with the oxygen saturation ranging between 39.7 to 65.3% (Merron and Bruton 1986). Duba lagoon, on the other hand, is situated in the upper permanent swamp, where the rate of flow of water is considerably less (Reed 2000). The oxygen values in these slow flowing parts are even less and can fall below 10% saturation when the waters recede (Merron and Bruton 1986). Sampling in both 1998 and 1999 was conducted in June and July, which is the time of year that the flood waters in the riverine panhandle and upper swamp has started to recede. Consequently the lower oxygen levels found in Duba lagoon could be a

reason for increased stress levels for the fish community and subsequently providing the opportunity for higher myxosporean infection prevalence.

Reed (2000) also compared the number of plasmodia per gill arch versus the host length using combined data from 1998 and 1999. It is generally accepted that a normal host/parasite relationship shows a number of individuals in a sample size that are not infected, a number of individuals that are moderately infected and a few individuals that are highly infected. The results obtained by Reed (2000) revealed a normal host/parasite distribution pattern for *M. macrolepidotus* infected with *H. macrolepidotus* (Fig. 5.4).

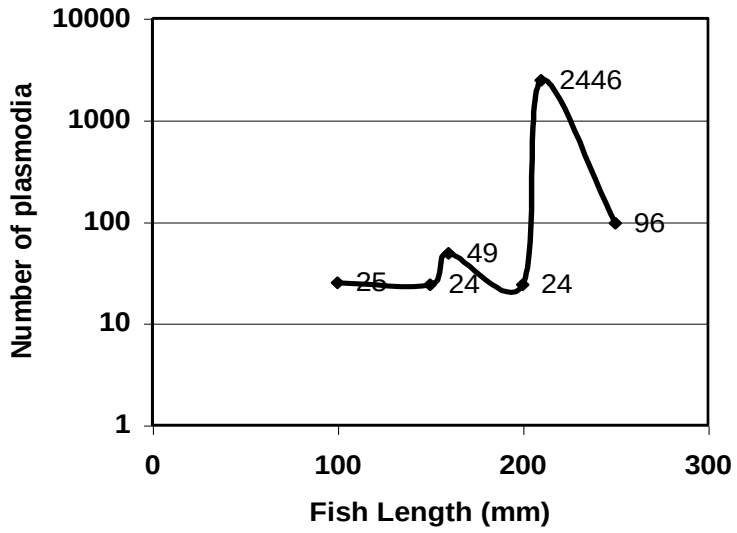


Figure 5.4. Logarithmic graph showing the number of plasmodia per *Marcusenius macrolepidotis* (Peters, 1852) gill arch versus the fish lengths for six individuals (from Reed 2000).

All of the *H. macrolepidotus* plasmodia were found infecting the gills of *M. macrolepidotus*. According to Reed (2000) a definite prevalence for the first two gill arches as well as the tips of the gill filaments were noted in the distribution of plasmodia in the gills (Fig. 5.5). A possible reason for this could be that *M. macrolepidotus* individuals have very small and narrow gill slits, with the gills situated quite deeply. Myxosporean spores situated in plasmodia at the tips of the gill filaments, near the gill slits would be more efficiently released into the water at the time of spore release, than if they were found deeper and subsequently trapped in the gill chamber. Furthermore, myxosporean plasmodia situated in the first two gill arches would also have the advantage of being nearest the gill slits, at the time of spore release (Reed 2000).

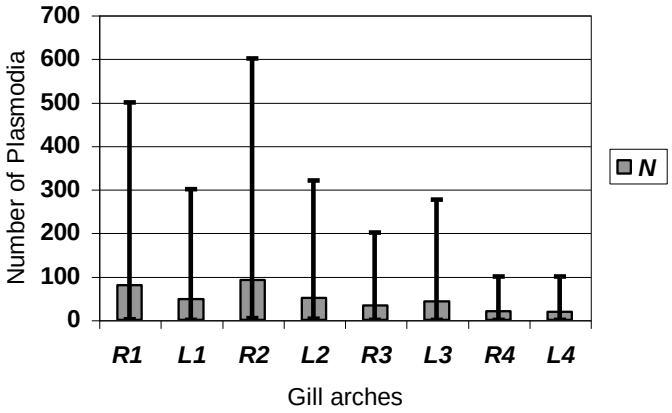


Figure 5.5 : Histogram showing the average number of plasmodia (**N**) per gill arches of seven *Marcusenius macrolepidotis* (Peters, 1852) specimens examined (**Y**-error bars- range, **L-** Left gill arches, **R-** Right gill arches, gill arches numbered 1-4) (from Reed 2000).

Family Cyprinidae

Cyprinids are primary freshwater fishes with a wide range of sizes and shapes, life-histories and habitat preferences. They characteristically lack teeth, but have strong pharyngeal bones with teeth (Skelton 2001). The family Cyprinidae boasts about 275 genera and more than 1600 species from Africa, Europe, Asia and North America (Skelton 2001). In Africa there are approximately 24 genera and 475 species with eight genera and 80 species found in southern Africa (Skelton 2001).

In the Okavango Delta 21 species of the family Cyprinidae are found. During the surveys conducted from 1997 to 2002, 16 of the 21 Okavango cyprinids were collected and examined for myxosporean infections. Three different myxosporeans from the genus *Myxobolus* were found infecting the skin and gills of primarily *Barbus* species in the Okavango Delta (Table 5.2). Two of these species, namely *Myxobolus paludinosus* and *M. etsatsaensis* were the first freshwater fish-infecting myxosporeans to be described from Botswana and from southern Africa (Reed *et al.* 2002b). The description of these two species brought the total number of myxosporeans infecting *Barbus* hosts in Africa to 10 (Table 5.6).

Table 5.6. Myxosporeans infecting *Barbus* hosts in Africa.

Myxosporean	Host	Organ	Country	Reference
Chloromyxum birgii Fomena and Bouix, 1994	*Barbus aspilus, B. martorelli, Amphilius longirostris*	Gall bladder	Cameroon	Fomena and Bouix (1994)
Myxidium mendehei Fomena and Bouix, 1994	*Barbus guirali, B. martorelli*	Kidneys	Cameroon	Fomena and Bouix (1994)
Myxidium nyongensis Fomena and Bouix, 1986	*Barbus aspilus, B. jae, B. guirali, B. martorelli, B. camptacanthus*	Gall bladder	Cameroon	Fomena and Bouix (1986)
Myxobolus etsatsaensis Reed, Basson and Van As, 2002	*Barbus thamalakanensis*	Gills	Botswana	Reed, Basson and Van As (2002b)
Myxobolus njinei Fomena, Bouix and Birgi, 1985	*Barbus campthacanthus, B. guirali, B. batesii, B. martorelli*	Gills	Cameroon	Fomena, Bouix and Birgi (1985)
Myxobolus nkolyaensis Fomena and Bouix, 1994	*Barbus jae*	Gills	Cameroon	Fomena and Bouix (1994)
Myxobolus nyongana Fomena, Bouix and Birgi, 1985	*Barbus aspilus, B. jae, B. campthacanthus, B. guirali, B. martorelli*	Gills	Nyong Basin (Cameroon)	Fomena, Bouix and Birgi (1985)
Myxobolus oloi Fomena and Bouix, 1994	*Barbus aspilus, B. guirali, B. camptacanthus*	Gills, kidneys, heart	Cameroon	Fomena and Bouix (1994)
Myxobolus paludinosus Reed, Basson and Van As, 2002	*Barbus paludinosus*	Gills	Botswana	Reed, Basson and Van As (2002b)
Thelohanellus valeti Fomena and Bouix, 1987	*Barbus aspilus, B. jae*	Operculum, stomach wall	Cameroon	Fomena and Bouix (1987)

Barbus afrovernayi Nichols and Boulton, 1927 (Fig. 5.9c)

The spottail barb, *Barbus afrovernayi* Nichols and Boulton, 1927 is a small species characterised by a large conspicuous black spot on its caudal peduncle. Widely distributed in the Cunene, Okavango, upper Zambezi and Kafue rivers it reaches an average of 45 mm in length. These fish are generally found in quite, well-vegetated waters feeding from the surface or on small invertebrates living on plant surfaces (Skelton 2001).

A total of 92 *B. afrovernayi* were examined for myxosporean infections during the various surveys conducted in the Okavango Delta from 1998 to 2001 (Table 5.2). The skin and gills of eight individuals (9%) were infected with *Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985) and this parasite was generally found infecting *B. afrovernayi* at four different localities with very low infection prevalences (Table 5.7). The only exception was at Etsatsa mainstream where one of two *B. afrovernayi* individuals examined were infected. This could simply be due to a chance sample. It could also be due to the fact that Nxameseri and Shakawe are situated within the upper panhandle where oxygen values tend to be higher than in the lower panhandle reaches where Etsatsa mainstream is situated. More *B. afrovernayi* would have to be sampled and examined from Etsatsa mainstream in order to validate this hypothesis.

Table 5.7. *Barbus afrovernayi* Nichols and Boulton, 1927 examined from 1998 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1998								
Guma lagoon	14	14	0	29 (25-33)	×	×	×	×
Shakawe backwaters	1	1	0	29	×	×	×	×
1999								
Etsatsa mainstream	2	2	0	30, 31	1	50	Gills	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)
Duba lagoon	1	0	1	30	×	×	×	×
Guma lagoon	3	3	0	23, 24, 25	×	×	×	×
Mohembo floodplains	3	0	3	25, 35, 35	×	×	×	×
2000								
Kalatog	3	3	0	30, 32, 38	×	×	×	×
Nxameseri	7	7	0	26 (23-34)	2	28	Gills, skin	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)
Shakawe backwaters	16	16	0	29 (19-40)	2	13	Gills	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)
2001								
Crocodile lagoon	1	1	0	29	×	×	×	×
Mohembo floodplains	2	2	0	35, 36	×	×	×	×
Nxameseri	3	3	0	22, 29, 36	×	×	×	×
Observation island	2	2	0	22, 39	×	×	×	×
Shakawe backwaters	14	14	0	39 (25-56)	1	7	Gills	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)
Tim's channel	20	20	0	35 (30-55)	2	10	Gills	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)
Total	**92**	88	4	**32 (19-56)**	**8**	**9**	n.a.	n.a.

Barbus barnardi Jubb, 1965 (Fig. 5.9d)

The blackback barb, *Barbus barnardi* Jubb, 1965 is characterised by a distinctive black stripe running from the tip of its snout to the caudal base, together with irregular black spots along the midline of the back as well as a black spot at the base of the anal fin (Skelton 2001). This species may reach an average of 70 mm in length and generally prefers shallow, well-vegetated streams, floodplains and marshes where it feeds on small aquatic insects and algae.

During the course of sampling in the Okavango Delta from 1997 to 2001 a total of 82 *B. barnardi* were collected and examined for the presence of myxosporean infections. The results revealed that the gills and skin of this fish species was infected by *M. nyongana* (Table 5.2). The infection prevalences varied greatly between years and localities. The highest sample size collected was at Picnic lagoon where 1/9 (11%) of the *B. barnardi* collected were infected (Table 5.8).

Table 5.8. *Barbus barnardi* Jubb, 1965 examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1997								
Mohembo floodplains	2	2	0	35, 41	×	×	×	×
Seronga backwaters	7	7	0	24 (20-40)	1	14	Gills	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)
Thamalakane river, Maun	6	6	0	37 (25-50)	×	×	×	×
1998								
Xaro	1	1	0	24	×	×	×	×
Nxameseri	1	1	0	25	×	×	×	×
1999								
Etsatsa mainstream	2	2	0	24, 47	×	×	×	×
Guma lagoon	1	1	0	26	×	×	×	×
Lechwe island	1	1	0	27	×	×	×	×
Little Duba	1	1	0	40	1	100	Gills	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)
Mohembo floodplains	3	3	0	25, 27, 27	×	×	×	×
Nxameseri fish farm	2	2	0	28, 25	×	×	×	×
Upper Thoage island	4	4	0	21, 25, 25, 32	×	×	×	×
2000								
Boro river	1	1	0	41	×	×	×	×
Mohembo floodplains	1	1	0	40	1	100	Gills	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)
Shakawe backwaters	1	1	0	40	1	100	Gills	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)

Table 5.8 continued. *Barbus barnardi* Jubb, 1965 examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
2001								
Mohembo floodplains	5	5	0	28, 30, 35, 36, 36	1	20	Gills	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)
Nxameseri	4	4	0	30, 30, 32, 35	×	×	×	×
Observation island	19	19	0	27 (25-33)	2	11	Gills, skin	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)
Picnic lagoon	9	9	0	29 (25-35)	1	11	Gills	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)
Shakawe backwaters	7	7	0	31 (20-40)	×	×	×	×
Tim's channel	4	4	0	30, 30, 32, 38	2	50	Gills	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)
Total	**82**	**82**	**0**	**31 (20-47)**	**10**	**12**	n.a.	n.a.

Barbus haasianus David, 1936 (Fig. 5.9e)

The sicklefin barb, *Barbus haasianus* is a very small species (32 mm) distributed throughout the Okavango, upper Zambezi, Kafue, lower Zambezi, Pungwe and Zambian Congo systems (Skelton 2001). This species is characterised by a thin black line running along the midbody and ending in a spot at the base of the caudal fin as well as a black triangular spot at the base of the dorsal fin. These fish generally inhabit swamps and floodplains in well-vegetated habitats (Skelton 2001).

Fifty-nine *B. haasianus* individuals were collected from various localities in the Okavango and examined for the presence of myxosporean infections from 1998 to 2001. The skin and gills of a single *B. haasianus* individual collected at Nxameseri during 2001 was infected with *Myxobolus* sp. 1 (Table 5.2). This infection was merely recorded and subsequently no final identification of the *Myxobolus* species could be made (Table 5.9). It is very likely that the species could possibly be *M. nyongana* since this myxosporean appears to be widespread amongst the *Barbus* species in the Okavango.

Table 5.9. *Barbus haasianus* David, 1936 examined from 1998 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1998								
Guma floodplains	3	3	0	25, 30, 31	×	×	×	×
Shakawe backwaters	4	4	0	23, 25, 26, 30	×	×	×	×
1999								
Etsatsa mainstream	1	1	0	24	×	×	×	×
Guma lagoon	3	3	0	26, 28, 36	×	×	×	×
Mohembo floodplains	14	14	0	26 (17-35)	×	×	×	×
2000								
Nxameseri	5	5	0	20, 20, 22, 22, 25	×	×	×	×
Thamalakane river, Maun	1	1	0	38	×	×	×	×
2001								
Mohembo floodplains	2	2	0	24, 30	×	×	×	×
Nxameseri	5	5	0	20, 21, 23, 25, 30	1	20	Gills, skin	*Myxobolus* sp. 1
Observation island	9	9	0	24 (19-30)	×	×	×	×
Picnic lagoon	7	7	0	27 (25-28)	×	×	×	×
Shakawe backwaters	1	1	0	36	×	×	×	×
Thamalakane river, Maun	2	2	0	30, 30	×	×	×	×
Tim's channel	2	2	0	17, 20	×	×	×	×
Total	**59**	**59**	**0**	**26 (17-38)**	**1**	**2**	n.a.	n.a.

Barbus miolepis Boulenger, 1902 (Fig. 5.9f)

The zigzag barb, *Barbus miolepis* is characterised by having a bold black zigzag band along its body to the end of the caudal peduncle with a parallel 'shadow' band above and below the main band (Skelton 2001). This species is found in the Okavango, Upper Zambezi, Kafue and Congo Systems and may reach 125 mm in length. A total of 43 *B. miolepis* individuals were collected from Shakawe backwaters and Mohembo floodplains, respectively, during 2000 and 2001 and examined for the presence of myxosporean parasites (Table 5.2). A histological section through the gills of a single *B. miolepis* collected from Shakawe backwaters during 2001 revealed the presence of *Myxobolus* sp. 2 (Table 5.10) (Fig. 5.8a). This species may also be *M. nyongana.* As reported

previously, it appears that this myxosporean is widespread amongst *Barbus* hosts in the Okavango.

Table 5.10. *Barbus miolepis* Boulenger, 1902 examined from 2000 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
2000								
Shakawe backwaters	42	42	0	52 (34-62)	1	2	Gills	*Myxobolus* sp. 2
2001								
Mohembo floodplains	1	1	0	75	×	×	×	×
Total	**43**	**43**	0	**53 (20-75)**	**1**	**2**	n.a.	n.a.

Barbus multilineatus Worthington, 1933 (Fig. 5.9g)

The copperstripe barb, *Barbus multilineatus* Worthington, 1933 is olive brown above with silvery sides, a black primary dorsal ray, yellow fins and a dark stripe from the tip of the snout to the base of the mid-caudal rays. This species reaches an average length of 45 mm and inhabits shallow, well-vegetated water in backwaters, floodplains and river margins (Skelton 2001). Forty-eight *Barbus multilineatus* were collected from various localities in the Okavango during 1997, 1998, 1999 and 2001. During 1999 the gills and skin of four individuals (57%) collected from Etsatsa mainstream were found infected with *M. nyongana* and the gills of three individuals (43%), also from Etsatsa mainstream, were infected with *M. etsatsaensis* (Table 5.2). A single individual collected from Tim's channel during 2001 was also infected with *M. nyongana* (Table 5.11). Figure 5.8b illustrates a plasmodium packed full of *M. nyongana* spores bursting from the gill filaments of *B. multilineatus*.

Table 5.11. *Barbus multilineatus* Worthington, 1933 examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1997								
Mohembo floodplains	1	1	0	35	×	×	×	×
1998								
Guma floodplains	7	7	0	26 (21-30)	×	×	×	×

Table 5.11 continued. *Barbus multilineatus* Worthington, 1933 examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; **×**- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
Shakawe backwaters	6	6	0	30 (26-34)	×	×	×	×
1999								
Etsatsa mainstream	19	7	12	27 (21-33)	3	43	Gills	*Myxobolus etsatsaensis* Reed, Basson and Van As, 2002
					4	57	Gills, skin	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)
Lechwe island	4	4	0	22, 23, 25, 27	×	×	×	×
Little Duba	3	3	0	25, 26, 34	×	×	×	×
Makwena	6	6	0	27 (25-30)	×	×	×	×
2001								
Shakawe backwaters	1	1	0	30	×	×	×	×
Tim's channel	1	1	0	30	1	100	Gills	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)
Total	**48**	**36**	**12**	**28 (21-35)**	**8**	**17**	n.a.	n.a.

Barbus paludinosus Peters, 1852 (Fig. 5.9h)

The straightfin barb, *Barbus paludinosus* is widespread in the east coastal rivers from East Africa south to the Vungu, KwaZulu-Natal, and from the southern Congo tributaries as well as the Quanza in Angola (Skelton 2001). This species is characterised by a pointed head and two pairs of short barbels, it has an average length of 150 mm. Preferring quiet well-vegetated habitats, it is a hardy species that feeds on a wide variety of small organisms including insects, small snails and crustaceans, algae diatoms and detritus (Skelton 2001).

The skin and gills of 81 *Barbus paludinosus* individuals were examined for myxosporean infections during 1997, 1998, 1999 and 2001 from various localities in the Okavango. Results revealed that two myxosporean species, namely *M. etsatsaensis* and *M. paludinosus*, predominantly infected this fish species (Table 5.2). *Myxobolus paludinosus* was originally recorded by Reed (2000) from *B. paludinosus* and subsequently described in Reed *et al.* (2002a). The gills and skin of nine *B. paludinosus* individuals were infected with *M. paludinosus* from a variety of localities in the Okavango (Table 5.12). Five of the *B. paludinosus* individuals from a number of

localities in the Okavango also showed gill infections with *M. etsatsaensis* (Table 5.12). The gills of two individuals one each from Etsatsa mainstream and Lechwe island were infected with both *M. etsatsaensis* and *M. paludinosus*. *Myxobolus* sp. 3 was recorded from the gills of a single *B. paludinosus* together with *M. paludinosus* collected at Little Duba island in 1999.

Table 5.12. *Barbus paludinosus* Peters, 1852 examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1997								
Mohembo floodplains	3	3	0	85, 85, 85	×	×	×	×
1998								
Guma floodplains	17	17	0	42 (24-70)	×	×	×	×
Nxameseri	12	12	0	35 (29-41)	×	×	×	×
1999								
Etsatsa mainstream	3	0	3	27, 36, 36	1	33	Gills	*Myxobolus etsatsaensis* Reed, Basson and Van As, 2002, *M. paludinosus* Reed, Basson and Van As, 2002
Lechwe island	2	2	0	54, 41	1	50	Gills	*Myxobolus etsatsaensis* Reed, Basson and Van As, 2002, *M. paludinosus* Reed, Basson and Van As, 2002
Duba lagoon	4	4	0	40, 38, 45, 46	1	25	Gills	*Myxobolus etsatsaensis* Reed, Basson and Van As, 2002
Little Duba	11	6	5	40 (26-57)	3	27	Gills	*Myxobolus etsatsaensis* Reed, Basson and Van As, 2002
					2	18	Gills and skin	*M. paludinosus* Reed, Basson and Van As, 2002
					1	9	Gills	*Myxobolus* sp. 3 *M. paludinosus* Reed, Basson and Van As, 2002
Upper Thoage	3	3	0	25, 35, 36	1	33	Gills	*M. paludinosus* Reed, Basson and Van As, 2002
2001								
Crocodile island	1	1	0	48	×	×	×	×
Mohembo floodplains	2	2	0	45, 48	×	×	×	×
Nxameseri	4	4	0	40, 40, 42, 46	×	×	×	×
Shakawe backwaters	19	19	0	59 (32-101)	3	16	Gills	*M. paludinosus* Reed, Basson and Van As, 2002
Total	**81**	**74**	**7**	**46 (24-101)**	n.a.	n.a.	n.a.	n.a.

Barbus poechii Steindachner, 1911 (Fig. 5.9i)

The dashtail barb, *Barbus poechii* Steindachner, 1911 is a common inhabitant of riverine and floodplain regions feeding on insects and small organisms (Skelton 2001). The species is characterised by a prominent oblong black dash on the caudal peduncle and is found in the Cunene, Okavango and upper Zambezi systems (Skelton 2001). Fifty-one individuals of *B. poechii* were collected and examined for myxosporean infections from various localities in the Okavango from 1997 to 2001. The gills and skin of eight *B. poechii* specimens were infected with *M. nyongana* (Table 5.2). Reed (2000) also recorded *M. nyongana* from a single *B. poechii* in 1999. The highest infection prevalence was recorded at Shakawe Backwaters in 2001 where 5/14 (36%) *B. poechii* were infected with *M. nyongana* (Table 5.13).

Table 5.13. *Barbus poechii* Steindachner, 1911 examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1997								
Drodsky's backwaters	8	8	0	76 (28-117)	1	13	Gills	*M. paludinosus* Reed, Basson and Van As, 2002
Mohembo backwaters	1	1	0	90	×	×	×	×
Seronga backwaters	1	1	0	88	×	×	×	×
1998								
Guma floodplains	3	3	0	62, 82, 92	×	×	×	×
Kalatog	13	13	0	29 (26-33)	×	×	×	×
Nxabega permanent swamp	2	2	0	40, 75	×	×	×	×
Nxabega temporary swamp	3	3	0	40, 40, 45	×	×	×	×
Xaro	5	5	0	22, 30, 88, 100, 102	1	20	Gills	*M. paludinosus* Reed, Basson and Van As, 2002,
1999								
Etsatsa mainstream	1	0	1	36	1	100	Gills	*M. paludinosus* Reed, Basson and Van As, 2002
2001								
Shakawe backwaters	14	14	0	79 (30-105)	5	36	Gills	*M. paludinosus* Reed, Basson and Van As, 2002
Total	**51**	**50**	**1**	**61 (22-117)**	**8**	**15**	n.a	n.a.

Barbus radiatus Peters, 1853 (Fig. 5.9j)

The Beira barb, *Barbus radiatus* Peters, 1853, has distinctive pit lines on the top of the head and on the cheeks, with a straight black band from the tip of the snout to the base of the caudal fin. The caudal fins are rose red with sooty black edges and the eyes are bright red (Skelton 2001). This is a very widespread species southwards from Uganda, including the Zambian Congo, Cunene, Okavango, Zambezi and east coast rivers south to the Phongolo system. These fish may reach 120 mm in length and favour marshes and marginal vegetation of streams, rivers and lakes where it is generally active at night (Skelton 2001). The gills and skin of 44 *B. radiatus* individuals were collected and examined for myxosporean infections from 1997 to 2001. The results revealed that the gills and skin of two of these fish, collected from Mohembo floodplains and Tim's channel during 2001, were infected with *M. nyongana* (Table 5.14).

Table 5.14. *Barbus radiatus* Peters, 1853 fishes from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1997								
Drodsky's backwaters	1	1	0	45	×	×	×	×
1998								
Shakawe backwaters	3	3	0	25, 27, 31	×	×	×	×
1999								
Upper Thoage Lagoon	2	2	0	22, 23	×	×	×	×
2000								
Nxameseri	1	1	0	26	×	×	×	×
2001								
Crocodile island	6	6	0	27 (22-37)	×	×	×	×
Mohembo floodplains	1	1	0	25	1	100	Gills, skin	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)
Nxameseri	19	19	0	28 (26-32)	×	×	×	×
Observation island	2	2	0	21, 28	×	×	×	×
Shakawe backwaters	4	4	0	35, 45, 50, 50	×	×	×	×
Tim's channel	5	5	0	28, 30, 32, 34, 55	1	20	Gills	*Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985)
Total	**44**	**44**	**0**	**30 (21-55)**	**2**	**5**	n.a.	n.a.

Barbus thamalakanensis Fowler, 1953 (Fig. 5.10a)

The Thamalakane barb, *Barbus thamalakanensis* is confined to the Okavango and Upper Zambezi systems where it is found in marginal vegetation feeding on insects and periphyton. This species is translucent brown on top with silvery white sides and two pairs of long barbels with a regular black stripe passing straight from the tip of the snout to the base of the caudal fin, ending in a black spot at the base of the caudal fin (Skelton 2001). Thirteen *B. thamalakanensis*, collected from Nxabega and Pepere backwaters during 1998 and Etsatsa mainstream during 1999, were examined for myxosporean infections (Table 5.2). The gills of four fish from all the collection localities (31%) were infected with *M. etsatsaensis*. Reed (2000) recorded this same myxosporean species from a single *B. thamalakanensis* during 1999 and subsequently *M. etsatsaensis* was described (Reed *et al.* 2002b) (Table 5.15).

Table 5.15. *Barbus thamalakanensis* Fowler, 1953 examined sites from 1998 to 1999 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1998								
Nxabega	7	7	0	24 (20-35)	2	29	Gills	*Myxobolus etsatsaensis* Reed, Basson, Van As, 2002
Pepere backwaters	5	5	0	20, 22, 35, 35, 55	1	20	Gills	*Myxobolus etsatsaensis* Reed, Basson, Van As, 2002
1999								
Etsatsa mainstream	1	0	1	30	1	100	Gills	*Myxobolus etsatsaensis* Reed, Basson, Van As, 2002
Total	**13**	**12**	**1**	**28 (20-55)**	**4**	**31**	n.a.	n.a.

Barbus unitaeniatus Günther, 1866 (Fig. 5.10b)

The longbeard barb, *Barbus unitaeniatus* is widely distributed in southern Africa and is found in a variety of habitats where it feeds on aquatic invertebrates and grass seeds. This species may reach 140 mm and has a characteristic dark lateral stripe and chevron marking on that lateral line (Skelton 2001). A single individual *B. unitaeniatus* was collected from the Boro River during 2000 and was found with a skin infection of *Myxobolus* sp. 4 (Table 5.16).

Table 5.16. *Barbus unitaeniatus* Günther, 1866 examined in 2000 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
2000								
Boro River	1	1	0	35	1	100	Skin	*Myxobolus* sp. 4
Total	**1**	**1**	**0**	**35**	**1**	**100**	n.a.	n.a

Coptostomabarbus wittei David and Poll, 1937 (Fig. 5.10c)

The upjaw barb, *Coptostomabarbus wittei*, is found in swamps and floodplains of shallow densely vegetated still water habitats where it feeds on minute planktonic organisms. This species is widespread throughout the Okavango Delta, upper Zambezi system, Kafue floodplains and Lualaba floodplains of the Congo and reaches a mere 40 mm in length (Skelton 2001). Eleven individual *C. wittei* were collected and examined for myxosporean infections in 1998, 2000 and 2001 (Table 5.2). The gills of one *C. wittei* collected from Shakawe during 2000 were infected with *Myxobolus* sp. 5 (Table 5.17).

Table 5.17. *Coptostomabarbus wittei* David and Poll, 1937 examined from 1998 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1998								
Guma lagoon	1	1	0	30	×	×	×	×
Thebe lagoon	1	1	0	26	×	×	×	×
Nxabega temporary swamp	2	2	0	27, 32	×	×	×	×
2000								
Kalatog	3	3	0	22, 25, 25	×	×	×	×
Nxameseri	1	1	0	22	×	×	×	×
Shakawe backwaters	2	2	0	18, 21	1	50	Gills	*Myxobolus* sp. 5
2001								
Mohembo floodplains	1	1	0	20	×	×	×	×
Total	**11**	**11**	**0**	**24 (18-32)**	**1**	**9**	n.a.	n.a.

Since *M. nyongana* was collected from many different *Barbus* sp. at various localities in both the Panhandle and Delta regions, it is possible that the species is well distributed throughout the Okavango Delta as a whole. Furthermore the large variety of hosts indicates that *M. nyongana* is not species specific, but possibly genus or family specific.

Family Characidae

The family name 'characidae' is derived from the Greek word meaning "pointed stake" and possibly arises from the sharp-pointed teeth that many of the species in this family have. Characins are easily distinguished from the cyprinids by having sharp teeth on their jaws and a small adipose fin (Skelton 2001). There are 18 genera and over a 100 species in Africa confined to the tropical waters, with five genera and six species in southern Africa (Skelton 2001).

***Hydrocynus vittatus* Castelnau, 1861 (Fig. 5.10d)**

The tigerfish, *Hydrocynus vittatus* Castelnau, 1861, is a very widespread and ferocious species distributed throughout Africa from the Nile and the major rivers of West Africa, south through the rift valley lakes to the Congo (Bruton 1984). The distribution of tigerfish in southern Africa is limited to the Okavango, Zambezi and lowveld reaches south to the Phongolo (Skelton 2001). Adult tigerfish have striking colours with a silvery-black head and body and a series of longitudinal black stripes. The fins vary from yellow to blood red with black trailing edges (Skelton 2001). These fish prefer well-oxygenated water in larger rivers and lakes, tending to frequent the surface layers where they often fall prey to the swooping African fish eagle.

A total of 51 *H. vittatus* individuals were collected from various localities in the Okavango and examined for myxosporean parasites from 1997 to 2001. The gills, gill arches and gill operculum of 11 individuals were infected with *Myxobolus hydrocyni* Kostoïngue and Toguebaye, 1994 (Tables 5.2, 5.18). *Myxobolus hydrocyni* was first described from the gills of *Hydrocyni forskali* in Chad by Kostoïngue and Toguebaye (1994). The plasmodia of *M. hydrocyni* are very inconspicuous and easily overlooked (Fig. 5.8c).

Table 5.18. *Hydrocynus vittatus* (Castelnau, 1861) examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	Organ	M
1997								
Drodsky's mainstream	18	18	0	260 (152-740)	×	×	×	×
1998								
Guma lagoon	2	2	0	165, 280	×	×	×	×
Pepere backwater	1	1	0	660	×	×	×	×
Xaro mainstream	8	8	6	227 (165-400)	4	50	Gill arches	*Myxobolus hydrocyni* Kostoïngue and Toguebaye, 1994
1999								
Duba lagoon	6	6	0	444 (305-540)	3	50	Gill operculum, gills	*Myxobolus hydrocyni* Kostoïngue and Toguebaye, 1994
Etsatsa mainstream	3		3	247, 470, 485	×	×	×	×
Nkoga mainstream	2	2	0	305, 540	×	×	×	×
Samochima lagoon	1	1	0	205	1	100	Gills	*Myxobolus hydrocyni* Kostoïngue and Toguebaye, 1994
2000								
Samochima lagoon	2	2	0	205, 530	×	×	×	×
Shakawe mainstream	2	2	0	170, 170	×	×	×	×
2001								
Mokoro lagoon	4	4	0	395, 610, 647, 680	3	75	Gill arches	*Myxobolus hydrocyni* Kostoïngue and Toguebaye, 1994
Samochima lagoon	2	2	0	175, 210	×	×	×	×
Total	**51**	**42**	**9**	**320 (100-740)**	**11**	**22**	n.a.	n.a.

Rhabdalestes maunensis (Fowler, 1935) (Fig. 5.10e)

The slender robber, *Rhabdalestes maunensis*, is a small slender characin with a silvery head and belly and a bluish green iridescent band extending along the body and a characteristic black band along the base of the anal fin (Skelton 2001). This species may reach 60 mm in length and prefers shallow well-vegetated habitats in the Cunene, Okavango and upper Zambezi and Kafue systems (Skelton 2001). A total of 88 *R. maunensis* were examined from 1998 to 2001 and the skin and gills of two fish collected in the Panhandle during 2000 were infected by *Myxobolus* sp. 6 (Tables 5.2, 5.19).

Table 5.19. *Rhabdalestes maunensis* (Fowler, 1935) examined 1998 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1998								
Xaro mainstream	18	18	0	36 (29-46)	×	×	×	×
1999								
Guma lagoon	1	1	0	36	×	×	×	×
Etsatsa mainstream	1	0	1	45	×	×	×	×
Upper Thoage	5	5	0	26, 32, 34, 34, 42	×	×	×	×
2000								
Boro river	1	1	0	46	×	×	×	×
Nxaraga	10	10	0	44 (26-55)	×	×	×	×
Nxameseri lagoon	3	3	0	44, 45, 48	×	×	×	×
Shakawe	14	14	0	53 (32-76)	×	×	×	×
Tim's channel	4	4	0	55, 60, 70, 80	×	×	×	×
2001								
Mohembo floodplains	2	2	0	40, 45	×	×	×	×
Nxameseri lagoon	11	11	0	38 (32-47)	×	×	×	×
Samochima	10	10	0	43 (40-45)	1	10	Skin	*Myxobolus* sp. 6
Shakawe	8	8	0	45 (40-52)	1	13	Skin, gills	*Myxobolus* sp. 6
Total	**88**	**87**	**1**	**43 (25-76)**	**2**	**2**	n.a.	n.a.

Family Hepsetidae

The endemic African family Hepsetidae is represented by only one genus, i.e. *Hepsetus* Swainson, 1838 which is monotypic.

Hepsetus odoe (Bloch, 1794) (Fig. 5.10f)

The African pike, *Hepsetus odoe* (Bloch, 1794) is easily recognized by its pointed head and crocodile-like jaws. This unique and widespread species is found in quiet, deep water in channels and lagoons of floodplains (Skelton 2001). Females reach an average length of 250 mm. Ninety-five *H. odoe* were examined for myxosporean parasites in the Okavango from 1997 to 2001. The skin and fins of 11 of these fish were infected with *Myxobolus africanus* Fomena, Bouix and Birgi, 1985 (Table 5.20). *Myxobolus africanus*

was originally described from the gills of *H. odoe* in Cameroon by Fomena, Bouix and Birgi (1985).

Table 5.20. *Hepsetus odoe* (Bloch, 1794) examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1997								
Samochima lagoon	6	6	0	227 (150-343)	×	×	×	×
1998								
Guma lagoon	24	18	6	303 (230-430)	7	29	Gills	*Myxobolus africanus* Fomena, Bouix and Birgi, 1985
Kalatog	1	1	0	300	×	×	×	×
Mokoro lagoon	19	0	19	299 (225-360)	×	×	×	×
Nxameseri	2	2	0	260, 320	×	×	×	×
Samochima lagoon	2	0	2	200, 230	×	×	×	×
Thebe lagoon	1	1	0	293	×	×	×	×
1999								
Upper Thoage	4	3	1	250, 265, 305, 305	×	×	×	×
2000								
Nxaraga	4	4	0	230, 280, 285, 300	3	75	Gills, fins	*Myxobolus africanus* Fomena, Bouix and Birgi, 1985
Mokoro lagoon	7	7	0	312 (200-380)	×	×	×	×
Samochima lagoon	6	6	0	262 (160-370)	1	17	Gills	*Myxobolus africanus* Fomena, Bouix and Birgi, 1985
2001								
Crocodile island	1	1	0	260	×	×	×	×
Kalatog channel	2	2	0	289, 317	×	×	×	×
Mokoro lagoon	6	6	0	353 (310-395)	×	×	×	×
Nxameseri	8	8	0	154 (135-175)	×	×	×	×
Samochima lagoon	2	2	0	300, 325	×	×	×	×
Total	**95**	**67**	**28**	**281 (135-395)**	**11**	**12**	n.a.	n.a.

Family Schilbeidae

The butterbarbels are shoaling catfishes found in Africa and Asia. They characteristically have sharp dorsal and pectoral fins and are treated with respect by fishermen. In Africa

the family Schilbeidae is represented by five genera and about 32 species. Only one genus, *Schilbe* Oken, 1897, occurs in southern Africa (Skelton 2001).

***Schilbe intermedius* Rüppell, 1832 (Fig. 5.10g)**

The silver catfish or butterbarbel, *Schilbe intermedius*, is widespread throughout southern Africa in the Cunene, Okavango and Zambezi systems southwards towards the Phongolo in northern Zululand. These fish are generally more active at night where they shoal in slow-flowing open water with emergent or submerged vegetation. They reach an average of about 300 mm in length and are an important subsistence species (Skelton 2001).

This fish host was one of the more abundant species caught during surveys conducted from 1997 to 2001, with a total of 211 *S. intermedius* individuals collected from many different localities in the Okavango river and Delta regions (Tables 5.2, 5.21). The gills of 74 of these were infected with *Henneguya xarensis* Reed, Basson and Van As (in prep.). Reed (2000) collected this species during 1998 and 1999 and described it as *Henneguya* sp. D and found that at least 60% of all the populations sampled at various localities were infected with this myxosporean. Reed (2000) also noted by counting plasmodia, that the parasite showed no preference for a particular gill arch (Fig. 5.6). The gills and gill slits of these fish are not deeply situated like those of *Marcusenius macrolepidotus* and spores can easily be released into the water from any of the gill arches (Reed 2000).

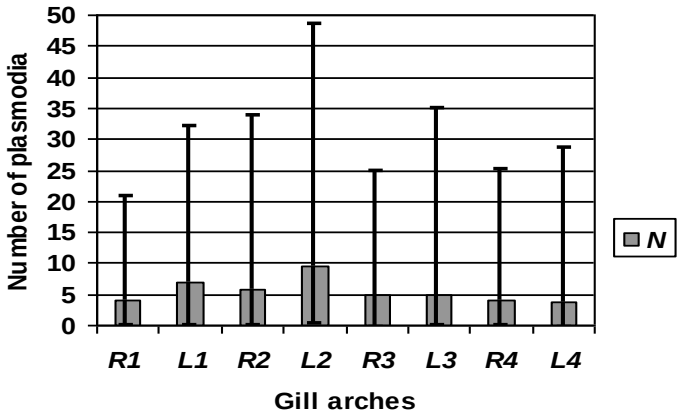


Figure 5.6: Histogram showing the average number of plasmodia (**N**) per gill arches of 14 *Schilbe intermedius* Rüppell, 1832 specimens examined (Y-error bars = fish length range, **L** = Left gill arche, **R** = Right gill arch) (from Reed 2000).

Furthermore, a relatively normal host/parasite distribution was noted, with one individual in the sample size having an extremely high infection (Fig. 5.7).

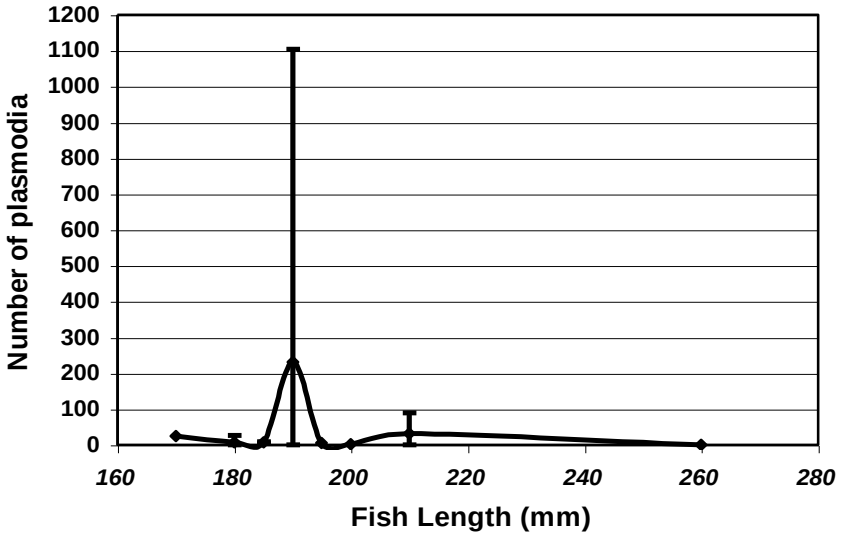


Figure 5.7: Line graph showing the relationship between the fish length and the average number of plasmodia (**A**) for 14 *Schilbe intermedius*. (Y-error bars = length range) [from Reed (2000)].

The plasmodia of this myxosporean are situated between the secondary gill lamellae (Fig. 5.8d, e, f). Histological sections conducted by Reed (2000) revealed no apparent host responses, with possibly only the sheer size of the plasmodia significantly distorting the shape of the secondary gill lamellae between which they develop. The surrounding gill lamellae were also severely compressed which may have reduced significantly the surface area of the infected gill filament (Reed 2000). This probably also resulted in a respiratory deficiency for the fish, especially since oxygen values in the water at the time of the receding flood were low (Merron and Bruton 1986). Living in an environment of reduced oxygen concentration, high levels of myxosporean infections in the gills of fishes could influence the productivity of the fish population (Reed 2000). Secondary bacterial and fungal infections in the gills may occur when plasmodia rupture to release the spores.

Table 5.21. *Schilbe intermedius* Rüppell, 1832 individuals examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1997								
Mohembo backwaters	3	3	0	60, 90, 82	×	×	×	×
Mohembo floodplains	2	2	0	100, 120	×	×	×	×

Table 5.21 continued. *Schilbe intermedius* Rüppell, 1832 individuals examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
Samochima lagoon	6	6	0	192 (137-225)	1	17	Gills	*Henneguya xarensis* Reed, Basson and Van As (in prep)
1998								
Guma lagoon	38	19	19	161 (80-270)	13	34	Gills	*Henneguya xarensis* Reed, Basson and Van As (in prep)
Nxabega permanent swamp	1	1	0	80	×	×	×	×
Pepere lagoon	3	3	0	200, 240, 240	1	33	Gills	*Henneguya xarensis* Reed, Basson and Van As (in prep)
Samochima lagoon	44	13	31	190 (120-260)	23	52	Gills	*Henneguya xarensis* Reed, Basson and Van As (in prep)
Thebe lagoon	5	5	0	194, 215, 216, 230, 265	×	×	×	×
1999								
Duba lagoon	12	0	12	203 (104-270)	11	92	Gills	*Henneguya xarensis* Reed, Basson and Van As (in prep)
Upper Thoage	26	0	17	209 (104-270)	12	46	Gills	*Henneguya xarensis* Reed, Basson and Van As (in prep)
2000								
Nxameseri	1	1	0	190	×	×	×	×
Nxaraga	5	5	0	90, 200, 260, 260, 280	1	20	Gills	*Henneguya xarensis* Reed, Basson and Van As (in prep)
Samochima	30	30	0	201 (90-307)	3	10	Gills	*Henneguya xarensis* Reed, Basson and Van As (in prep)
2001								
Crocodile lagoon	4	4	0	32, 315, 315, 210	×	×	×	×
Kalatog channel	1	1	0	308	×	×	×	×
Mokoro lagoon	14	14	0	245 (200-290)	7	50	Gills	*Henneguya xarensis* Reed, Basson and Van As (in prep)
Picnic lagoon	2	2	0	210, 342	1	50	Gills	*Henneguya xarensis* Reed, Basson and Van As (in prep)
Samochima lagoon	9	9	0	100 (78-130)	1	11	Gills	*Henneguya xarensis* Reed, Basson and Van As (in prep)
Tim's channel	5	5	0	125, 200, 259, 289, 330	×	×	×	×
Total	**211**	**132**	**79**	**192 (32-342)**	**74**	**35**	n.a.	n.a.

Family Clariidae

Clariids are African and Asian catfishes that are well known for their hardiness and ability to breath air and survive in a desiccating environment (Skelton 2001). The family is represented by 12 genera in Africa and 74 species. In southern Africa three genera and eight species are found.

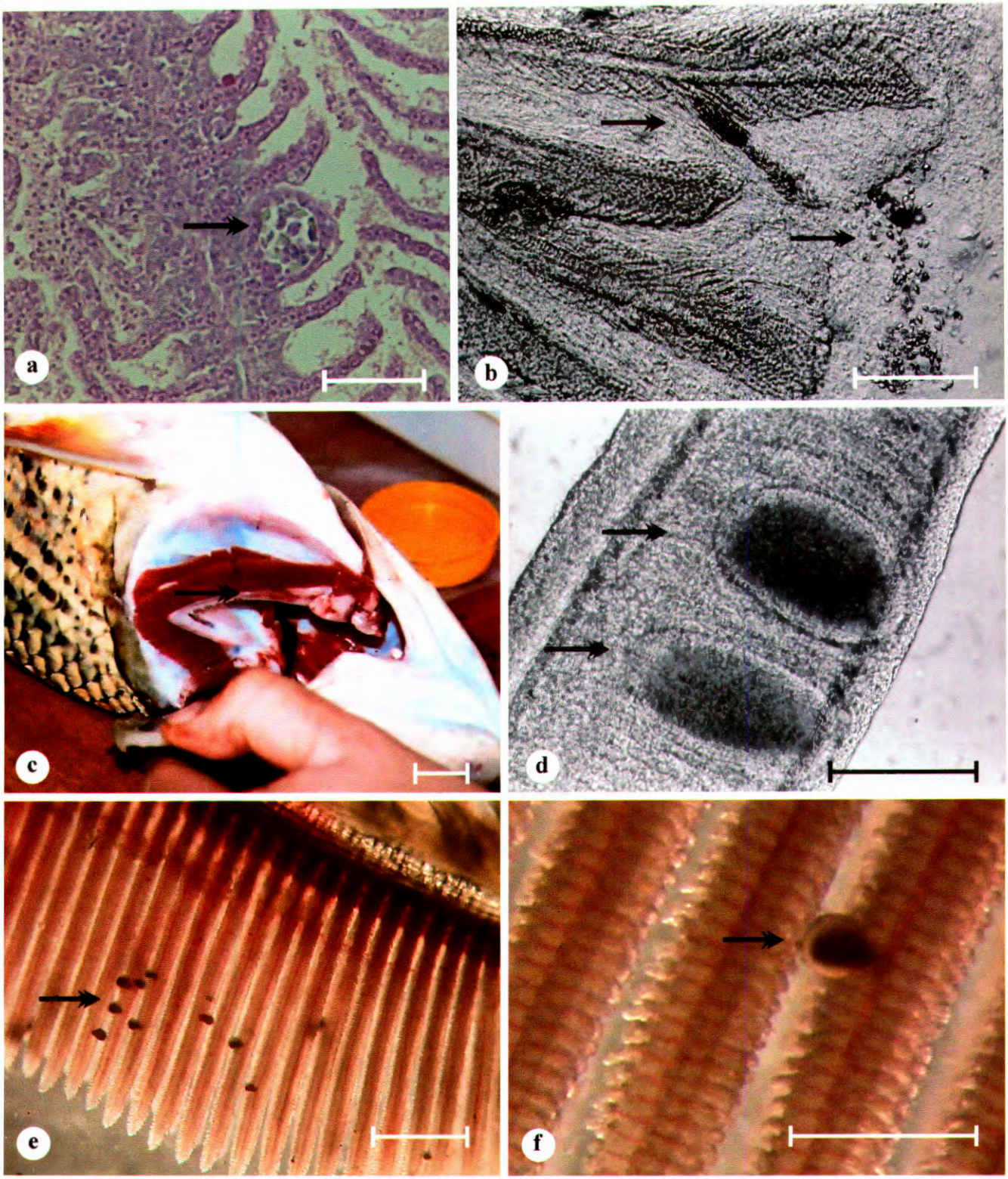


Figure 5.8. **a.** Histological section through the gills of *Barbus miolepis* Boulenger, 1902 showing a small plasmodium packed full of *Myxobolus* Butschli, 1882 sp. 1 spores (arrow). **b.** Micrograph of squashed *Barbus multilineatus* Worthington, 1933 gills showing a bursting plasmodium releasing *Myxobolus nyongana* (Fomena, Bouix and Birgi, 1985) spores (arrows). **c.** Photograph of the gills of *Hydrocynus vittatus* Castelnau, 1861 showing a plasmodium of *Myxobolus hydrocyni* Kostoïngue and Toguebaye, 1994 (arrow). **d.** Squash preparation of a *Schilbe intermedius* Rüppell, 1832 gill filament showing a plasmodium packed full with *Henneguya xarensis* spores (arrow). **e, f.** Dissection microscope photographs of *S. intermedius* gill filaments showing *H. xarensis* plasmodia (arrow). Scale bars: **a, b, e, f.** 5 mm, **c, d.** 10 mm.

***Clarias gariepinus* (Burchell, 1822) (Fig. 5.10h)**

The sharptooth catfish, *Clarias gariepinus*, is probably the most widespread fish species in Africa and is found throughout the woodland savanna zones of the Afro-tropical region from the Nile to as far south as Western Cape in South Africa (Skelton 2001). They are found in almost any habitat and can endure harsh conditions, reaching an average of 1.4 metres in length. These fish can migrate overland if need be in times of drought. They are omnivores and prey, scavenge and grub on virtually anything (Skelton 2001).

A total of 45 individual *C. gariepinus* were captured and examined for myxosporean parasites from various Okavango localities from 1997 to 2001 (Table 5.22). Three different myxosporeans from two genera were found infecting the sharptooth catfishes. The secondary accessory-breathing organs of two individual *C. gariepinus* collected from Duba lagoon in 1999 and Mokoro lagoon in 2001 were infected with *Henneguya suprabranchiae* Landsberg, 1987. This species was originally described from the same host in Israel by Landsberg (1987). The gills of catfish are reduced making them reliant on the secondary accessory-breathing organ for survival in oxygen deficient environments. Histological sections through the secondary accessory-breathing organs of infected individuals revealed that the *H. suprabranchiae* plasmodia severely displace the cartilage in this organ. Infections such as these that might impair the functioning of this important organ could have devastating effects on a fish population living in an environment where oxygen concentrations in the water may become very low during times of receding floods. Catfish tend to escape receding water levels by migrating over land, and consequently they depend solely on the functioning of the secondary-accessory breathing organ to do so successfully.

The gills of five *C. gariepinus* individuals collected from Nxabega permanent swamp in 1998, Duba lagoon in 1999, Nxaraga and Tim's channel in 2000 and Mokorol agoon in 2001 were infected with *H. samochimensis*. The plasmodia of this myxosporean occupies about two-thirds of the entire primary gill filaments. High infections could affect the respiratory function of the gills (Reed 2000). The ovaries of four individual *C. gariepinus* collected from Duba lagoon in 1999 and Mokoro lagoon in 2001 were infected with *Myxobolus gariepinus*. As reported by Reed (2000) infections in the reproductive organs of fishes may be more serious than they appear. This is because even though the fish may appear healthy externally and macroscopically, the reproductive potential might be

severely affected. The plasmodia of this species are situated within the blood vessels supplying circulating blood to the ovaries. Plasmodia blocking these blood vessels may result in the sterilisation of the infected individual (Reed 2000).

Table 5.22. *Clarias gariepinus* (Burchell, 1822) examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1997								
Samochima lagoon	3	3	0	180, 370, 400	×	×	×	×
1998								
Guma lagoon	7		1	287 (40-570)	×	×	×	×
Mokoro lagoon	4		2	475, 500, 530, 955	×	×	×	×
Nxabega permanent swamp	2			380, 425	2	100	Gills	*Henneguya samochimensis* Reed, Basson and Van As, 2003
Nxabega temporary swamp	1			400	×	×	×	×
Pepere backwaters	1			400	×	×	×	×
1999								
Duba lagoon	6	0	6	557 (430-740)	1	17	Accessory-breathing organ	*Henneguya suprabranchiae* Landsberg, 1987
					1	17	Gills	*Henneguya samochimensis* Reed, Basson and Van As, 2003
					2	33	Ovaries	*Myxobolus gariepinus* Reed, Basson and Van As, 2003
Etsatsa mainstream	2	2	0	300, 340	×	×	×	×
Guma lagoon	3			350, 400, 720	×	×	×	×
2000								
Boro river	1			530	×	×	×	×
Nxaraga	3			400, 470, 640	1	33	Gills	*Henneguya samochimensis* Reed, Basson and Van As, 2003
Tim's channel	3			380, 400, 640	1	33	Gills	*Henneguya samochimensis* Reed, Basson and Van As, 2003
2001								
Mokoro lagoon	3	3	0	455, 580, 690	1	33	Accessory-breathing organ	*Henneguya suprabranchiae* Landsberg, 1987
							Gills	*Henneguya samochimensis* Reed, Basson and Van As, 2003
							Ovaries	*Myxobolus gariepinus* Reed, Basson and Van As, 2003
Samochima lagoon	6			597 (200-840)	1	17	Ovaries	*Myxobolus gariepinus* Reed, Basson and Van As, 2003
Total	**45**	**36**	**9**	**465 (40-955)**	n.a.	n.a.	n.a.	n.a.

Clarias stappersii Boulenger, 1915 (Fig. 5.10i)

The blotched catfish, *Clarias stappersii*, is characterised by a large, oblong head, relatively short barbels and a heavily botched color pattern with a clearly outlined lateral line. This species is distributed throughout the Cunene, Okavango, upper Zambezi and Kafue systems where it reaches and average length of 410 mm (Skelton 2001). A total of 15 *C. stappersii* were collected from various localities throughout the Okavango and examined for myxosporean parasites in 1998 and 2001 (Tables 5.2, 5.23). The accessory-breathing organ of one individual collected from Mokoro lagoon in 2001 was infected with *H. suprabranchiae*. This infection was initially recorded by Reed (2000). Another individual collected during 2001 from Tim's channel showed a single plasmodium underneath the skin on the belly of the fish. The plasmodium was filled with spores of *Myxobolus* sp. 7.

Table 5.23. *Clarias stappersii* Boulenger, 1915 examined from 1998 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1998								
Samochima lagoon	2	2	0	30, 150	×	×	×	×
2001								
Mokoro lagoon	2	2	0	410, 485	1	50	Accessory-breathing organ	*Henneguya suprabranchiae* Landsberg, 1987
Nxameseri	4	4	0	42, 42, 50, 60	×	×	×	×
Observation island	1	1	0	50	×	×	×	×
Samochima lagoon	2	2	0	40, 60	×	×	×	×
Tim's channel	4	4	0	42, 42, 50, 62	1	25	Skin	*Myxobolus* sp. 7
Total	**14**	**14**	**0**	**105 (40-485)**	**1**	**7**	n.a.	n.a.

Clarias theodorae Weber, 1897 (Fig. 5.10j)

The snake catfish, *Clarias theodorae*, is characterised by a small, short head with long barbels reaching to behind the head. This fish species is widespread in southern Africa and even occurs in the coastal rivers of southern KwaZulu Natal in South Africa. Snake catfish prefer dense, marginal vegetation along banks of slow-flowing rivers and reach an average of 350 mm in length (Skelton 2001). Twenty-seven *C. theodorae* individuals were collected and examined for myxosporean parasites in the Okavango River and Delta

from 1997 to 2001 (Table 5.2). A single individual collected from Duba lagoon in 1999 was infected with *H. suprabranchiae* in the accessory-breathing organ (Reed 2000). During 2000 a small plasmodium situated under the skin of another individual collected from Samochima lagoon was found filled with spores from the genus *Myxobolus* (Table 5.24). This appears to be the same *Myxobolus* sp. 7 found under the skin of *C. stappersii* (see above) collected during 2001 from Tim's channel.

Table 5.24. *Clarias theodorae* Weber, 1897 examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts; **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1997								
Mohembo backwaters	2	2	0	100, 100	×	×	×	×
Mohembo floodplains	1	1	0	145	×	×	×	×
1999								
Duba lagoon	1	0	1	150	×	×	×	×
Etsatsa mainstream	6	6	0	32 (23-42)	×	×	×	×
Little Duba	5	5	0	55, 135, 185, 190, 210	×	×	×	×
Sepopa lagoon	2	2	0	150, 220	×	×	×	×
2000								
Samochima lagoon	6	6	0	191 (114-237)	1	17	Skin	*Myxobolus* sp. 7
2001								
Picnic lagoon	1	1	0	80	×	×	×	×
Shakawe backwaters	3	3	0	40, 44, 45	×	×	×	×
Total	**27**	**26**	**1**	**115 (23-237)**	**1**	**4**	n.a.	n.a.

Family Cichlidae

Members of the family Cichlidae form a large group of fresh and brackish water fishes distributed throughout Africa, South and central America, Madagascar, the Levant, parts of Arabia and India (Skelton 2001). Many species are important food fishes. Cichlids are the largest fish family in Africa with about 900 known species. In southern Africa there are eight genera and 42 species.

Oreochromis andersonii (Castelnau, 1861) (Fig. 5.11a)

The threespot tilapia, *Oreochromis andersonii* (Castelnau, 1861), may reach an average length of 500 mm in length and is found in the Cunene, Okavango, upper Zambezi and Kafue systems. This popular angling species is tolerant of both fresh and brackish water, preferring slow-flowing or standing water where it feeds on detritus, diatoms and zooplankton (Skelton 2001). A total of 82 *O. andersonii* individuals were captured and examined for the presence of myxosporean parasites from various localities in the Okavango from 1997 to 2001 (Table 5.2). Results revealed that the gills, skin and buccal cavity of eight of these *O. andersonii* individuals, collected during 1998 were infected with *Myxobolus camerounensis* Fomena, Marques and Bouix, 1993 (Table 5.25).

Table 5.25. *Oreochromis andersonii* (Castelnau, 1861) examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1997								
Drodsky's mainstream	1	1	0	310	×	×	×	×
Mohembo floodplains	16	16	0	109 (70-140)	×	×	×	×
1998								
Kalatog channel	1	1	0	265	×	×	×	×
Mohembo backwaters	2	2	0	110, 120	1	50	Skin	*Myxobolus camerounensis* Fomena, Marqués and Bouix, 1993
Nxabega temporary swamp	1	1	0	200	×	×	×	×
Nxameseri	9	9	0	103 (76-144)	1	11	Gills	*Myxobolus camerounensis* Fomena, Marqués and Bouix, 1993
Xaro mainstream	16	9	7	149 (105-375)	6	38	Buccal cavity	*Myxobolus camerounensis* Fomena, Marqués and Bouix, 1993
1999								
Etsatsa mainstream	1	1	0	380	×	×	×	×
Nxameseri fish farm	3	3	0	135, 250, 300	×	×	×	×
2000								
Boro river	8	8	0	62 (45-80)	×	×	×	×
2001								
Kalatog channel	6	6	0	350 (293-430)	×	×	×	×
Mokoro lagoon	3	3	0	135, 303, 305	×	×	×	×
Samochima lagoon	1	1	0	326	×	×	×	×

Table 5.25 continued. *Oreochromis andersonii* (Castelnau, 1861) examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
Shakawe mainstream	14	14	0	167 (105-370)	×	×	×	×
Total	**82**	**75**	**7**	**160 (45-430)**	**8**	**10**	n.a.	n.a.

Oreochromis macrochir (Boulenger, 1912) (Fig. 5.11b)

The greenhead tilapia, *O. macrochir* (Boulenger, 1912), is distributed widely throughout southern Africa and is found in quiet waters along margins and backwaters of the Cunene, Okavango, upper Zambezi and Lake Kariba (Skelton 2001). These fish are important aquaculture fishes and are also popular angling species and reach an average of 400 mm in length. A total of 17 *O. macrochir* individuals were captured and examined for the presence of myxosporean parasites in 1997, 1998 and 2001 (Table 5.2). The gills of a single individual collected from Samochima lagoon during 2001 were infected with *M. camerounensis* (Table 5.26).

Table 5.26. *Oreochromis macrochir* (Boulenger, 1912) examined 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1997								
Mohembo backwaters	1	1	0	40	×	×	×	×
Thamalakane river, Maun	7	7	0	39 (20-85)	×	×	×	×
1998								
Thebe lagoon	1	1	0	173	×	×	×	×
Samochima lagoon	6		1	254 (150-329)	×	×	×	×
2001								
Samochima lagoon	1	1	0	184	1	100	Gills	*Myxobolus camerounensis* Fomena, Marqués and Bouix, 1993
Shakawe backwaters	1	1	0	80	×	×	×	×
Total	**17**	**16**	**1**	**134 (20-329)**	**1**	**6**	n.a.	n.a.

Pseudocrenilabrus philander (Weber, 1897) (Fig. 5.11c)

The southern mouthbrooder, *Pseudocrenilabrus philander*, is distributed from the Orange River and southern KwaZulu-Natal northwards throughout southern Africa (Skelton 2001). These fish may reach an average of 130 mm in length and some natural populations are threatened due to introduced fishes, habitat destruction and insecticide pollution (Skelton 2001). A total of 351 *P. philander* individuals were collected and examined for myxosporean parasites from many different localities in the Okavango from 1997 to 2001 (Table 5.2). The skin of 14 of these were infected with *Myxobolus* sp. 8 (Table 5.27).

Table 5.27. *Pseudocrenilabrus philander* (Weber, 1897) examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1997								
Drodsky's	5	5	0	30, 40, 45, 64, 75	×	×	×	×
Mohembo floodplains	10	10	0	26 (18-40)	3	30	Skin	*Myxobolus* sp. 8
Seronga backwaters	3	3	0	70, 100, 111	×	×	×	×
1998								
Guma floodplains	2	2	0	20, 25	×	×	×	×
Guma lagoon	15	15	0	29 (14-58)	×	×	×	×
Makwena lagoon	14	14	0	24 (20-33)	×	×	×	×
Mohembo backwaters	11	3	8	23 (20-30)	×	×	×	×
Nxabega permanent swamp	1	1	0	20	×	×	×	×
Nxameseri backwater	10	10	0	24 (20-34)	×	×	×	×
Shakawe backwater	4	4	0	25, 31, 37, 40	×	×	×	×
Thebe lagoon	17	17	0	22 (16-40)	×	×	×	×
Xaro backwaters	14	6	8	24 (18-34)	×	×	×	×
1999								
Duba lagoon	9	9	0	22 (19-25)	×	×	×	×
Etsatsa mainstream	10	10	0	31 (16-45)	×	×	×	×
Guma floodplains	19	19	0	22 (15-36)	×	×	×	×
Guma lagoon	5	5	0	20, 21, 21, 22, 27	×	×	×	×
Lechwe island	15	15	0	25	×	×	×	×

Table 5.27 continued. *Pseudocrenilabrus philander* (Weber, 1897) examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
Leopard channel	1	1	0	24	×	×	×	×
Makwena lagoon	1	1	0	17	×	×	×	×
Mohembo floodplains	15	15	0	31 (20-63)	×	×	×	×
Sepopa floodplains	11	11	0	26 (20-40)	×	×	×	×
Thebe lagoon	21	21	0	21 (16-44)	×	×	×	×
Upper Thoage	4	4	0	21, 22, 23, 25	×	×	×	×
2000								
Boro River	7	7	0	35 (22-64)	2	29	Skin	*Myxobolus* sp. 8
Mohembo floodplains	3	3	0	34, 40, 45	×	×	×	×
Nxameseri backwater	3	3	0	24, 30,31	×	×	×	×
Nxaraga floodplains	4	4	0	34, 38, 40, 49	×	×	×	×
Shakawe backwaters	11	11	0	36 (22-92)	3	27	Skin	*Myxobolus* sp. 8
Tim's channel	2	2	0	59, 60	×	×	×	×
2001								
Crocodile island	20	20	0	32 (14-42)	4	20	Skin	*Myxobolus* sp. 8
Mohembo floodplains	19	19	0	28 (18-40)	×	×	×	×
Nxameseri	6	6	0	26 (18-31)	×	×	×	×
Observation island	11	11	0	27 (15-65)	×	×	×	×
Picnic lagoon	7	7	0	38 (30-53)	×	×	×	×
Shakawe	28	28	0	39 (20-66)	1	4	Skin	*Myxobolus* sp. 8
Thamalakane river, Maun	2	2	0	30, 45	×	×	×	×
Tim's channel	11	11	0	35 (20-58)	1	9	Skin	*Myxobolus* sp. 8
Total	**351**	**335**	**16**	**29 (14-111)**	**14**	**4**	n.a.	n.a.

Tilapia rendalli (Boulenger, 1896) (Fig. 5.11d)

The redbreast tilapia, *Tiliapia rendalli*, is widespread throughout the Cunene, Okavango, Zambezi system, east coastal rivers south to the Phongolo and coastal lakes to Lake Sibaya. This species is tolerant of a wide range of temperatures and high salinities. It is a

popular angling species, valued in aquaculture and fisheries and is used for weed control in dams. It may reach 400 mm in length (Skelton 2001).

A total of 71 individual *T. rendalli* were collected and examined for the presence of myxosporean parasites (Table 5.2). The gills of five individuals collected during 1998 and 2001 from Shakawe backwaters were infected with *Myxobolus* cf. *tilapiae* Abolarin, 1974. *Henneguya* sp. 1 was recorded from the gills of a single *T. rendalli* collected during 1999 from Mohembo floodplains (Table 5.28).

Table 5.28. *Tilapia rendalli* (Boulenger, 1896) examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1997								
Mohembo backwaters	5			69, 69, 70, 73, 115	×	×	×	×
1998								
Mohembo backwaters	5	0	5	60, 60, 66, 70, 71	×	×	×	×
Nxabega temporary swamp	1	1	0	62	×	×	×	×
Thebe lagoon	26	26	0	122 (90 -175)	1	4	Gills	*Myxobolus cf. tilapiae* Abolarin, 1974.
Xaro backwaters	17	0	2	114 (50-173)	3	18	Gills	*Myxobolus cf. tilapiae* Abolarin, 1974.
1999								
Mohembo floodplains	1	0	1	34	1	100	×	*Henneguya* sp. 1
2001								
Kalatog channel	1	1	0	293	×	×	×	×
Shakawe backwaters	15	15	0	107 (65-120)	1	7	Gills	*Myxobolus cf. tilapiae* Abolarin, 1974.
Total	**71**	**63**	**8**	**110 (34-293)**	n.a.	n.a.	n.a.	n.a.

Tilapia ruweti (Poll and Thys van den Audenaerde, 1965) (Fig. 5.11e)

The Okavango tilapia, *T. ruweti*, is found distributed throughout the Okavango Delta, upper Zambezi and southern tributaries of the Congo River system (Skelton 2001). These fish are found in swamps and floodplain habitats where they feed on soft plants and insect larvae. They reach around 104 mm in length. Thirteen *T. ruweti* individuals were collected and examined for myxosporean infections in the Okavango in 1998 and 1999 (Table 5.2). The gills of one of these fish collected at Etsatsa mainstream during 1999

were infected with *M. camerounensis*. The skins of four individuals collected from Pepere lagoon during 1998 were infected with *Myxobolus* sp. 9 (Table 5.29).

Table 5.29. *Tilapia ruweti* (Poll and Thys van den Audenaerde, 1965) examined 1998 to 1999 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1998								
Pepere backwaters	3	3	0	18, 20, 20	×	×	×	×
Pepere lagoon	9	9	0	61 (55-70)	4	44	Gills	*Myxobolus* sp. 9
1999								
Etsatsa mainstream	1	0	1	100	1	100	Gills	*Myxobolus camerounensis* Fomena, Marqués and Bouix, 1993
Total	**13**	**12**	**1**	**55 (18-100)**	n.a.	n.a.	n.a.	n.a.

Tilapia sparrmanii Smith, 1840 (Fig. 5.11f)

The banded tilapia *T. sparrmanii* is widely distributed throughout southern Africa and has even been translocated to south of the Orange River to the Cape Province of South Africa (Skelton 2001). This omnivorous species is tolerant of a wide range of habitats, feeding on small invertebrates or even small fish. They are an important subsistence species and reach an average of 230 mm in length. A total of 148 individual *T. sparrmanii* from the Okavango were collected and examined for myxosporean parasites. The gills of three individuals were infected with *Myxobolus* sp. A (Table 5.30).

Table 5.30. *Tilapia sparrmanii* A. Smith, 1840 examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1997								
Mohembo backwaters	8	8	0	79 (50-95)	×	×	×	×
1998								
Guma floodplains	15	15	0	35 (20-52)	×	×	×	×
Nxabega temporary swamp	10	10	0	63 (15-142)	×	×	×	×
Nxameseri	1	1	0	20	×	×	×	×
Pepere backwaters	4	4	0	30, 30, 80, 100	1	25	Skin	*Myxobolus* sp. A

Table 5.30 continued. *Tilapia sparrmanii* A. Smith, 1840 examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
Pepere lagoon	3	3	0	45, 85, 177	×	×	×	×
Thebe lagoon	14	14	0	76 (22-165)	×	×	×	×
Xaro backwaters	1	1	0	150	×	×	×	×
1999								
Etsatsa mainstream	6	6	0	40 (28-54)	×	×	×	×
Guma floodplains	6	6	0	25 (21-30)	×	×	×	×
Lechwe island	27	27	0	33 (22-46)	×	×	×	×
Makwena lagoon	2	2	0	28, 33	×	×	×	×
Thebe lagoon	11	1	10	131 (98-140)	×	×	×	×
Upper Thoage	3	3	0	37, 39, 40	×	×	×	×
2000								
Boro river	8	8	0	45 (32-49)	1	13	Skin, gills	*Myxobolus* sp. A
Nxameseri backwaters	4	4	0	32, 36, 36, 46	×	×	×	×
Shakawe backwaters	7	7	0	67 (32-190)	1	14	Gills	*Myxobolus* sp. A
Thamalakane river	5	5	0	45, 52, 55, 55, 65	×	×	×	×
2001								
Crocodile island	1	1	0	28	×	×	×	×
Mohembo floodplains	1	1	0	100	×	×	×	×
Nxameseri	1	1	0	40	×	×	×	×
Observation island	2	2	0	30, 95	×	×	×	×
Shakawe backwaters	8	8	0	94 (65-125)	×	×	×	×
Total	**148**	**138**	**10**	**59 (15-190)**	**3**	**2**	n.a.	n.a.

Family Anabantidae

The family Anabantidae is one of the "labyrinth" fish families. These fishes have accessory-breathing organs within the chambers above the gills since most species live in waters where low oxygen conditions often occur (Skelton 2001).

Ctenopoma multispine Peters, 1844 (Fig. 5.11g)

The many-spined climbing perch, *Ctenopoma* Peters, 1844 lives in vegetated riverine backwaters, floodplain lagoons, swamps and isolated pans, preying on suitably small creatures such as shrimps and small fish. These fish reach an average of 135 mm in length and can endure warm, stagnant waters, often leaving the water and moving overland to alternative sites in wet weather or at night (Skelton 2001).

A total of 21 individual *C. multispine* were collected from various localities throughout the Okavango from 1997 to 2001 and examined for myxosporean infections (Table 5.2). Three different myxosporeans were found infecting the gills of this fish host (Table 5.31). A single individual collected from Guma floodplains during 1998 was infected with *Myxobolus* sp. 10 while another individual collected from Pepere Backwaters during the same year was infected with *Myxobolus* sp. 11. A third individual collected from the Upper Thoage during 1999 was infected with *Henneguya* sp. 2.

Table 5.31. *Ctenopoma multispine* Peters, 1844 examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf	P (%)	O	M
1997								
Mohembo backwaters	8	8	0	60 (40-90)	×	×	×	×
1998								
Guma floodplains	4	4	0	20, 40, 40, 42	1	25	Gills	*Myxobolus* sp. 10
Pepere backwaters	3	3	0	19, 20, 20	1	33	Gills	*Myxobolus* sp. 11
1999								
Little Duba	1	1	0	93	×	×	×	×
Upper Thoage	1	1	0	43	1	100	Gills	*Henneguya* sp. 2
2001								
Nxameseri	1	1	0	75	×	×	×	×
Shakawe	2	2	0	80, 86	×	×	×	×
Tim's channel	1	1	0	73	×	×	×	×
Total	**21**	**21**	**0**	**54 (19-93)**	n.a.	n.a.	n.a.	n.a.

Microctenopoma intermedium (Pellegrin, 1920) (Fig. 5.11h)

The blackspot climbing perch, *Microctenopoma intermedium*, occurs in dense marginal vegetation of rivers, lakes, lagoons and channels of swamps and floodplains where it preys on insects and other small organisms (Skelton 2001). These fish are found in the Okavango, upper and lower Zambezi and Kafue rivers as well as the St. Lucia basin and may reach an average of 55 mm in length.

A total of 33 *M. intermedium* were caught from various localities in the Okavango Delta. A single *M. intermedium* collected from Pepere Backwaters during 1998 was infected with *Henneguya* sp. 3 (Table 5. 32).

Table 5.32. *Microctenopoma intermedium* (Pellegrin, 1920) examined from 1997 to 2001 in the Okavango River and Delta, Botswana [Key: **Inf**.- Number of host infected; **M**- Myxosporean species infecting the fish hosts; **N**- Total number of fish examined; **O**- Organs of fish hosts infected; **P**- Prevalence expressed as a percentage (%); **PS**- Present study; **R**- Data from Reed (2000); **S**- Mean size and size range of fish hosts (mm); **n.a.**- Not applicable; ×- Not infected].

Locality	N	PS	R	S	Inf.	P (%)	O	M
1997								
Mohembo backwaters	14	14	0	31 (21-45)	×	×	×	×
1998								
Pepere backwaters	2	2	0	45, 50	1	50	Gills	*Henneguya* sp. 3
1999								
Etsatsa mainstream	1	1	0	25	×	×	×	×
Guma floodplains	1	1	0	35	×	×	×	×
Guma lagoon	3	3	0	30, 34, 40	×	×	×	×
Little Duba	5	5	0	18, 23, 24, 26, 30	×	×	×	×
Mohembo floodplains	1	1	0	32	×	×	×	×
Sepopa	1	1	0	46	×	×	×	×
2000								
Samochima lagoon	3	3	0	35, 38, 40	×	×	×	×
2001								
Nxameseri backwaters	1	1	0	20	×	×	×	×
Tim's channel	1	1	0	20	×	×	×	×
Total	**33**	**33**	**0**	**32 (18-50)**	**1**	**3**	n.a.	n.a.

6. Myxosporeans infecting Intertidal Fishes along the Cape South Coast, South Africa

The southern African coastline, stretching from northern Namibia to southern Moçambique has one of the most diverse marine fauna and flora compositions in the world. Over 10 000 species are known from this coastline, comprising almost 15% of all known marine species worldwide (Branch, Griffiths, Branch and Beckley 2002). Incredibly, 12% of all the coastal marine species along the southern African coastline are endemic (Branch *et al.* 2002). The main reason for this diversity is the influence of two major ocean currents that sweep the coastline (Fig. 6.1).

The Agulhas Current, which is one of the most powerful ocean currents in the world, brings warm water from the Equatorial tropical regions to the east coast of southern Africa. This current is up to 160 km wide and flows at a speed of 2.6 metres per second, transporting 80 million tonnes of water per second (Branch and Branch 1995). In fact, the entire Indian Ocean is a huge mass of water, driven by strong winds, circulating in an anti-clockwise direction. This water mass splits when it reaches Madagascar with part of it moving around the island and down the coast of Moçambique, where it is called the Moçambique Current. The two split currents meet again as they flow past the east coast of South Africa, forming an input to the mighty Agulhas Current (Branch and Branch 1995). The Moçambique Current then moves down the continental shelf of the East coast, widening along the Transkei Coast and forcing the Agulhas Current offshore and resulting in the coastal waters becoming cooler (Branch *et al.* 2002). Eventually the Agulhas swings back in an eastward direction, joining the large mass of water circulating around the basin of the Indian Ocean.

Along the West Coast of southern Africa a totally different situation occurs. The Benguela Current originates from a large, cold current travelling from west to east in the subantarctic Southern Ocean, namely the Antarctic Circumpolar Current. North of this circles the South Atlantic Circulation, which brings cold water from the southern Antarctic regions, to the West Coast of southern Africa, giving rise to the Benguela Current (Branch and Branch 1995). Since this water originates at great depths, where it is too dark for plant life to grow, it is not only cold, but also very rich in nutrients, which in turn gives rise to very productive food chains along the west coast (Branch *et al.* 2002).

The nutrient rich water along the West Coast culminates into one of the richest fishing grounds in the world and as a result supports large colonies of sea birds and seals (Branch and Branch 1995).

The great diversity of coastal marine fauna and flora can be explained by the massive influence these two currents have along the coastline. Although productivity is high on the West Coast, its supports relatively few species, compared to the East Coast, which is particularly diverse due to the large suite of tropical Indo-Pacific species that contributes to the fauna and flora. The different water temperatures influence the type of species living in certain areas and of course where the two currents meet, a mixture of both the warm water species and the cold water species is found, giving an even greater species diversity for that specific region. These two ocean currents meet along the Cape south coast of South Africa.

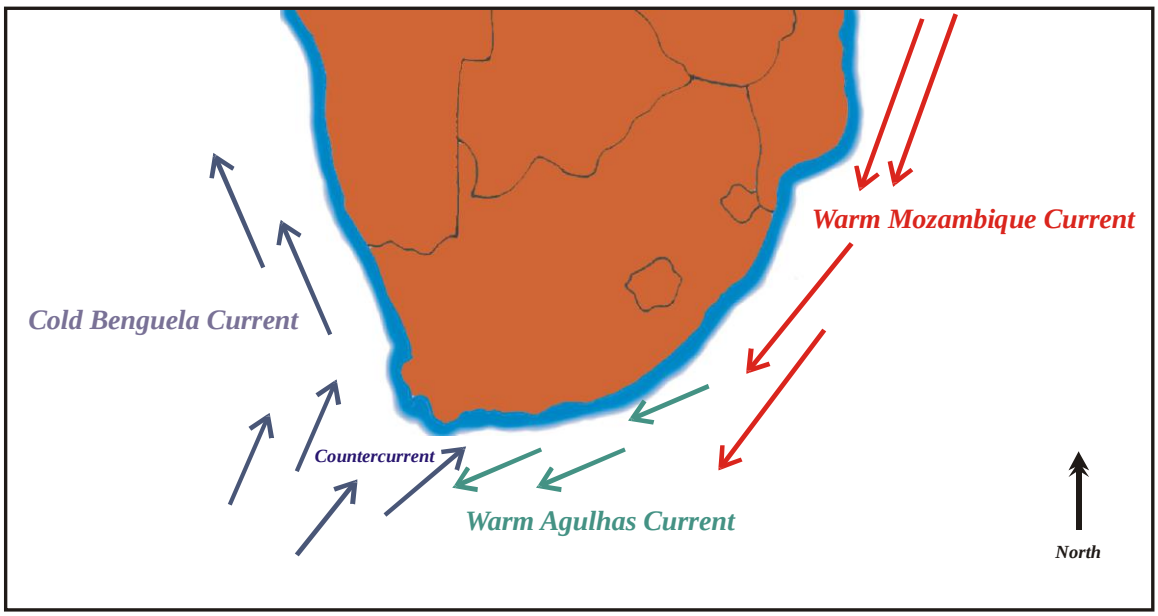


Figure 6.1. Map of southern Africa illustrating the major ocean currents contributing to the unique species diversity found along the Cape south coast of South Africa.

Sampling localities

Surveys conducted for the purpose of this study were undertaken at three different localities along the Cape south coast (see Fig 4.4, Chapter 4). The majority of data collected were obtained from the *De Hoop Nature Reserve* (Fig. 4.4a), which is situated approximately 40 km east of the southern most tip of Africa and is found more or less in the region where the Agulhas Current swings back to the east. This enormous reserve is 36 000 ha in extent and is one of the largest protected natural areas in South Africa. The

adjacent De Hoop Marine Reserve is the largest of its kind in Africa and stretches as far as five kilometers out to sea. As can be expected, the diversity of marine fauna is incredible and very little or no impacts have been associated with this region. This locality could most probably be classified as a pristine environment, reflecting how the entire southern Cape coast region might have looked before the onset of anthropogenic influences. De Hoop was proclaimed a nature reserve in 1957 and was initially used to breed rare and endangered species such as the bontebok and Cape zebra. The protected adjacent marine area was proclaimed protected in March 1986 (Cowling and Richardson 1995).

Almost adjacent to the De Hoop Nature Reserve is the *De Mond Nature Reserve*. The reserve lies at the mouth of the Heuningsnes River between the villages of Arniston and Struisbaai. De Mond is 954 ha in size and comprises former sections of the farms Zoetendals Vallei and Bushy Park. It was proclaimed as a nature reserve in 1986 and is managed as a satellite of the De Hoop Nature Reserve.

The third sampling locality was at the fishing/tourist town of *Jeffrey's Bay*, which is situated East of De Hoop Nature Reserve. This town does not fall within a protected reserve and is exposed to a booming fishing industry and many tourists.

Results

Results obtained from surveys conducted along the Cape south coast of South Africa are presented in this chapter. These results include descriptions of new species from the genera *Ceratomyxa*, *Henneguya*, *Myxidium*, *Myxobolus* and *Sphaeromyxa* Thélohan, 1892. Also included are myxosporean species noted, but not completely described due to insufficient material.

Species descriptions

Three species from the genus *Ceratomyxa*, one species from the genus *Henneguya*, two species from the genus *Myxidium*, one species from the genus *Myxobolus* and one species from the genus *Sphaeromyxa* were collected. A brief literature review of each of these genera in Africa is provided followed by the species descriptions.

Genus *Ceratomyxa* Thélohan, 1892

The genus *Ceratomyxa* is probably the most widely distributed genus amongst coelozoic myxosporean infecting the gall bladders and urinary tracts of most marine fishes throughout the world (Brickle, Kalavati and MacKenzie 2001). Thélohan established this genus in 1892 with the discovery of its type species, *Ceratomyxa arcuata* Thélohan, 1892 in the gall bladder of *Pagellus bograveo* (Sarkar and Pramanik 1993). Since the discovery of this genus, more than 130 species have been described from fishes in all parts of the world. Most species are found coelozoically in marine fish, meaning that they are found within organ cavities such as gall bladders and urinary bladders. Some species have been found encysting histozoically with even a few species described from freshwater hosts (Lom and Dyková 1992).

Members of the genus *Ceratomyxa* are characterised by elongated, crescent-shaped or arcuate spores, with shell valves that are often conical, exceeding the axial diameter of the spore. These mostly contain sub-spherical polar capsules that have capsular foramina near the sutural line at the anterior pole of the spore, usually with a binucleate sporoplasm that does not fill the entire spore cavity (Lom and Dyková 1992). Unfortunately most of the more than 157 known *Ceratomyxa* species were described many years ago, using poor data and illustrations (Sitjá-Bobadilla, Palenzuela and Álvarez-Pellitero 1995). Even many recent reports do not completely follow the guidelines for species descriptions established by Lom and Arthur (1989), making it extremely difficult for taxonomic comparisons, whilst describing new species. Ultrastructural data on *Ceratomyxa* species is also very scarce (Sitjá-Bobadilla *et al.* 1995).

In Africa nine *Ceratomyxa* species have been described from marine fish hosts (see Chapter 3, Table 3.4) (Dubina and Isakov 1976; Gaevskaya and Kovaleva 1979; Kpatcha, Diebakate, Faye and Toguebaye 1996b). Seven of these species were described from fishes collected off the coast of Senegal by Kpatcha *et al.* (1996b). As mentioned earlier in this thesis, Fantham (1919, 1930) conducted some myxosporean research along the South African coast during the early 1900's. One species he described, *Leptotheca obovalis*, from the gall bladders of intertidal hosts (Fantham 1930) appears to rather be a *Ceratomyxa* species (see Chapter 3; Table 3.3; Fig. 3.3). Since his species descriptions are not regarded as valid, it can merely be noted that he recorded what appeared to be a

Ceratomyxa species infecting some of the intertidal fishes along the Cape south coast of South Africa.

The first official description of a *Ceratomyxa* species from the African coast was completed in 1976 by two Russian scientists, Dubina and Isakov, who described *C. shulmani* Dubina and Isakov, 1976 from a deep sea fish, *Alepocephalus australis*, off the coast of South Africa. Three years later in 1979, another two Russian scientists, Gaevskaya and Kovaleva described *C. australis* Gaevskaya and Kovaleva, 1979 from *Trachurus trachurus capensis* off the coast of Namibia. Remarkably, seventeen years passed before more *Ceratomyxa* species were described from the African coast, with Kpatcha *et al.* (1996b) describing seven new species from fishes off the coast of Senegal.

Table 3.4 in Chapter 3 provides a complete list of *Ceratomyxa* species described and recorded from Africa. Therefore, in this chapter only a table of comparative species dimensions is provided (Table 6.1).

Ceratomyxa species from the Cape south coast, South Africa

Results obtained from the surveys conducted along the Cape south coast revealed three *Ceratomyxa* species infecting the gall bladders of intertidal fish hosts in the De Hoop Nature Reserve and Jeffrey's Bay.

***Ceratomyxa* sp. A.**

(Figs. 6.2; 6.3a, b)

Hosts: *Clinus superciliosus* (Linnaeus, 1758)

Site of infection: Gall bladder and lumen of kidney tubules.

Localities: De Hoop Nature Reserve (34°28'S, 20°30'E), Jeffrey's Bay (34°2.2'S; 24°56.5'E), South Africa.

Total prevalence: 84 % (110/130).

Reference material: Deposited in the Aquatic Parasitology Research Group, Department of Zoology and Entomology, University of the Free State, Bloemfonteins' Parasite Collection.

Description of vegetative stages: Plasmodia are coelozoic and mostly spherical, transparent, with numerous refractile granules and inner generative cells (Fig. 6.2a), often

with long extensions connecting the disporous trophozoites (Figs. 6.2b, c, d). Some appear to be associated with gall bladder and kidney epithelium (Figs. 6.2e, f). These varied greatly in size (5 – 20 µm) and shape (Figs. 6.2e, f).

***Description of spores (based on 38 live spores)*:** Mature spores are transversely elongated and narrowly crescent-shaped with a slightly convex anterior and concave posterior (Figs. 6.3a, b), measuring 4.0 – 5.5 (4.5 ± 0.5) µm long × 12.0 –17.5 (15.4 ± 1.4) µm wide. Spore shell valves are equal in length and have a smooth surface (Figs. 6.2g, h), each tapering to a rounded end. The sutural line is thin and straight. Two spherical to ovoid polar capsules are situated on either side of the sutural line (Figs. 6.2g, h; 6.3a), measuring 2.0 – 3.0 (2.7 ± 0.3) µm long × 2.0 – 2.5 (2.1 ± 0.2) µm wide. The number of coils per polar filament was not observed. A single binucleate sporoplasm fills almost the entire spore cavity and contains a single, small iodinophilous vacuole (Fig. 6.3a).

Remarks: *Ceratomyxa* sp. A shows morphological similarities with only two of the nine species found infecting marine fishes in Africa. *Ceratomyxa fistulariae* Kpatcha, Diebakate, Faye and Toguebaye, 1996, described from the bile ducts of *Fistularia petimba* in Senegal by Kpatcha *et al.* (1996b) is similar in general spore shape, but has a much greater spore width than *Ceratomyxa* sp. A (Table 6.1). Comparatively, *C. truncata* Thélohan, 1895 found infecting the bile ducts of *Sardinella madarensis* also in Senegal by Kpatcha *et al.* (1996b), has a much broader spore (Table 6.1), is more strongly arched and has a prominent sutural ridge, unlike the smaller less arched spores of *Ceratomyxa* sp. A. Compared with species from around the world, *Ceratomyxa* sp. A resembles *C. arripica* Su and White, 1994 described from the gall bladder of *Arripis trutta* in Tasmania, Australia by Su and White (1994). The spores of *Ceratomyxa* sp. A are, however, broader and do not have an almost straight posterior end, as in the case of *C. arripica*. *Ceratomyxa* sp. A is most similar to *C. sparusaurati* Sitjá-Bobadilla, Palenzuela and Álvarez-Pellitero, 1995 described from the gall bladder of *Sparus aurata* in Spain by Sitjá-Bobadilla *et al.* (1995). The spore dimensions are very similar, but the spores of *C. sparusaurati* have a slightly more convex anterior and concave posterior end, compared with the more straightened spores of *Ceratomyxa* sp. A. *Ceratomyxa* sp. A does not conform to the description of any known *Ceratomyxa* species.

***Ceratomyxa* sp. B**

(Figs. 6.3. c, d)

Host: *Clinus cottoides* Valenciennes, 1836.

Site of infection: Gall bladder and lumen of kidney tubules.

Locality: De Hoop Nature Reserve (34°28‘S, 20°30’E), South Africa.

Total prevalence: 59 % (26/44).

Reference material: Deposited in the Aquatic Parasitology Research Group, Department of Zoology and Entomology, University of the Free State, Bloemfonteins’ Parasite Collection.

***Description of vegetative stages*:** Disporic, coelozoic trophozoites floating within the gall bladder bile. Plasmodia are mostly spherical to elongate and refractile with numerous granules and inner generative cells ranging in size from 5 – 20 µm.

***Description of spores (based on 20 live spores)*:** Mature spores are broadly elliptical to crescent-shaped with a rounded convex anterior and an almost straight posterior end, measuring 6.5 – 8.0 (7.0 ± 0.6) µm long × 17.0 – 22.0 (18.2 ± 1.7) µm wide (Figs. 6.3c, d). Shell valves are smooth with one occasionally tapering to a greater degree than the other. The sutural line is straight with two spherical to ovoid polar capsules situated medially. Polar capsules measure 2.3 – 3.0 (2.7 ± 0.4) µm long × 2.0 – 3.0 (2.4 ± 0.4) µm wide (Figs. 6.3c, d). There appears to be three to four coils per polar filament (Fig. 6.3c). The uninucleate sporoplasm is transversely elongated, extending into both the shell valves.

Remarks: *Ceratomyxa* sp. B is possibly the same species as *Leptotheca obovalis*, collected on several occasions from the gall bladders of intertidal fishes in Table Bay and False Bay, South Africa by Fantham (1930) (see Chapter 3; Table 3.3; Figs. 3.3a-c) due to similar morphological characteristics. Amongst the *Ceratomyxa* species found infecting African marine fishes, *Ceratomyxa* sp. B closely resembles *C. australis* Gaevskaya and Kovaleva, 1979 (Gaevskaya and Kovaleva 1979). The spores of *C. australis* are, however, smaller and have a shorter spore length (Table 6.1) giving them a narrower appearance compared to the more broadly rounded spores of *Ceratomyxa* sp. B. The polar capsules of *C. australis* are also more teardrop-shaped compared to the almost spherical polar capsules of *Ceratomyxa* sp. B. *Ceratomyxa* sp. B resembles *C.*

lagocephali Kpatcha, Diebakate, Faye and Toguebaye, 1996 described from the gall bladder of *Lagocephalus laevigatus* off the coast of Senegal by Kpatcha *et al.* (1996b). The spores of *C. lagocephali* are even more broadly crescent-shaped than *Ceratomyxa* sp. B (Table 6.1). Furthermore, the spherical polar capsules of *C. lagocephali* are larger than the smaller, almost spherical polar capsules of *Ceratomyxa* sp. B. Compared with species from around the world, *Ceratomyxa* sp. B also resembles *C. arripica* from Tasmania by Su and White (1994). The spores of *C. arripica* are, however, smaller than *Ceratomyxa* sp. B. Furthermore, the spores of *C. arripica* have a very prominent convex anterior, tapering to two equally rounded ends, unlike the spores of *Ceratomyxa* sp. B, which have more broadly rounded ends, with one end occasionally tapering to a greater degree. *Ceratomyxa* sp. B has some morphological similarities with *C. buri* Yokoyama and Fukuda, 2001 described from the gall bladder of *Seriola quinqueradiata* in Japan by Yokoyama and Fukuda (2001). The spores of *C. buri* have the same average spore length, but have a narrower spore width than the spores of *Ceratomyxa* sp. B. Based on these differences in morphological characteristics, geographical distribution and host species, *Ceratomyxa* sp. B is considered to be new.

***Ceratomyxa* sp. C.**

(Figs. 6.3e, f)

Host: *Amblyrhynchotes honkenii* (Bloch, 1795).

Site of infection: Gall bladder and lumen of kidney tubules.

Localities: De Hoop Nature Reserve (34°28‘S, 20°30’E), Jeffrey’s Bay (34°2.2’S; 24°56.5’E), South Africa.

Total prevalence: 43 % (6/14).

Reference material: Deposited in the Aquatic Parasitology Research Group, Department of Zoology and Entomology, University of the Free State, Bloemfonteins’ Parasite Collection.

***Description of vegetative stages*:** Disporic spherical trophozoites were observed floating within gall bladder bile. The trophozoites were mostly transparent with refractile granules ranging in size from 5 – 20 µm.

***Description of spores (based on 20 live spores)*:** Mature spores are transversely elongated, very slightly crescent-shaped and broadly concave, measuring 7.5 – 8.0 (7.8 ±

0.3) µm long × 18.0 – 21.0 (19.0 ± 1.4) µm wide (Fig. 6.3e). The shell valves are smooth and equal in size, tapering to a broadly rounded end while the sutural line is straight with two almost spherical polar capsules situated medially (Figs. 6.3e, f). The polar capsules measure 3.0 – 3.2 (3.1 ± 0.08) µm long × 3.0 – 3.1 (3.0 ± 0.04) µm wide, with polar filaments that have two to three coils in each polar capsule. The uninucleate sporoplasm is also transversely elongated and extends into each of the two shell valves, almost filling the entire spore cavity (Figs. 6.3e, f).

Remarks: Amongst the three *Ceratomyxa* species collected from the De Hoop Nature reserve, *Ceratomyxa* sp. C is has the longest spore length and most box-like appearance. Morphologically the most similar African species is *C. lagocephali* (Kpatcha *et al.* 1996b), but has a relatively longer spore body length than *Ceratomyxa* sp. C (Table 6.1) giving the spores of *Ceratomyxa* sp. C a narrower appearance than the broader spores of *C. lagocephali*. Another similar African species is *C. acanthuri* Kpatcha, Diebakate, Faye and Toguebaye, 1996 described from the gall bladder of *Acanthurus monroviae* in Senegal (Kpatcha *et al.* 1996b). *Ceratomyxa acanthuri* does, however, have a much longer spore length and narrower spore width (Table 6.1) than the slightly more transversely elongated spores of *Ceratomyxa* sp. C. Compared with species throughout the world, *Ceratomyxa* sp. C is similar to *C. buri* described from Japan by Yokoyama and Fukuda (2001). The spores of *C. buri* have a narrower spore width and is anteriorly more convex, compared to the broadly crescent-shaped spores of *Ceratomyxa* sp. C. *Ceratomyxa* sp. C does not conform to the description of any known *Ceratomyxa* species.

Table 6.1. Spore measurements of African *Ceratomyxa* Thélohan, 1892 species including those from the present study [Key: **PC** – polar capsule; **np** – not provided; * - species has both spherical and pyriform-shaped polar capsules].

Species	Spore length (µm)	Spore width (µm)	PC length (µm)	PC width (µm)	Reference
Ceratomyxa acanthuri Kpatcha, Diebakate, Faye and Toguebaye, 1996	10.54 ± 0.8 (10.0-12.0)	16.57 ±0.9 (16.0-18.0)	2.75 ± 0.6 (2.0-3.20)	np	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Ceratomyxa australis Gaevskaya and Kovaleva, 1979	4.0-5.3	13.3-15.0	2.0-2.6	1.3	Gaevskaya and Kovaleva (1979)
* *Ceratomyxa fistulariae* Kpatcha, Diebakate, Faye and Toguebaye, 1996	10.25 ± 0.6 (10.0-12.0)	39.64 ± 0.56 (38.8-40.0)	5.21 ± 0.5 (4.5-5.5) in diameter	np	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
			5.15 ± 0.38 (4.5-6.0)	4.21 ± 0.41 (4.0-4.5)	
Ceratomyxa lagocephali Kpatcha, Diebakate, Faye and Toguebaye, 1996	21.68 ± 0.6 (20.0-22.5)	9.28 ± 0.4 (9.0-10.50)	4.29 ± 0.48 (3.5-4.5) µm in diameter	np	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Ceratomyxa shulmani Dubina and Isakov, 1976	17	120	11.0	10.0	Dubina and Isakov (1976)
Ceratomyxa syacii Kpatcha, Diebakate, Faye and Toguebaye, 1996	23.0 ± 0.9 (22.5-25.0)	23.55 ± 0.9 (22.5-25.0)	1.87 ± 0.1 (1.5-2.0) µm in diameter	np	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Ceratomyxa trachinocephali Kpatcha, Diebakate, Faye and Toguebaye, 1996	11.5 ±0.8 (10-12)	49.66 ±0.7 (48-50)	2.7 ±0.4 (2.0-3.0) in diameter	np	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Ceratomyxa. trichuiri Kpatcha, Diebakate, Faye and Toguebaye, 1996	10.62 ± 0.9 (10.0-12.0)	99.2 ± 0.9 (98.0-100.0)	4.85 ± 0.2 (4.5-5.0) in diameter	np	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Ceratomyxa. truncata Kpatcha, Diebakate, Faye and Toguebaye, 1996	6.08 ± 0.16 (5.0-7.0)	26.05 ± 0.7 (25.5-27.0)	2.17 ± 0.1 (2.0-2.25) in diameter	np	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Ceratomyxa Thélohan, 1892 sp. A	4.0 - 5.5 (4.5 ± 0.5)	12.0 - 17.5 (15.4 ± 1.4)	2.0 – 3.0 (2.7± 0.3)	2.0 - 2.5 (2.1 ± 0.2)	Present study
Ceratomyxa sp. B	6.5 – 8.0 (7.1 ± 0.6)	17.0 – 22.0 (18.2 ± 1.7)	2.3 - 3.0 (2.7 ± 0.4)	2.0 – 3.0 (2.4 ± 0.4)	Present study
Ceratomyxa sp. C	7.5 – 8.0 (7.8 ± 0.3)	18.0 – 21.0 (19.0 ± 1.4)	3.0 – 3.2 (3.1 ± 0.08)	3.0 – 3.1 (3.0 ± 0.04)	Present study

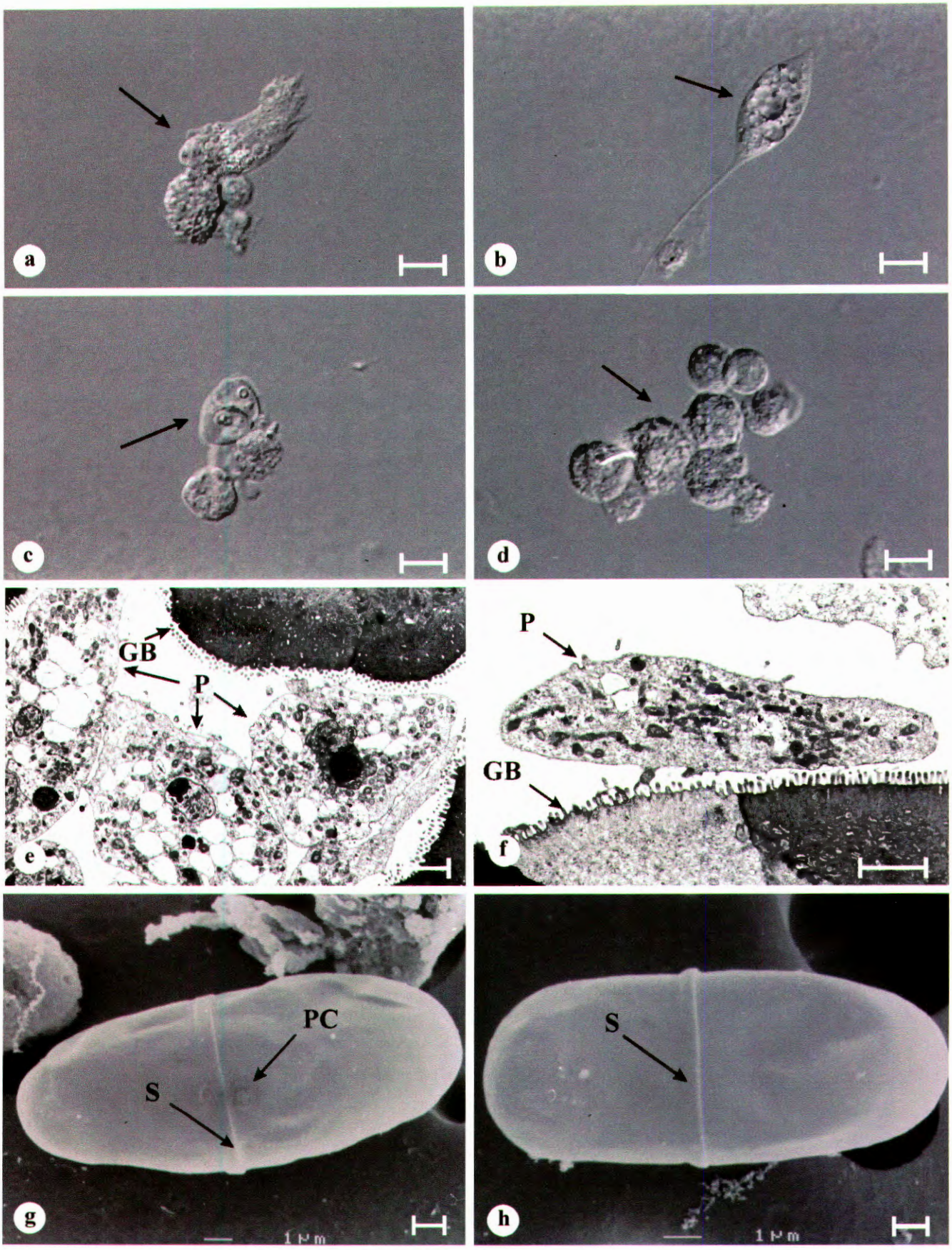


Figure 6.2. Light micrographs (**a-d**), transmission electron micrographs (**e, f**) and scanning electron micrographs of *Ceratomyxa* Thélohan, 1892 sp. A infecting the gall bladder of *Clinus superciliosus* (Linnaeus, 1758) from the Cape south coast of South Africa. **a-d**. Live plasmodia (arrows). **e, f.** Plasmodia (P) seen associated with the gall bladder epithelium (GB). **g, h.** Spores showing the sutural ridge (S) and polar filament discharge ducts (PC). Scale bars: **a-d**. 10 µm. **e-h**. 1µm.

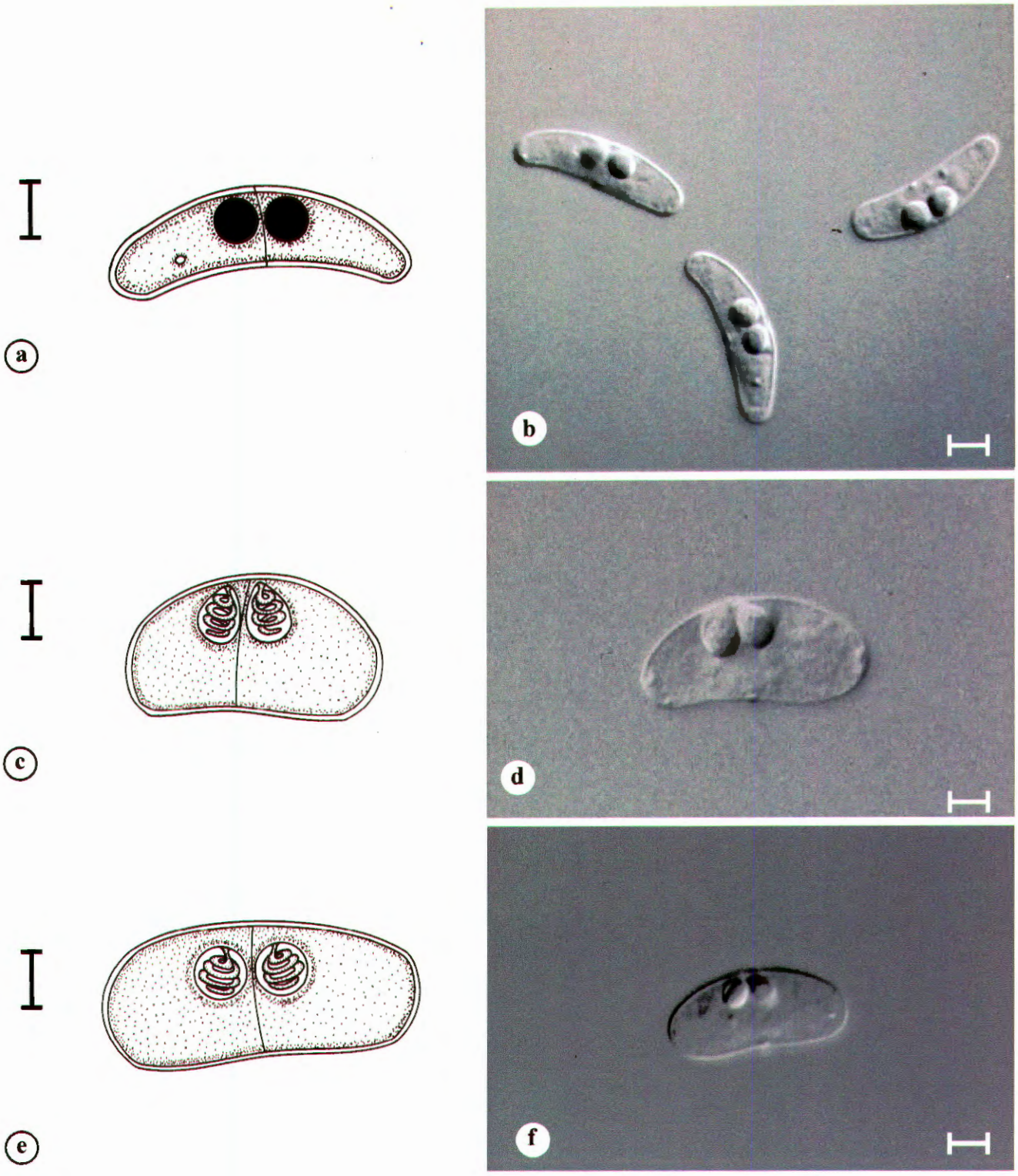


Figure 6.3. Line drawings (**a, c, e**) and micrographs of live spores (**b, d, f**) of *Ceratomyxa* Thélohan, 1892 species infecting the gall bladders of intertidal fishes along the Cape south coast, South Africa. **a, b.** *Ceratomyxa* sp. A from *Clinus superciliosus* (Linneaus, 1758). **c, d.** *Ceratomyxa* sp. B from *C. cottoides* Valenciennes, 1836. **e, f.** *Ceratomyxa* sp. C from *Amblyrhynchotes honckenii* (Bloch, 1795). Scale bars: 10 µm.

Genus *Henneguya* Thélohan, 1892

The genus *Henneguya* comprises well over 174 known species throughout the world. The majority of these species have been described from freshwater fishes and are occasionally also found parasitising marine fishes (Hallett and Diamant 2001). A recent publication by Eiras (2002), contains a comprehensive synopsis of the species of the genus *Henneguya* that would facilitate any research of this genus. Myxosporeans of the genus *Henneguya* are characterised by having rounded, ellipsoid or spindle-shaped spores that are biconvex in sutural view. The spores have two smooth shell valves with an extended caudal projection and two polar capsules, which may sometimes be very elongated.

Henneguya species are important fish pathogens, with the gills often being the most heavily infected organ (Azevedo and Matos 1995). In Africa only eight *Henneguya* species have been described from marine fishes (see Chapter 3, Table 3.4). All of these species have been described from the coast of Senegal (Kpatcha *et al.* 1997). The only other record of a *Henneguya* species is that of Bahri, Hassine and Marqués (1996) who noted the presence of a *Henneguya* sp. infecting the gills of *Sparus aurata* in Tunisia.

***Henneguya* species from the Cape south coast, South Africa**

The results of this study revealed the presence of one *Henneguya* species infecting the gills of two intertidal fish hosts at both the De Hoop Nature Reserve and Jeffrey's Bay.

***Henneguya* sp. B.**

(Fig. 6.4)

Hosts: *Clinus superciliosus* (Linnaeus, 1758), *C. cottoides* Valenciennes, 1836

Site of infection: Gills and gill arches.

Localities: De Hoop Nature Reserve (34°28'S, 20°30'E), Jeffrey's Bay (34°2.2'S; 24°56.5'E), South Africa.

Total prevalence: 2.3 % (3/131).

Reference material: Deposited in the Aquatic Parasitology Research Group, Department of Zoology and Entomology, University of the Free State, Bloemfonteins' Parasite Collection.

Description of vegetative stages: Large histozoic polysporic plasmodia were found within the blood vessels of the gills and gill arches. Plasmodia were white in colour and varied in shape and size measuring 1 – 3 mm in length.

***Description of spores (based on 20 live spores)*:** Mature spores are ovoid to spherical in valvular view and bi-convex in sutural view (Figs. 6.4a, b). The anterior and posterior ends are equally rounded with the spore body measuring 9.0 – 11.0 (10.0 ± 0.61) µm long × 7.0 – 8.5 (7.9 ± 0.37) µm wide. The shell valves are smooth and equal in size with a very wide sutural ridge visible (Figs. 6.4a, b, e, f). Two separate, very long and thin filiform caudal projections extend from the posterior of the spore. The total length of the spores is 43.0 – 46.0 (44.6 ± 1.97) µm. Two pyriform-shaped polar capsules are situated in the anterior end of the spore and measure 4.0 – 4.2 (4.0 ± 0.06) µm long × 2.0 – 2.5 (2.17 ± 0.19) µm wide (Figs. 6.4c, d). Four to five coils can be seen in the polar filament (Fig. 6.4d). A binucleate sporoplasm is situated directly behind the two polar capsules, almost filling the entire spore cavity.

***Remarks*:** All of the eight African marine *Henneguya* species described from fishes along the Senegalese coast by Kpatcha *et al.* (1997) have very similar morphological appearances. One very prominent characteristic that they all exhibit is a very wide sutural ridge. The same characteristic was found in *Henneguya* sp. B. Although all the species described in Senegal are very similar to *Henneguya* sp. B, they each exhibit one or more distinguishing characteristics.

The spores of *H. brachydeuteri* Kpatcha, Diebakate, Fall and Toguebaye, 1997 from the heart of *Brachydeuterus auritus* are generally shorter in total length (Table 6.2) and appear to have a much wider sutural ridge than *Henneguya* sp. B. *Henneguya jaolensis* Kpatcha, Diebakate, Fall and Toguebaye, 1997, from the kidney of *Cephalopholis taeniops*, have the same average total spore length, but have a shorter spore body length (Table 6.2) compared to that of *Henneguya* sp. B. The spores of *H. kayarensis* Kpatcha, Diebakate, Fall and Toguebaye, 1997, from the liver of *Galeoides decadactylus*, are much longer in total spore length and generally have a smaller spore body (Table 6.2) than *Henneguya* sp. B. *Henneguya lutjani* Kpatcha, Diebakate, Fall and Toguebaye, 1997, from the gills of *Lutjanus agennes*, also have much longer spores that are generally larger than those of *Henneguya* sp. B. The spores of *H. mbourensis* Kpatcha, Diebakate, Fall

and Toguebaye, 1997, from the kidney of *Dentex canariensis*, are much shorter in total length than the spores of *Henneguya* sp. B. Morphologically the spores of *H. oukamensis* Kpatcha, Diebakate, Fall and Toguebaye, 1997, from the gills of *Mugil cephalus*, are most distinct from *Henneguya* sp. B. These are much shorter and have an almost spherical spore body compared with the more elongated spores of *Henneguya* sp. B that do not have a totally spherical spore body. *Henneguya priacanthi* Kpatcha, Diebakate, Fall and Toguebaye, 1997, from the gills of *Pricanthus arenatus*, is most similar to *Henneguya* sp. B, but has a relatively shorter total spore length and generally smaller polar capsules (Table 6.2). The spores of *H. yoffensis* Kpatcha, Diebakate, Fall and Toguebaye, 1997, from the gills and heart of *Sparus caeruleosticutus*, have the same average total spore length, but have a larger spore body (Table 6.2) than *Henneguya* sp. B.

Compared with marine species from around the world *Henneguya* sp. B differs in the following ways. *Henneguya lesteri* Hallet and Diamant, 2001 from the gills of *Sillago analis* in Queensland, Australia has generally smaller spores that are morphologically very different (Hallett and Diamant 2001).

Henneguya sp. B does therefore not conform to the description of any marine *Henneguya* species. No *Henneguya* species have ever been recorded from the South African coast and since *Henneguya* sp. B differs morphologically and morphometrically from any known *Henneguya* species, it can be regarded as a new species.

Table 6.2. Spore measurements of African *Henneguya* Thélohan, 1892 species including those from the present study [Key: **CL** – caudal length; **P** – present study; **PC** – polar capsule; **R** – reference; **SBL** – spore body length; **SBW** – spore body width; **TL** -total length; *- species has both spherical and pyriform-shaped polar capsules; 1 – Kpatcha, Faye, Diebakate, Fall and Faye (1997)].

Species	TL (µm)	SBL (µm)	CL (µm)	SBW (µm)	PC length (µm)	PC width (µm)	R
Henneguya brachydeuteri Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	37.18 ± 0.98 (36.0-41.0)	11.5 ± 0.5 (10.0-12.0)	26.9 ± 0.9 (26-29)	8.36 ± 0.75 (7-9)	4.33 ± 0.5 (4.0-5.0)	2.6 ± 0.5 (2.0-3.0)	1
Henneguya joalensis Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	44.81 ± 0.2 (44.5-45.0)	8.9 ± 0.1 (8.5-9.0)	35.25 ± 0.97 (34.0-36.0)	6.37 (6.0-7.0)	Smaller: 3.73 ± 1.18 (3.4 - 4.5)	Smaller: 1.86 ± 0.09 (1.8 – 2.0)	1
					Larger: 4.78 ± 0.45 (4.5-5.5)	Larger: 2.53 ± 0.21 (2.25-3.0)	
Henneguya kayarensis Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	54.70 ± 0.83 (52.0-56.5)	8.41 ± 0.65 (7.0-9.0)	46.29 ± 0.98 (45.0-47.5)	6.6 ± 0.41 (6.0-7.0)	4.32 ± 0.19 (4.0-4.5)	2.36 ± 0.11 (2.25-2.5)	1

Table 6.2 continued. Spore measurements of African *Henneguya* Thélohan, 1892 species, including those from the present study [Key: **CL** – caudal length; **P** – present study; **PC** – polar capsule; **R** – reference; **SBL** – spore body length; **SBW** – spore body width; **TL** -total length; *- species has both spherical and pyriform-shaped polar capsules; 1 – Kpatcha, Faye, Diebakate, Fall and Faye (1997)].

Species	TL (µm)	SBL (µm)	CL (µm)	SBW (µm)	PC length (µm)	PC width (µm)	R
Henneguya lutjani Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	49.96 ± 0.98 (47.25-50.4)	11.86 ± 0.6 (11.25-13.0)	37.22 ± 0.98 (36.0-38.25)	7.29 ± 0.73 (6.0-8.0)	3.84 ± 0.58 (3.0-4.5)	2.96 ± 0.44 (2.25-3.5)	1
Henneguya mbourensis Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	29.62 ± 0.99 (28.0-33.)	10.26 ± 0.44 (10.0-11.0)	20.66 ± 0.99 (20.0-22.5)	7.98 ± 0.98 (6.5-9.0)	4.78 ± 0.5 (3.5-5.0)	2.4 ± 0.5 (2.0-3.5)	1
Henneguya oukamensis Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	20.86 ± 1.47 (16.0-24.0)	10.9 ± 0.57 (9.0-13.0)	9.9 ± 1.36 (6.0-14.0)	9.0 ± 0.44 (5.0-9.0)	3.78 ±0.48 (3.0-4.0)	2.43 ± 0.42 (2.0-3.0)	1
Henneguya priancanthi Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	39.74 ± 0.99 (36.5-41.0)	9.18 ± 0.22 (9.0-9.5)	28.12 ± 0.1 (22.5-31.5)	7.32 ± 0.5 (6.5-8.0)	2.16 ± 0.1 (2.0-2.5)	1.34 ± 0.1 (1.0-2.0)	1
Henneguya yoffensis Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	46.18 ± 0.36 (37.0-50.0)	13.38 ± 0.19 (12.0-15.0)	32.13 ± 0.27 (24.0-36.0)	9.13 ± 0.31 (8.0-11.0)	3.47 ± 0.19 (3.0-4.0)	2.30 ± 0.13 (2.0-3.0)	1
Henneguya Thélohan, 1892 sp. B	43.0 – 46.0 (44.6 ± 1.97)	9.0 – 11.0 (10.0 ± 0.61)	34.0 – 35.0 (34.0 ± 1.36)	7.0 – 8.5 (7.9 ± 0.37)	4.0 – 4.2 (4.0 ± 0.06)	2.0 – 2.5 (2.17 ± 0.19)	P

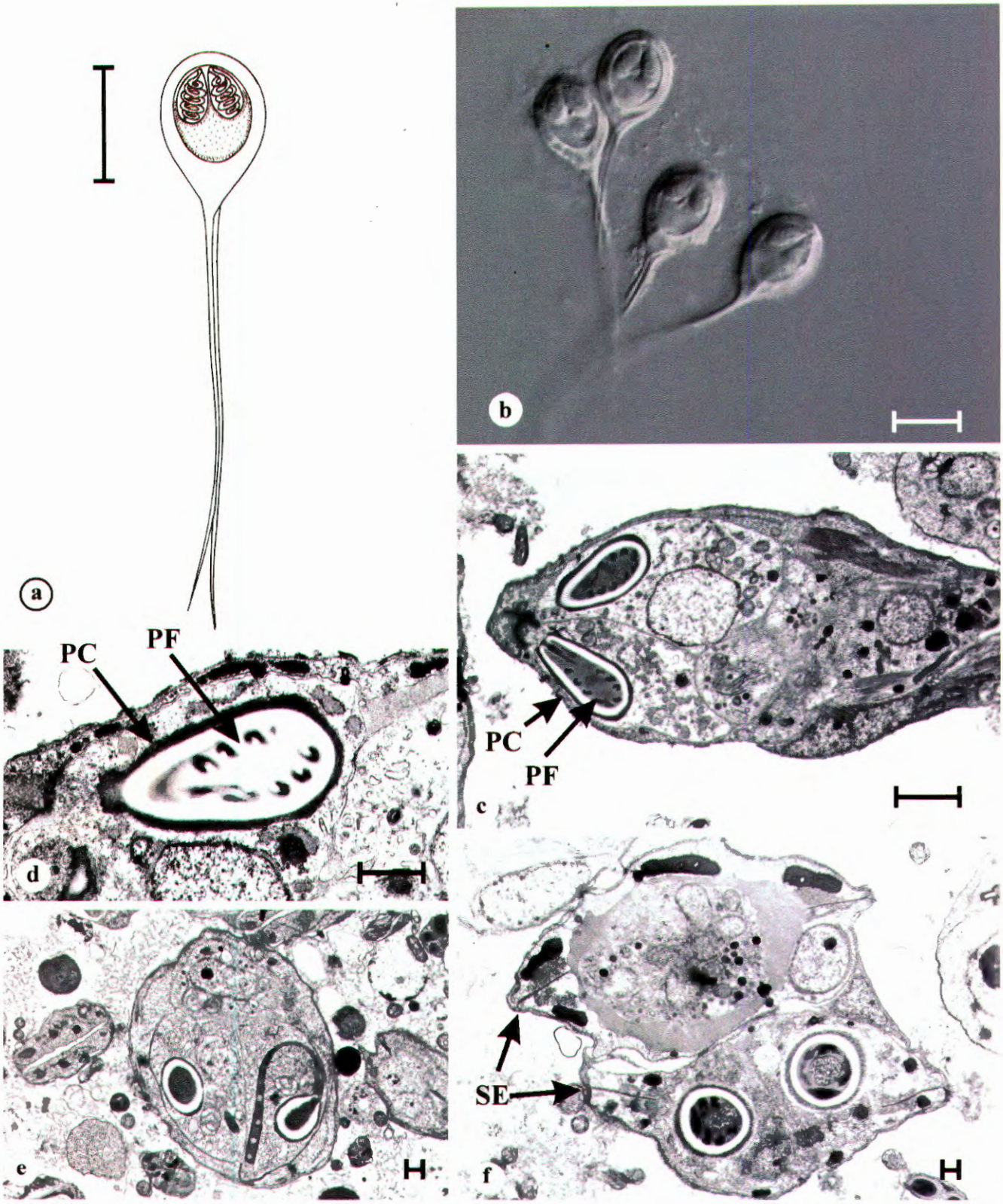


Figure 6.4. Line drawing (**a**), micrograph of live spores (**b**) and scanning electron micrographs (**c-f**) of *Henneguya* Thélohan, 1892 sp. B from the gills of *Clinus superciliosus* (Linnaeus, 1758) collected from the Cape south coast, South Africa. **a, b**. Spores. **c.** Section through spore illustrating two polar capsules (PC) with polar filaments (PF). **d.** Section through polar capsule (PC) illustrating the coiled polar filament (PF). **e.** Section through spore body showing developing polar capsule and polar filament. **f.** Transverse section though two adjacent spores showing the shell valves (SV) joining along a sutural edge (SE). Scale bars: **a, b.** 10 µm, **d-f.** 1µm.

Genus *Myxidium* Bütschli, 1882

The genus *Myxidium* is widely distributed in both marine and freshwater fish and occasionally occurs in reptiles and amphibians (MacKenzie and Kalavati 1995). Over 190 species have been described from both freshwater and marine fish throughout the world (Canning, Curry, Anderson and Okamura 1999). The first species to be described in this genus was *M. lieberkuehni* Bütschli, 1882 (Jayasri and Hoffmann 1982).

Members of the genus *Myxidium* are characterised by having spores that are fusiform, straight or slightly sigmoid, with more or less pointed ends. The shell valves are either smooth or have ridges with a sutural line bisecting the spore. Two mostly pyriform polar capsules are situated at each end of the spore. One binucleate sporoplasm is located as a rule between the polar capsules (Lom and Dyková 1992). They are primarily coelozoic, invading the gall bladder, urinary bladder and kidney tubules of marine and freshwater fishes. Most species have a wide geographical distribution and are host specific (Padma-Dorothy and Kalavati 1992). A few histozoic species have been described in freshwater hosts (Diamant, Lom and Dyková 1994).

As with most of the marine myxosporean research, very little is known about the genus *Myxidium* along the African coastline. A mere four species are known from the entire African coast, three of which were described from Senegal (Kpatcha *et al.* 1996a) (see Chapter 3, Table 3.4). As mentioned in Chapter 3, Fantham (1930) recorded three different species from the genus *Myxidium* whilst conducting a survey of the marine parasitic fauna along the southern Cape coast of South Africa. In this paper, he described *Myxidium contortum* Fantham, 1930, from the gall bladder of the blenny *Blennius cornutus* in False Bay, *M. pagelli* Fantham, 1930 from the bile of white steenbras, *Lithognathus lithognathus* bought at a fish market in Cape Town and probably caught in False Bay and *M. parvoviforme* Fantham, 1930 from the bile of a cob, *Argyrosomus hololepidotus* at Kalk Bay (see Chapter 3; Table 3.3; Figs. 3.3f, g, h).

The first valid species from the genus *Myxidium* to be described from the African coast was *Myxidium gigantissimum* Dubina and Isakov, 1976 from the gall bladder of the deep-sea fish *Alepocephalus australis* off the coast of South Africa (Dubina and Isakov 1976). Many years later *Myxidium giganteum* Doflein, 1898 was found infecting the gall bladder of *Raja miraletus* off the coast of Senegal by Kpatcha *et al.* (1996a). *Myxidium*

abudefdufi Kpatcha, Diebakate and Toguebaye, 1996 and *M. elopsi* Kpatcha, Diebakate and Toguebaye, 1996 were described from the gall bladder of *Abudefduf marginatus* and the intestine of *Elops senegalensis*, respectively, off the coast of Senegal by Kpatcha *et al.* (1996a).

Myxidium species from the Cape south coast, South Africa

Results obtained from the surveys conducted along the Cape south coast of South Africa revealed two myxosporeans from the genus *Myxidium* infecting the gall bladders of two intertidal fishes.

Myxidium sp. A

(Figs. 6.5a, b, c)

Host: *Chorisochimus dentex* (Bloch, 1795).

Site of infection: Gall bladder and lumen of kidney tubules.

Localities: De Hoop Nature Reserve (34°28‘S, 20°30’E), Jeffrey’s Bay (34°2.2’S; 24°56.5’E), South Africa.

Total prevalence: 100 % (5/5).

Reference material: Deposited in the Aquatic Parasitology Research Group, Department of Zoology and Entomology, University of the Free State, Bloemfonteins’ Parasite Collection.

***Description of vegetative stages*:** Many tiny rounded to sub-spherical plasmodia were seen drifting in the bile of the gall bladder. The plasmodia were transparent and granular, sometimes with fingerlike projections extending from the clusters of trophozoites measuring 5 – 20 µm in length.

***Description of spores (based on 20 live spores)*:** Mature spores are broadly fusiform to oval with the ends pointed diagonally towards opposite sides in sutural view, measuring 8.0-9.5 (8.7 ± 0.44) µm long × 5.0 – 6.5 (5.6 ± 0.47) µm wide (Figs. 6.5a, b, c). Two smooth equal shell valves join along a narrow sutural line. Two equal pyriform-shaped polar capsules are situated diagonally in opposite ends of the spore cavity, measuring 2.8 – 4.0 (3.4 ± 0.48) µm long × 1.5 – 2.2 (2.1 ± 0.24) µm wide. There appears to be four to five coils in each polar filament (Fig. 6.5a). A single binucleate sporoplasm fills almost the entire spore cavity.

***Remarks*:** *Myxidium* sp. A. differs from all four the African species, not even conforming to any of the species recorded by Fantham (1930) (see Fig. 3.3, Chapter 3). Compared with the slender, arcuate and transversely elongated spores of *M. gigantissimum* (Table 6.3), the spores of *Myxidium* sp. A are more rounded and very much smaller. On the other hand, the spores of *M. giganteum* are fusiform with more sharply pointed ends and are generally larger than the spores of *Myxidium* sp. A (Table 6.3). Furthermore, the polar capsules of *M. giganteum* are situated directly opposite each other and are also generally larger and more pyriform-shaped than the diagonally situated, smaller polar capsules of *Myxidium* sp. A. *Myxidium* sp. A also differs from *M. abudefdufi*. The spores of the latter have polar capsules situated directly opposite each other, unlike the diagonal polar capsules of *Myxidium* sp. A. Amongst the African *Myxidium* species, *Myxidium* sp. A is most similar to *M. elopsi*. The spore dimensions are very similar, with the only difference being that the polar capsules of *M. elopsi* are not diagonally situated, as in the case of *Myxidium* sp. A.

Compared to marine species from the rest of the world, the following differences can be noted. The spores of *Myxidium* sp. A differ from *M. giardi* Cèpéde, 1906 by having diagonally placed polar capsules that lie in the plane of the sutural line. *Myxidium* sp. A does not conform to any of the known species from the genus *Myxidium.*

***Myxidium* sp. B**

(Figs. 6.5d, e, f)

Host: *Diplodus sargus* (Smith, 1844).

Site of infection: Gall bladder and lumen of kidney tubules.

Locality: De Hoop Nature Reserve (34°28‘S, 20°30’E), South Africa.

Total prevalence: 14% (5/36).

Reference material: Deposited in the Aquatic Parasitology Research Group, Department of Zoology and Entomology, University of the Free State, Bloemfonteins’ Parasite Collection.

***Description of vegetative stages*:** Many tiny elongated, finger-like plasmodia were seen drifting in the bile of the gall bladder. The plasmodia were transparent and granular

measuring 4 – 5 µm in length. Infected gall bladders were dark yellow in color and the epithelium appeared thicker than normal.

***Description of spores (based on 20 live spores)*:** Mature spores are broadly fusiform to oval in valvular view, measuring 5.5 – 8.0 (6.7 ± 0.6) µm long × 9.0 – 11.0 (6.7 ± 0.6) µm wide (Figs. 6.5 d, e, f). Two ridged shell valves adhere along a narrow sutural ridge (Fig. 6.5e). The polar capsules are almost spherical in shape and situated opposite each other, one at each end of the spore, measuring 2.0 – 3.5 (10.2 ± 0.7) µm long × 2.0 – 3.5 (2.7 ± 0.33) µm wide. The number of coils per polar filament is difficult to observe. A single binucleate sporoplasm is situated between the polar capsules, almost filling the entire spore cavity.

Remarks: *Myxidium* sp. B is possibly the same species collected by Fantham (1930) (see Chapter 3, Fig. 3.3g), which he named *M. parvoviforme*, from the bile of the cob, *Argyrosomus hololepidotus* from Kalk Bay. The spores of *Myxidium* sp. B are distinct from all the known African species, since they exhibit ridged shell valves. Three species described from fishes in Brazil also exhibit ridged shell valves, but *Myxidium* sp. B differs from them in the following ways. *Myxidium cruzi* Penido, 1927, *M. gurgeli* Pinto, 1928 and *M. cholecysticum* Cordeiro and Gioa, 1990 all exhibit pointed shell valves (Gioia and Cordeiro 1996), compared with the more rounded shell valves of *Myxidium* sp. B.

Table 6.3. Spore measurements of African Marine *Myxidium* Bütschli, 1882 including the species from the present study [Key: **PC** – polar capsule; **np** – not provided].

Species	Spore length (µm)	Spore width (µm)	PC length (µm)	PC width (µm)	Reference
Myxidium abudefdufi Kpatcha, Diebakate and Toguebaye, 1996	9.14 ± 0.3 (9.9)	6.79 ± 0.12 (6.75 – 7.20)	2.72 ± 0.06 (2.7 – 2.9)	2.25	Kpatcha, Diebakate and Toguebaye (1996)
M. elopsi Kpatcha, Diebakate and Toguebaye, 1996	9.0 ± 0.94 (7.0 – 10.0)	5.41 ± 0.94 (4.5 – 8.0)	2.82 ± 0.59 (2.0 – 3.5)	1.74 ± 0.5 (1.5 – 2.7)	Kpatcha, Diebakate and Toguebaye (1996)
M. giganteum Doflein, 1898	19.93 ± 0.24 (19.0-20.0)	9.54 ± 0.8 (8.0-10.0)	4.67 ± 0.62 (4.0-5.4)	2.87 ± 0.21 (2.0-3.0)	Kpatcha, Diebakate and Toguebaye (1996)
M. gigantissimum Dubina and Isakov, 1976	42.5 – 97.5	5.0 – 8.5	np	np	Dubina and Isakov (1976)
Myxidium Bütschli, 1882 sp. A	8.0-9.5 (8.7 ± 0.44)	5.0 – 6.5 (5.6 ± 0.47)	2.8 – 4.0 (3.4 ± 0.48)	1.5 – 2.2 (2.1 ± 0.24)	Present study
Myxidium sp. B	9.0 – 11.0 (6.7 ± 0.6)	5.5 – 8.0 (6.7 ± 0.6)	2.0 – 3.5 (2.7 ± 0.33)	2.0 – 3.5 (10.2 ± 0.7)	Present study

Genus *Myxobolus* Bütschli, 1882

The genus *Myxobolus* forms an enormous group with more than 690 species described from fishes throughout the world (Lom and Dyková 1992). This genus is characterised by having spores that are ovoid or rounded in valvular view and biconvex in sutural view with smooth shell valves. Usually two pyriform-shaped polar capsules are found in the spore body, with a sutural ridge that may extend to a cresentic ledge. A binucleate sporoplasm is present, often with an iodinophilous vacuole and the trophozoites are also mostly large and polysporic with pansporoblast formation. Most species are found histozoically in freshwater fishes with a few in marine and estuarine fishes. Some species have also been recorded from amphibians.

Only approximately 24 *Myxobolus* species in the world have been described from marine fish hosts (Lom and Dyková 1994). Approximately 62 *Myxobolus* species are known from Africa of which only 11 have been found infecting African marine fishes (see Chapter 3, Table 3.4). All these species have been collected from mullet hosts in Africa. With the exception of *M. episquamalis* Egusa, Maeno and Sorimachi, 1990 (a possible junior synonym of *M. exiguus* Thélohan, 1892), *M. exiguus*, *M. mülleri* Bütschli, 1882 and *M. spinacuravature* Maeno, Ogawa and Egusa, 1990, all the species were originally described in Africa.

The genus *Myxobolus* has often been associated with mullet species throughout the world, with many histozoic *Myxobolus* species known to induce severe harm to these hosts (Sitjá-Bobadilla and Alvarez-Pellitero 1993). The family Mugilidae has a worldwide distribution with members living in diverse environmental conditions. Mullet culture is a flourishing industry in many parts of the world especially in Mediterranean countries such as Italy, Israel, Egypt and Tunisia. A notorious example of such a pathogenic *Myxobolus* species is *M. exiguus*, which was reported to be responsible for devastating infections in the Black Sea provoking serious lesions in the gills and leading to the death of 600 kg of mullet per kilometer of coast (Shulman 1966; Bahri *et al.* 1995). More than 22 *Myxobolus* species have been described from mugilid fishes around the world (Landsberg and Lom 1991; Lom and Dyková 1994; Bahri and Marqués 1996; Fall *et al.* 1997; Faye *et al.* 1999).

Mullet are one of the most important resources of the Tunisian lagoons and represent a high percentage of the fish catches (Bahri and Marqués 1996). *Mugil cephalus* from

Tunisia has been found infected with several species of the genus *Myxobolus*. In Tunisia many mullet caught are rejected because of their unpleasant appearance thought to be caused by the skin myxosporean, *M. exiguus* (Bahri *et al.* 1995). Recognising the importance of mullet in aquaculture, Bahri and Marqués (1996) investigated the *Myxobolus* species infecting *Mugil cephalus* in Ichkeul Lagoon in Tunisia. They collected *M. episquamalis* from the distal parts of the scales and *M. spinacurvatura* from the mesentric vessels. *Myxobolus bizerti* Bahri and Marqués, 1996 was described from the gill filaments and *M. ichkeulensis* Bahri and Marqués, 1996 from the gill arches. Bahri and Marqués (1996) found that the pathological effects of the species were very variable. *Myxobolus episquamalis* invaded the whole body of the mullet, debilitating it and leading to its commercial rejection. *Myxobolus ichkeulensis* weakened the cartilaginous tissue of the gill arches and the cysts of *M. bizerti* possibly blocked the lumen of the blood vessels of the gill lamellae. Mullets infected with *M. episquamalis* had no commercial value even though they did not differ in behavior and condition of normal fish (Egusa, Maeno and Sorimachi 1990).

Mugil cephalus is also an economically important fish species in Senegal and forms a large part of the total catch in the area. Fall *et al.* (1997) collected five myxosporeans from the genus *Myxobolus* from *M. cephalus* in this region. *Myxobolus exiguus* and *M. mülleri* were recorded for the first time in Senegal. *Myxobolus hannensis* Fall, Kpatcha, Diebakate, Faye and Toguebaye, 1997, *M. goreensis* Fall, Kpatcha, Diebakate, Faye and Toguebaye, 1997 and *M. raibuti* Fall, Kpatcha, Diebakate, Faye and Toguebaye, 1997 were described as new species. Two years later Faye *et al.* (1999) reported a third new species, *M. hani* Faye, Kpatcha, Diebakate, Fall and Toguebaye, 1999, from the gills of *Mugil curema* in Senegal.

Myxobolus species from the Cape south coast, South Africa

During surveys conducted along the Cape south coast, a *Myxobolus* species was discovered infecting the gills of *Liza richardsonii* at the De Mond Nature Reserve. In Table 6.4 comparative spore measurements of *Myxobolus* species described from African *Myxobolus* species are provided.

***Myxobolus* sp. B**

(Figs. 6.5g, h, i)

Type host: *Liza richardsonii* (Smith, 1846)

Site of infection: Gills.

Localities: De Mond Nature Reserve**,** De Hoop Nature Reserve (34°28‘S, 20°30’E), South Africa.

Total prevalence: 10 % (5/48).

Reference material: Deposited in the Aquatic Parasitology Research Group, Department of Zoology and Entomology, University of the Free State, Bloemfonteins’ Parasite Collection.

***Description of vegetative stages*:** Many tiny rounded to sub-spherical sporogonic plasmodia were found infecting the primary gill lamellae. They were whitish in colour and measured 0.5 mm – 1 mm in diameter.

***Description of spores (based on 25 fixed spores)*:** Mature spores are sub-spherical to spherical in valvular view with two smooth shell-valves joining along relatively well-defined, smooth-edged sutural ridge (Figs. 6.5g, h, i). The spore measurements are 6.5 – 9.0 (7.9 ± 0.8) µm long × 6.0 – 7.5 (6.9 ± 0.5) µm in width. No intercapsular process is visible. Two pyriform-shaped polar capsules are situated in the anterior of the spore extending to at least the mid-length of the spore, measuring 1.5 – 3.0 (2.3 ± 0.5) µm long × 1.5 – 1.72 (1.6 ± 0.1) µm wide. Each polar capsule contains a polar filament with three to four filaments turns. No mucous envelope or obvious iodinophilous vacuole is visible.

***Remarks*:** *Myxobolus* sp. B resembles *M. bizerti*, described from Tunisia by Bahri and Marqués (1996). The spores of *M. bizerti* are, however, generally larger and have numerous notches along the sutural edge, which are absent in the smaller spores of *Myxobolus* sp. B. The spores of *M. cephalus* Iversen, Chitty and Van Meter, 1971 described from *M. cephalus* in the U.S.A by Iversen, Chitty and Van Meter (1971) are also spherical in shape, but the presence of an intercapsular process distinguishes this species from *Myxobolus* sp. B. *Myxobolus* sp. B differs from *M. ichkeulensis*, also described from the gills of *M. cephalus* in Tunisia by Bahri and Marqués (1996) in having smaller spores that have a smooth sutural lining. This compares with the larger spores of *M. ichkeulensis*, which have distinct sutural markings. Finally, compared with *M.*

mülleri, *Myxobolus* sp. B again lacks an intercapsular process and distinct notches along the sutural edge, which are both present in *M. mülleri*. Since *Myxobolus* sp. B does not conform to the description of any known *Myxobolus* species infecting mugilid hosts, it is described as a new species. This is the first record of a myxosporean infection in mugilid hosts in South Africa.

Table 6.4. Spore measurements of *Myxobolus* Bütschli, 1882 species infecting fishes in Africa.

Species	Spore body (µm)	Polar capsules (µm)	Reference
Myxobolus bizerti Bahri and Marques, 1996	14.2 (14.0-14.5)	6.5 (6.0-7.0) × 5.75 (5.5-6.0)	Bahri and Marques (1996)
Myxobolus episquamalis Egusa, Maeno and Sorimachi, 1990	8.6 (7.5-9.5) × 6.8 (6.0-7.5)	4.4 (3.8-5.0) × 2.2 (2.0-3.0)	Egusa, Maeno and Sorimachi (1990)
Myxobolus exiguus Thélohan, 1882	8.0-9.5 × 6.0-7.5	1.5 × 4.4-4.8	Fall, Kpatcha, Diebakate, Faye and Toguebaye (1997)
Myxobolus goreensis Fall, Kpatcha, Diebakate, Faye and Toguebaye, 1997	10.9 (10-13) in diamter	4.4 (4-5) × 3.0 (2-4)	Fall, Kpatcha, Diebakate, Faye and Toguebaye (1997)
Myxobolus hannensis Fall, Kpatcha, Diebakate, Faye and Toguebaye, 1997	13.9 (13-15) in diameter	8.9 (7-9) × 5.7 (5-6)	Fall, Kpatcha, Diebakate, Faye and Toguebaye (1997)
Myxobolus hani Faye, Kpatcha, Diebakate, Fall and Toguebaye, 1999	8.0 (7-9) × 7.1 (7-8)	n.p.	Faye, Kpatcha, Diebakate, Fall and Toguebaye (1999)
Myxobolus ichkeulensis Bahri and Marques, 1996	13.5 (13.0-14.0) × 12.5 (12.0-13.0)	5.5 (5.0-6.0) × 4.15 (4.0-4.3)	Bahri and Marques (1996)
Myxobolus mugilis Negm-Eldin, Govedich and Davies, 1999	7.4 × 7.3	Larger: 3.6 × 2.1, Smaller: 2.4 ×1.21	Negm-Eldin, Govedich and Davies (1999)
Myxobolus mülleri Bütschli, 1882	Oval spores: 10.0-12.0 µm × 9.0-11.0 µm; Spherical spores: 9.0 µm in diameter.	2.0-3.0 × 4.0-5.0	Bütschli (1882); Fall, Kpatcha, Diebakate, Faye and Toguebaye (1997)
Myxobolus raibauti Fall, Kpatcha, Diebakate, Faye and Toguebaye, 1997	15.3 (14.0-16.0) × 12.1 (14.0-16.0)	5.9 (5.0-6.5) × 3.6 (3.0-4.0)	Fall, Kpatcha, Diebakate, Faye and Toguebaye (1997)
Myxobolus spinacurvatura Maeno, Sorimachi, Ogawa and Egusa, 1990	11.0 (10.2-13.4) × 12.9 (11.8-13.5)	3.8 (3.6-4.1) × 5.6 (4.7-6.3)	Maeno, Sorimachi, Ogawa and Egusa (1991); Bahri and Marques (1996)
Myxobolus Bütschli, 1882 sp. B	7.9 (6.5–9.0) × 6.9 (6.0–7.5)	2.3 (1.5–3.0) × 1.6 (1.5–1.72)	Present study

Genus *Sphaeromyxa* Thélohan, 1892

The genus *Sphaeromyxa* is characterised by having two polar capsules lying in the opposite and truncate ends of the elongated, sometimes curved spores. The polar capsules open in the level of the sutural line, connecting both ends and bisecting the spore. The shell valves may be smooth or ridged and one binucleate sporoplasm is present. Large polysporous plasmodia live in the gall bladder, pansporoblast formation is observed. The type species is *S. balbianii* Thélohan, 1892 (Lom and Noble 1984).

Sphaeromyxa species are gall bladder parasites of marine fishes and approximately 30 species have been described throughout the world. In Africa only one species of

Sphaeromyxa has been found infecting a marine fish host. *Sphaeromyxa balbianii* was found infecting the gall bladders of *Abudefduf marginalis* and *Sardinella madarensis* in Senegal by Kpatcha *et al*. (1996a) (see Table 3.4, Chapter 3).

Sphaeromyxa species from the Cape south coast, South Africa

A single species of *Sphaeromyxa* was found infecting *Pavoclinus graminis* in the De Hoop Nature Reserve, South Africa. For comparative purposes, Table 6.5 provides the spore measurements of *S. balbiani*.

Sphaeromyxa sp. A

(Figs. 6.5j, k)

Type host: *Pavoclinus graminis* (Gilchrist and Thompson, 1908)

Site of infection: Gills.

Locality: De Hoop Nature Reserve (34°28‘S, 20°30’E), South Africa.

Total prevalence: 14 % (1/7).

Reference material: Deposited in the Aquatic Parasitology Research Group, Department of Zoology and Entomology, University of the Free State, Bloemfonteins’ Parasite Collection.

***Description of vegetative stages*:** Coelozoic pansporoblasts were seen floating in the gall bladder of the host. The trophozoites were small, leaflike structures containing the developing spores ranging in size from 6 – 10 µm.

***Description of spores (based on 20 live spores)*:** Mature spores are transversely elongated, slightly arched and fusiform in valvular view with truncate or bluntly rounded ends, measuring 5.0 – 5.2 (5.0 ± 0.08) µm long × 26.5 – 27.5 (26.8 ± 0.5) µm wide (Figs. 6.5j, h). Shell valves are smooth and a narrow sutural ridge bisects the spores. Two large elongated-ovoid polar capsules are situated in opposite ends of the spore, measuring 7.0 – 9.0 (7.8 ± 0.76) µm long × 2.0 – 3.0 (2.5 ± 0.3) µm wide. Each polar capsule contains a short polar filament, not spirally wound, but folded two to three times. A single binucleate sporoplasm is situated between the two polar capsules without the presence of an iodinophlious vacuole.

***Remarks*:** *Sphaeromyxa* sp. A differs considerably from *S. balbiani* (Kpatcha *et al.* 1996a). The spores of *Sphaeromyxa* sp. A are slightly arched compared to the more ellipsoidal spores of *S. balbiani* and furthermore, the spores of *Sphaeromyxa* sp. A are much larger in overall morphology than the spores of *S. balbiani* (Table 6.5). *Sphaeromyxa* sp. A resembles *S. zabrazesi* Laveran and Mesnil, 1900 described from the gall bladder of syngnathid hosts in the Mediterranean (Lom and Dyková 1992). The spores of *Sphaeromyxa* sp. A are, however, slightly larger and are more boomerang-shaped than the briefly arched spores of *S. zabrazesi*. *Sphaeromyxa* sp. A differs from *S. magna* Zhukov, 1964 described from the Pacific (Lom and Dyková 1992) since *S. magna* has spores with a ridged surface and also has generally longer polar capsules than *Sphaeromyxa* sp. A. The spores of *S. lateralis* Noble, 1941, from the tide-pool fish *Artedius fenestralis* has broadly ovoid, curved spores (Lom and Dyková 1992) which differ from the elongated arched spores of *Sphaeromyxa* sp. A. The polar filaments of *S. lateralis* only folds one and a half times compared to the two to three folds of *Sphaeromyxa* sp. A. *Sphaeromyxa* sp. A does not conform to the description of any known *Sphaeromyxa* species. This is the first description of this species in Africa and the first record of this genus in South Africa.

Table 6.5. Spore measurements of African marine *Sphaeromyxa* Thélohan, 1892 species including the species from the present study [Key: **PC** – polar capsules].

Species	Spore length (µm)	Spore width (µm)	PC length (µm)	PC width (µm)	Coils	Reference
Sphaeromyxa balbiani Thélohan, 1892	3.6 – 4.5 (4.23 ± 0.4)	13.5 – 14.6 (14.2 ± 0.4)	3.37 – 4.5 (4.17 ± 0.4)	2.25 – 2.7 (2.4 ± 0.4)	4	Kpatcha, Diebakate and Toguebaye (1996a)
Sphaeromyxa lateralis Noble, 1941	8.0	26.0	8.6	6.3	1.5	Lom and Dyková (1992)
Sphaeromyxa magna Zhukov, 1964	6.0	23	8.5	4.0	4	Lom and Dyková (1992)
Sphaeromyxa zabrazesi Laveran and Mesnil, 1900	4.0	25.0	9.0	3.0	4	Lom and Dyková (1992)
Sphaeromyxa Thélohan, 1892 sp. A.	5.0 – 5.2 (5.0 ± 0.08)	26.5 – 27.5 (26.8 ± 0.5)	7.0 – 9.0 (7.8 ± 0.76)	2.0 – 3.0 (2.5 ± 0.3)	2 - 3	Present study

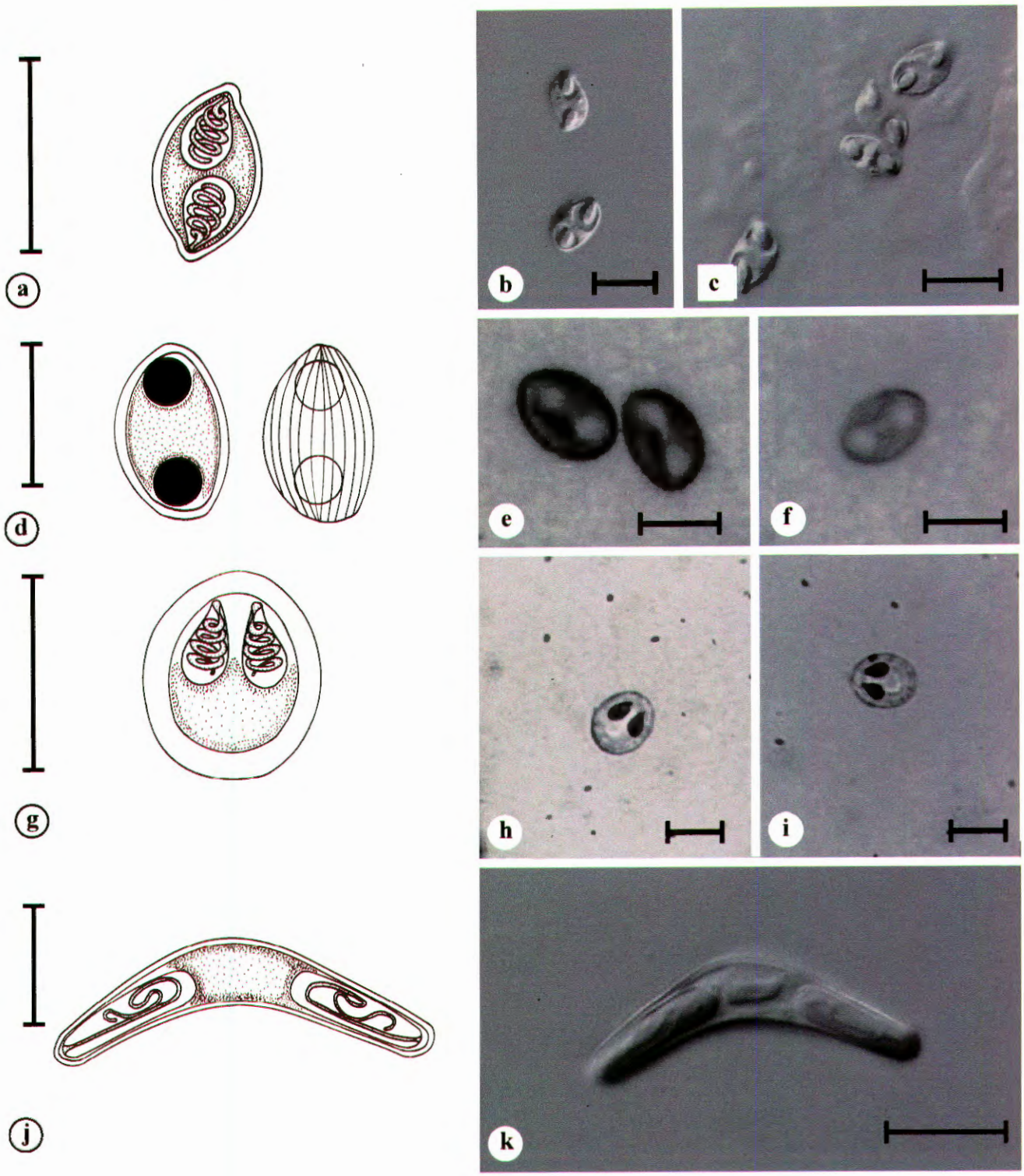


Figure 6.5. Line drawings (**a, d, g, j**), micrographs of live spores (**b, c, k**), Giemsa stained spores (**e, f**) and silver impregnated spores (**h, i**) of myxosporean species infecting the fishes along the Cape south coast of South Africa. **a, b, c.** *Myxidium* Bütschli, 1882 sp. A from the gall bladder of *Chorisochismus dentex* (Bloch, 1795). **d, e, f.** *Myxidium* sp. B from the gall bladder of *Diplodus sargus capensis* (Smith, 1844). **g, h, i.** *Myxobolus* Bütschli, 1882 sp. B from the gills of *Liza richardsonii* (Smith, 1846). **j, k.** *Sphaeromyxa* Thélohan, 1892 sp. A infecting the gall bladder of *Pavoclinus graminis* (Gilchrist and Thompson, 1908). Scale bars: 10 µm.

Discussion

The southern African coastline harbors over 2000 fish species, ranging in size from tiny, cryptic cling fishes to huge, but harmless whale sharks (Branch *et al.* 2002). During the nine surveys conducted since March 1998, a total of 410 fishes representing 33 species collected at the three localities were examined for the presence of myxosporean infections (Table 6.6). Amongst the 33 fish species examined, 15 different myxosporean species were recorded, of which eight have been described earlier in this chapter. The remaining eight myxosporean species were merely noted since insufficient material made it impossible to positively identify or describe them. They will be mentioned in the discussion that follows. A summary of all data collected is provided in Table 6.6, including those species merely noted. The relationships between each fish host and the myxosporean species infecting it are discussed below. The discussion takes place in order of fish families.

Table 6.6. Data of the various myxosporean species recorded from the Cape South Coast, South Africa [Key: **ML-** Mean fish length; **N-** Number of fishes examined; **P-** Prevalence; × = not infected]. Host names listed alphabetically.

Fishes				**Myxosporeans**	
Fish species	**N**	**ML (Range) mm**	**Organ infected**	**P (%)**	**Species**
De Hoop March 1998					
Boopsoidea inornata Castelnau, 1861	2	140, 170	×	×	×
Clinus cottoides Valenciennes, 1836	11	87.3 (71 – 115)	Gall bladder	5/11 (46)	*Ceratomyxa* sp. B
Clinus superciliosus (Linnaeus, 1752)	12	111.3 (59 – 219)	Gall bladder	7/12 (58)	*Ceratomyxa* sp. A
Dichistius capensis (Cuvier, 1831)	2	300, 340	×	×	×
Diplodus sargus capensis (Smith, 1844)	12	272 (196 – 350)	Gall bladder	4/12 (33.3)	*Myxidium* sp. B
Sarpa salpa (Linnaeus, 1758)	2	120, 140	×	×	×
De Mond March 1998					
Liza richardsonii (Smith, 1846)	17	118 (80 – 216)	Gills	4/17 (24)	*Myxobolus* sp. B
Jeffreys Bay January 1999					
Amblyrhynchotes honckenii (Bloch, 1795)	2	181, 185	Gall bladder	1/2 (50)	*Ceratomyxa* sp. C
Caffrogobius caffer (Günther, 1874)	1	90	×	×	×
Cheilodactylus fasciatus Lacepède, 1803	1	147	×	×	×
Chorisochismus dentex (Pallas, 1769)	3	39, 85, 201	Gall bladder	3/3 (100)	*Myxidium* sp. A
Clinus cottoides Valenciennes, 1836	3	70, 85, 102	Gall bladder		
Clinus superciliosus (Linnaeus, 1752)	29	130.1 (100 – 195)	Gall bladder	29/29 (100)	*Ceratomyxa* sp. A
			Gills	1/29 (3.4)	*Henneguya* sp. B
Galeichtys ater Castelnau, 1861	1	72	×	×	×
Solea bleekeri Boulenger, 1898	1	40	×	×	×
De Hoop March 1999					
Boopsoidea inornata Castelnau, 1861	1	170	×	×	×
Chorisochismus dentex (Pallas, 1769)	1	160	Gall bladder	1/1 (100)	*Myxidium* sp. A
Clinus cottoides Valenciennes, 1836	8	74 (41 – 100)	Gall bladder	5/8 (62.5)	*Ceratomyxa* sp. B
Clinus superciliosus (Linnaeus, 1752)	23	121.1 (73 – 200)	Gall bladder	19/23 (83.1)	*Ceratomyxa* sp. A

Table 6.6 continued. Data of the various myxosporean species recorded from the Cape South Coast, South Africa [Key: **ML-** Mean fish length; **N-** Number of fishes examined; **P-** Prevalence; × = not infected]. Host names listed alphabetically.

Fishes				Myxosporeans	
Fish species	**N**	**ML (Range) mm**	**Organ infected**	**P (%)**	**Species**
Clinus taurus Gilchrist and Thompson, 1908	1	145	×	×	×
Diplodus cervinus hottentotus (Smith, 1844)	1	339	×	×	×
Diplodus sargus capensis (Smith, 1844)	10	153.3 (5 – 375)	×	×	×
Kuhlia mugil (Schneider, 1801)	1	94	×	×	×
Liza richardsonii (Smith, 1846)	19	102.3 (68 – 207)	Gall bladder	3/19 (16)	*Ceratomyxa* sp.
			Gills	1/19 (5.2)	*Myxobolus* sp.B
Neoscorpis lithophilus (Gilchrist and Thompson, 1908)	17	105 (70 – 125)	×	×	×
Sparodon durbanensis (Castelnau, 1861)	4	147, 140, 105, 135	×	×	×
Sarpa salpa (Linnaeus, 1758)	1	112	×	×	×
Torpedo fuscomaculatus Peters, 1855	1	550	Gall bladder	1/1 (100)	*Chloromyxum* sp.
De Hoop November 1999					
Amblyrhynchotes honckenii (Bloch, 1795)	4	155, 170, 175, 180	Gall bladder	3/4 (75)	*Ceratomyxa* sp. C
Boopsoidea inornata Castelnau, 1861	1	190	×	×	×
Caffrogobius caffer (Günther, 1874)	8	86.6 (65 – 115)	×	×	×
Caffrogobius nudiceps (Valenciennes, 1827)	4	68, 70, 70, 100	×	×	×
Chirodactylus brachydactylus (Cuvier, 1830)	1	65	×	×	×
Chorisochismus dentex (Pallas, 1769)	1	180	Gall bladder	1/1 (100)	*Myxidium* sp. A
Clinus cottoides Valenciennes, 1836	8	77 (25 – 95)	Gall bladder	7/8 (87.5)	*Ceratomyxa* sp. B
Clinus superciliosus (Linnaeus, 1752)	24	94.1 (30 – 155)	Gall bladder	24/24 (100)	*Ceratomyxa* sp. A
				5/24 (21)	Possible *Sphaerospora* sp.
Dichistius capensis (Cuvier, 1831)	2	310, 320	×	×	×
Diplodus sargus capensis (Smith, 1844)	6	250 (120 – 340)	Gall bladder	1/6 (16.6)	*Myxidium* sp. B
Gymnocrotaphus curvidens Günther, 1859	1	207	×	×	×
Haploblepharus edwardsii (Voight, 1832)	3	448, 510, 610	×	×	×
Liza richardsonii (Smith, 1846)	5	50, 50, 70, 70, 90	Gall bladder	2/5 (40)	*Ceratomyxa* sp.
			Gills	1/5 (20)	*Myxobolus* sp.
De Hoop November 2000					
Amblyrhynchotes honckenii (Bloch, 1795)	4	138, 140, 171, 200	Gall bladder	2/4 (50)	*Ceratomyxa* sp. C
Caffrogobius nudiceps (Valenciennes, 1827)	1	80	×	×	×
Chorisochismus dentex (Pallas, 1769)	1	180	Gall bladder	1/1 (100)	*Myxidium* sp. A
Clinus cottoides Valenciennes, 1836	8	74.4 (50 – 95)	Gall bladder	6/8 (75)	*Ceratomyxa* sp. B
				1/8 (12.5)	*Henneguya* sp. B
Clinus superciliosus (Linnaeus, 1752)	14	130 (40 – 200)	Gall bladder	11/14 (79.1)	*Ceratomyxa* sp. A
			Urinary bladder	2/14 (14.2)	*Myxobolus* sp.
Diplodus sargus capensis (Smith, 1844)	1	100	×	×	×
Fucumimus mus (Gilchrist and Thompson, 1908)	3	75, 90, 100	×	×	×
Galeichtys ater Castelnau, 1861	2	240, 255	×	×	×
Haploblepharus edwardsii (Voigt, 1832)	4	518, 555, 577, 645	×	×	×
Pavoclinus graminis (Gilchrist and Thompson, 1908)	5	55, 60, 100, 140, 145	Gall bladder	1/5 (20)	*Sphaeromyxa* sp. A
Jeffreys Bay March 2001					
Clinus superciliosus (Linnaeus, 1752)	9	111.3 (75 – 160)	Gall bladder	6/9 (67)	*Ceratomyxa* sp. A
			Urinary bladder	4/9 (44)	*Myxobolus* sp.

Table 6.6 continued. Data of the various myxosporean species recorded from the Cape South Coast, South Africa [Key: **ML-** Mean fish length; **N-** Number of fishes examined; **P-** Prevalence; × = not infected]. Host names listed alphabetically.

Fishes				Myxosporeans	
Fish species	**N**	**ML (Range) mm**	**Organ infected**	**P (%)**	**Species**
Pavoclinus graminis (Gilchrist and Thompson, 1908)	2	67, 85	×	×	×
Stephanolepis auratus (Castelnau, 1861)	1	60	×	×	×
De Hoop March 2001					
Amblyrhynchotes honckenii (Bloch, 1795)	4	105, 115, 117, 125	Gall bladder	2/4 (50)	*Ceratomyxa* sp. C
Argyrosomus hololepidotus (Lacepède, 1801)	2	400, 450	×	×	×
Boopsoidea inornata Castelnau, 1861	1	186	×	×	×
Caffrogobius caffer (Günther, 1874)	1	96	×	×	×
Chirodactylus brachydactylus (Cuvier, 1830)	2	97, 140	×	×	×
Clinus cottoides Valenciennes, 1836	4	75 (64 – 90)	Gall bladder	3/4 (75)	*Ceratomyxa* sp. B
Clinus superciliosus (Linnaeus, 1752)	10	150.5 (135 – 169)	Gall bladder	8/10 (80)	*Ceratomyxa* sp. A
			Gills	1/10 (10)	*Henneguya* sp. B
			Urinary bladder	6/10 (60)	*Myxobolus* sp.
Clinus taurus Gilchrist and Thompson, 1908	1	166	×	×	×
Dichistius capensis (Cuvier, 1831)	2	380, 400	×	×	×
Diplodus sargus capensis (Smith, 1844)	5	123, 220, 270, 270, 285	×	×	×
Galeichtys ater Castelnau, 1861	2	41, 395	×	×	×
Haploblepharus edwardsii (Voigt, 1832)	2	500, 660	×	×	×
Lithognathus lithognathus (Cuvier, 1830)	1	450	Liver/kidney	1/1	*Sphaeromyxa* development stages
Liza richardsonii (Smith, 1846)	3	80, 99, 108	Gall bladder	1/3 (33)	*Zschokella* sp.
Parablennius cornutus (Linnaeus, 1758)	4	25, 30, 45, 55	×	×	×
Pomatomus saltatrix (Linneaus, 1766)	2	445, 572	×	×	×
Rhinobatus annulatus Smith, 1841	8	695 (74 – 900)	×	×	×
Sparodon durbanensis (Castelnau, 1861)	4	115, 140, 140, 128	×	×	×
De Hoop March 2002					
Argyrosomus hololepidotus (Lacepède, 1801)	2	420, 450	×	×	×
Boopsoidea inornata Castelnau, 1861	1	210	×	×	×
Caffrogobius caffer (Günther, 1874)	4	77, 100, 130, 130	×	×	×
Chorisochismus dentex (Pallas, 1769)	1	115	Gall bladder	1/1 (100)	*Myxidium* sp. A
Clinus cottoides Valenciennes, 1836	2	54, 85	Gall bladder	1/2 (50)	*Ceratomyxa* sp. B
Clinus superciliosus (Linnaeus, 1752)	10	147 (100 – 180)	Gall bladder	7/10 (70)	*Ceratomyxa* sp. A
Diplodus sargus capensis (Smith, 1844)	2	200, 270	Gall bladder	1/2 (50)	*Myxidium* sp. B
Fucumimus mus (Gilchrist and Thompson, 1908)	7	203 (198 – 222)	Gall bladder	3/7 (43)	*Ceratomyxa* sp.
Galeichtys ater Castelnau, 1861	2	300, 410	×	×	×
Haploblepharus edwardsii (Voigt, 1832)	1	690	×	×	×
Liza richardsonii (Smith, 1846)	4	95, 99, 110, 130	×	×	×
Pomatomus saltatrix (Linneaus, 1766)	3	400, 410, 405	×	×	×
Psammogobius knysnaensis Smith, 1936	2	41, 40	×	×	×
Rhinobatus annulatus Smith, 1841	1	400	×	×	×

Family Clinidae

Members of the Clinidae are small, well camouflaged fishes found among weeds of under stones in estuaries, tidal pools and sub-tidally down to at least 50m. About 80 species are known in this family of which each is carnivorous and endemic to its own region (Smith and Heemstra 1986). Thirty-eight species are known from southern Africa.

***Clinus cottoides* Valenciennes, 1836 (Fig. 6.9a)**

The bluntnose klipfish, *Clinus cottoides* Valenciennes, 1836 is a small, mottled intertidal klipfish characterised by a black blotch on the gill cover. This species is endemic to southern Africa and is found only along the Cape South Coast, generally hiding in tidal pools, where it feeds on small invertebrates (Branch *et al.* 2002).

A total of 44 individuals of *C. cottoides* were collected during seven surveys (De Hoop March 1998, March 1999, November 1999, November 2000, April 2001, March 2002, Jeffrey's Bay 1999) (Table 6.6). *Ceratomyxa* sp. B was abundantly found infecting the gall bladders of 59% (26/44) of the entire sample collected from all the various localities. No specific pattern could be recognised between the different surveys. The infection prevalence varied randomly, possibly coinciding with different sample sizes. A comparison of general infection prevalence between March and November collections at De Hoop Nature Reserve revealed that infections in November appeared to be higher (Table 6.6). It could be an indication of a slight seasonal trend, but more material needs to be examined to confirm these observations.

***Clinus superciliosus* Linnaeus, 1752 (Fig. 6.9b)**

The super klipfish, *Clinus superciliosus* Linnaeus, 1752 is found abundantly along the coast of South Africa to the coast of Namibia. It is also endemic to the region and is characterised by having thick fleshy lips and a distinct notch between the third and fourth dorsal spines. It may reach 30cm in length and is found abundantly in tidal pools (Branch *et al.* 2002).

This was the most abundant fish species collected during all of the surveys. A total of 131 individual *C. superciliosus* were caught and examined for the presence of myxozoan infections from all the sampling localities with the exception of De Mond Nature Reserve.

These fish were infected with four different myxosporean species, two of which have been described earlier in this Chapter.

The results revealed that 84% (110/131) of the entire sample was infected with *Ceratomyxa* sp. A in the gall bladder, kidneys and liver. In two surveys (Jeffrey's Bay January 1999 and De Hoop November 1999) 100% of the sample collected and examined was infected. The lowest infection prevalence was recorded in De Hoop during March 1998. No definite seasonal variations were noted between surveys conducted during January, March and November at all the sites. It appears as if *Ceratomyxa* sp. A is found associated with *C. superciliosus* all year round in all the collection localities.

Although many more fishes were collected at De Hoop Nature Reserve, a general comparison between the infection prevalence between Jeffrey's Bay and De Hoop Nature Reserve revealed that Jeffrey's Bay fishes showed a slightly higher level of infection. A possible reason could be that De Hoop Nature Reserve is a protected marine area, whilst Jeffrey's Bay is fishing/tourist destination with no protected or reserved areas. The intertidal fish species in Jeffrey's Bay are exposed to many more anthropogenic influences, such as pollution from the local fishing industry as well as simply the presence of many people living in the area. All these influences could possibly increase the fish's susceptibility to parasitic infections. Since such a high overall prevalence of infection was recorded, it is possible that *Ceratomyxa* sp. A is permanently associated with *C. superciliosus*. More material should be examined in greater detail to confirm this observation.

Fresh squash preparations of the gall bladder contents of *C. superciliosus* revealed masses of plasmodia and spores of *Ceratomyxa* sp. A floating in the bile of the gall bladders (see Figs. 6.2a, b, c, d). The plasmodia varied greatly in shape often having long extensions attached to the masses. The squash preparations revealed that the plasmodia were typically disporic, meaning that only two spores develop within in a single plasmodium (Fig. 6.2c).

Transmission electron micrographs and histological sectioning reveal that the plasmodia appear to be closely associated with the gall bladder epithelium (Figs. 6.2e, f; 6.6a, b). This observation was also noted by Alvarez-Pellitero and Sitjá-Bobadilla (1993b)

working on *Ceratomyxa labracus* and *C. diplodae* parasitising Mediterranean Sea bass *Dicentrarchus labrax*. In both wild and cultured conditions trophozoites appeared to line the gall bladder epithelium frequently, closely attached to the cell surface and even forming invaginations in it. Histopathological damage to the gall bladder of the infected fish might include vacuolation, deformation and even necrosis of epithelial cells (Alvarez-Pellitero and Sitjá-Bobadilla 1993b).

In many cases the livers of infected individuals were very light in colour and the bile appeared thick, opaque and dark green. Histological sections of the liver showed that the plasmodial stages of *Ceratomyxa* sp. A were found to develop mostly in the intra- but also in the extra-hepatic bile ducts (Figs. 6.6c, d, e). The masses of spores appear to cause severe obstruction in the bile ducts and in the infected specimens the bile ducts were all distended and packed full with plasmodial stages and developing spores. Sections stained with Massons Trichome revealed marked increase in fibrous tissue growth around the infected bile ducts. It is very likely that the normal bile drainage of the liver was affected due to the extremely reduced diameter of the lumen. Interestingly, a regular centripetal arrangement of the long axis of the spores was observed in the spores maturing in the plasmodial stages (Fig. 6.6d). Thickening and inflammation of the subepithelial connective tissue and damage to the neighboring pancreatic tissue might also occur. In other ceratomyxoses, spread of the parasites to other organs was observed in very intense infections and stress situations, such as starvation, seem to favor the appearance of ceratomyxosis (Sitjá-Bobadilla and Alvarez-Pellitero 1993b).

The second myxosporean described from *C. superciliosus* earlier in this chapter, *Henneguya* sp. B, was found infecting the cartilage and blood vessels of the gill arches. Macroscopic white plasmodia could be seen in the gill cartilage of the infected individuals. Squash preparations of these plasmodia revealed masses of *Henneguya* sp. B spores. This myxosporean species showed a very low infection prevalence and was only collected during three surveys (Jeffreys Bay January 1999; De Hoop November 1999; De Hoop March 2001) (Table 6.6). In each case, only one individual of the entire sample collected was infected with *Henneguya* sp. B. The overall infection prevalence of *Henneguya* sp. B for all the surveys during this study was approximately 2.3% (3/131), which was very low.

Histological sectioning through the infected gill arches revealed that the massive plasmodia severely distorted the entire gill arch and many of the gill lamellae. The large plasmodia have compressed many of the smaller gill filaments, severely decreasing the surface area for oxygen uptake by the gills (Figs. 6.6 f, g, h, i). These fish spend their entire lives in intertidal pools, which are subjected to daily variations in oxygen concentrations, salinity and temperature as a result of tidal movements. It is possible that an infection such as this, which appears to affect the respiratory function of the gills, could have an effect on the ability of these fish to survive in the harsh tidal pool environment, particularly during low tides when the oxygen concentrations in the intertidal pools drop dramatically.

During three surveys (De Hoop November 2000; Jeffrey's Bay March 2001; De Hoop March 2001) a myxosporean species from the genus *Myxobolus* was observed infecting the urinary bladders of 12 *C. superciliosus* individuals. This relatively large, but difficult to detect species, appeared to have almost heart-shaped spores floating in the urinary bladder. Unfortunately more material needs to be examined to confirm the identification of this species.

Five *C. superciliosus* specimens sampled during the De Hoop November 1999 survey, examined histologically, revealed the presence of plasmodial stages resembling developmental stages of a *Sphaerospora* sp. in the renal tubules, together with developmental stages making their way in the kidney parenchyma through the epithelium to the tubular lumina. Unfortunately no mature spores were found in fresh squash preparations of the kidney and consequently the species could not be identified.

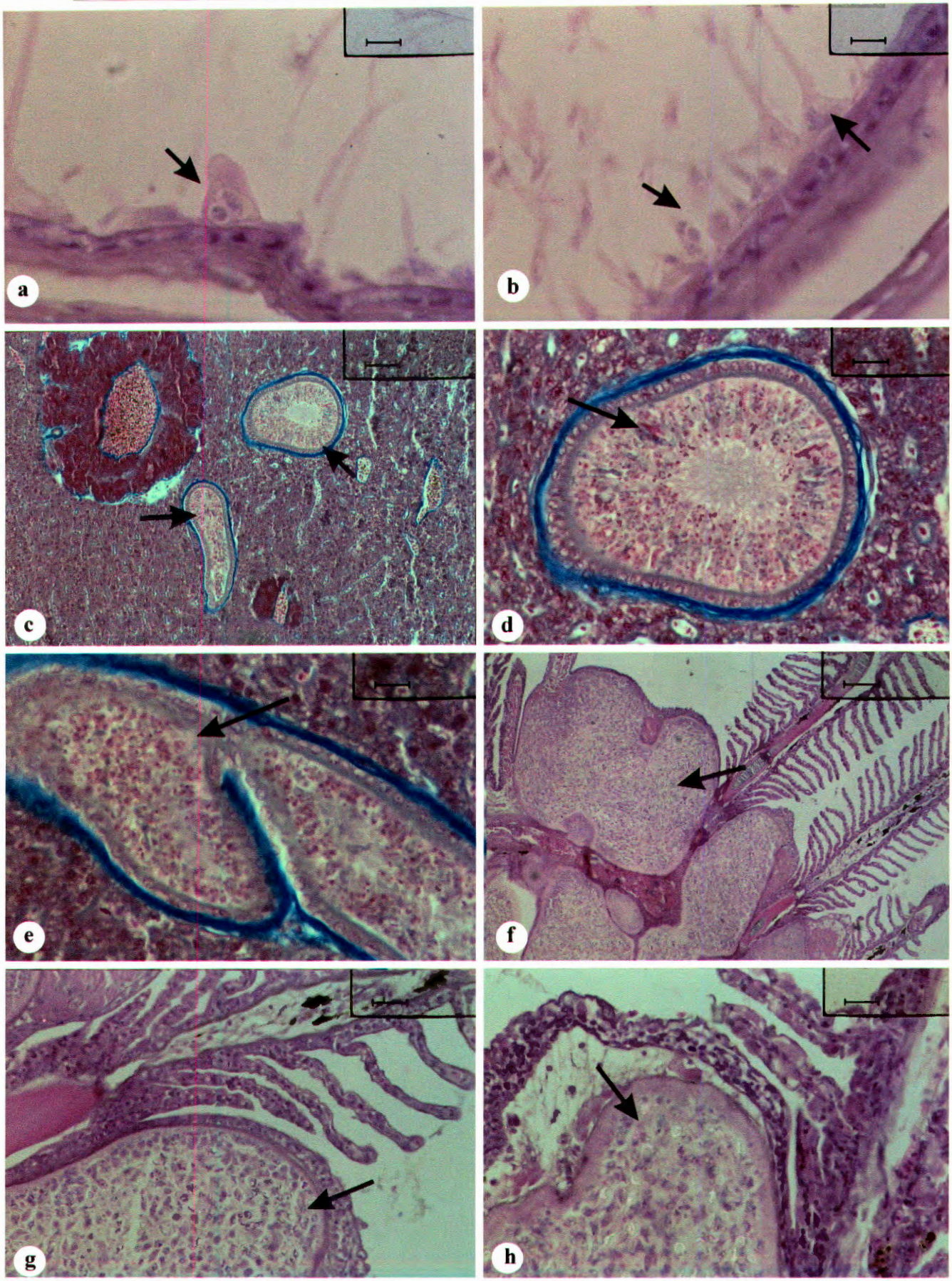


Figure 6.6. Histological sections (**a-i**) of fish organs infected with myxosporeans from the Cape south coast of South Africa. **a, b**. *Clinus superciliosus* (Linnaeus, 1758) gall bladder showing *Ceratomyxa* Thélohan, 1892 sp. A. plasmodia and spores (arrows) closely associated with the gall bladder epithelium. Sections stained with haematoxylin and eosin. **c-e**. *C. superciliosus* liver showing plasmodia and spores (arrows) of *Ceratomyxa* sp. A filling the bile ducts. Sections stained with Masson's Trichome Stain. **f-g.** *C. superciliosus* gills showing plasmodia packed with *Henneguya* Thélohan, 1892 sp. B spores. Sections stained with haematoxylin and eosin. Scale bars: a, b. 10 µm. c, f. 30 µm. d, e, g, h. 15 µm.

***Fucomimus mus* Smith, 1946 (Fig. 6.9c)**

The mousy klipfish, *Fucumimus mus* Smith, 1946 is cryptically coloured, being reddish, green or brown. This monotypic genus is characterised by a small mouth with two rows of teeth on each jaw (Smith and Heemstra 1986).

During two De Hoop surveys conducted in November 2000 and March 2002 a total of 10 *F. mus* were caught and examined for myxosporean infections. A *Ceratomyxa* sp. was recorded from the gall bladders of three individuals caught during the March 2002 survey. A general infection prevalence of 30% (3/10) was observed, but, insufficient material prevented the full description of this species.

***Pavoclinus graminis* (Gilchrist and Thompson, 1908) (Fig. 6.9d)**

The grass klipfish, *Pavoclinus graminis* (Gilchrist and Thompson, 1908) is a small, elongated, mottled and highly variable in colour. A conspicuous white stripe runs from the tip of the snout to the origin of the dorsal fin (Branch *et al.* 2002). It reaches 20 cm in length and is found along the coast from Moçambique to Cape point. Only seven of these tiny fish were collected during two surveys (De Hoop November 2000; Jeffrey's Bay 2001). The gall bladder of only one specimen, caught at De Hoop, was infected with *Sphaeromyxa* sp. A. The overall infection prevalence was thus only 14 % (1/7).

Family Gobiesocidae

Fishes in this family are characterised by a unique joint between the supracleithrum and the cleithrum bones of the pectoral girdle, as well as a distinctive gobiesocid sucking disc that is formed by the modified pelvic fins (Smith and Heemstra 1986).

***Chorisochismus dentex* (Pallas, 1769) (Fig. 6.9e)**

The rocksucker, *Chorisochismus dentex* (Pallas, 1769), is an endemic species found along the entire South African coast. These fish are found mostly in tidal pools and shallow water, feeding on urchins and in particular, limpets (Branch *et al.* 2002).

A total of five *C. dentex* were collected during four surveys (Jeffrey's Bay January 1999, De Hoop March 1999, November 2000, March 2002) (Table 6.6). Every individual collected was infected with *Myxidium* sp. A giving a 100% (5/5) infection prevalence for this myxosporean species. Since *C. dentex* was not readily collected, it is not possible to

conclude that *Myxidium* sp. A is always associated with this specific host along the South African coast.

Family Mugilidae

Members of this family are circumglobal fishes of commercial value and are found in all but the coldest seas, near the coast and in estuaries. Fifteen species are known from southern Africa (Smith and Heemstra 1986).

***Liza richardsonii* (Smith, 1846) (Fig. 6.9f)**

The southern mullet, *Liza richardsonii* (Smith, 1846) is an elongated silver fish with a dark dorsal surface and a characteristic yellow spot on its gill cover. It is endemic to southern Africa and are most commonly found in the Western Cape where it may reach 40 cm in length (Branch *et al.* 2002).

A total of 48 *L. richardsonii* were collected during five surveys (De Mond March 1998; De Hoop March 1999; De Hoop November 1999; De Hoop March 2001; De Hoop March 2002). *Myxobolus* sp. B was found infecting the gills of *L. richardsonii* collected from De Mond in March 1998. During this survey a total of 17 fish were caught and examined. The results revealed that approximately 24% (4/17) of the De Mond sample was infected with *Myxobolus* sp. B. During the De Hoop November 1999 survey one specimen of *L. richardsonii* was infected with *Myxobolus* sp. B. The overall infection prevalence for the entire sample was only 10 % (5/48).

During the De Hoop March 1999 survey three of the 19 *L. richardsonii* collected appeared to have a *Ceratomyxa* sp. infecting the gall bladders. Furthermore a single *L. richardsonii* collected during the De Hoop March 2001 survey possibly had a *Zschokkella* sp. infecting its gall bladder. Both these observations need to be verified and can only be noted.

Family Sparidae

Sparids occur in temperate and tropical waters of all oceans and are usually concentrated along the shore in shallow water. They are important food and angling fishes (Smith and Heemstra 1986)

***Diplodus sargus capensis* (Smith, 1844) (Fig. 6.9g)**

The blacktail, *Diplodus sargus capensis* (Smith, 1844) is oval-shaped in side view and characterised by a marked black patch on its tail. This ubiquitous fish is found all around the coast of southern Africa in a range of habitats. It is omnivorous and spawns all year round (Branch *et al.* 2002).

A total of 36 *D. s. capensis* were collected during six De Hoop surveys (March 1998; March 1999; November 1999; November 2000; March 2001; March 2002) and examined for the presence of myxosporean infections. The gall bladders of 14% (5/36) of the total *D. s. capensis* sample were infected with *Myxidium* sp. B. The initial survey during March 1998 at De Hoop revealed the highest infection prevalence of 30% (4/12). The species was only again recorded four years later in March 2002, with only one of two individuals being infected. During the survey at De Hoop in March 1998 the highest numbers of individual *D. s. capensis* were caught, but from there the sample sizes decreased. *Myxidium* sp. B appears to have generally low infection prevalence.

***Lithognathus lithognathus* Cuvier, 1830 (Fig. 6.9h)**

The white steenbras, *Lithognathus lithognathus* Cuvier, 1830 is an elongate and silvery fish with a long forehead and pig-like snout. This species is characterized by dark bars along its flanks and is a prized angling species that is caught along sandy beaches and in estuaries (Branch *et al.* 2002).

Histological sections of the kidney of a single *L. lithognathus* individual caught during the March 2001 De Hoop survey revealed developmental stages of what appears to be a *Sphaerospora* species (Fig. 6.7). No spores were observed in fresh squash preparations. More material must be examined to confirm this identification.

Family Tetraodontidae

Members of this family are commonly known as blaasops of puffer fishes since they are able to inflate their bodies by swallowing water or air to form an almost spherical, generally spiny ball to deter predators (Smith and Heemstra 1986).

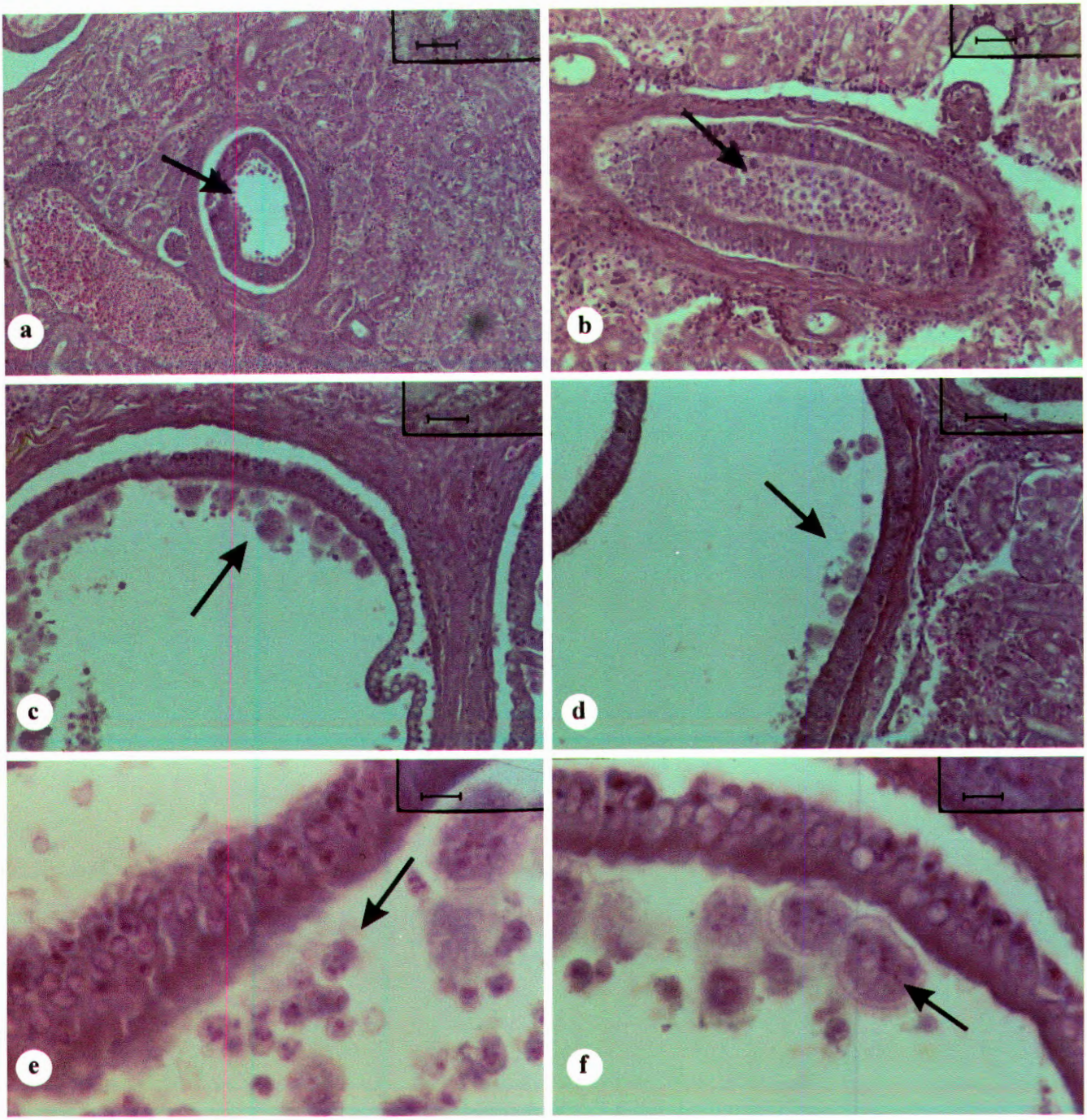


Figure 6.7. Histological sections (**a-f**) of liver from *Lithognatus lithognathus* Cuvier, 1830 collected from the Cape south coast, South Africa.. **a-f**. Developmental stages of a possible *Sphaerospora* Thélohan, 1892 species (arrows). Sections stained with haematoxylin and eosin. Scale bars: a. 30 µm. b. 20 µm. c, d. 20 µm. e, f. 10 µm.

***Amblyrhynchotes honckenii* (Bloch, 1795) (Fig. 6.9i)**

The evil eye blaasop (puffer), *Amblyrhynchotes honckenii* (Bloch, 1795), is an Indo Pacific fish species that is found over reefs, sandy areas and in the lower reaches of estuaries (Branch *et al.* 2002). They may reach 30 cm in length and are able to inflate themselves when provoked. Furthermore, their flesh is extremely poisonous and they often bury themselves in the sand while awaiting unwary prey such as crabs and other small fish.

A total of 14 *A. honckenii* specimens were collected during four surveys (Jeffrey's Bay January 1999, De Hoop November 1999, De Hoop November 2000, De Hoop March 2001) (Table 6.6). Although not many specimens were caught, at least 50% of each sample was infected with *Ceratomyxa* sp. C, with the overall infection prevalence being 43% (6/14). The bile of these fish tended to be normally thick and dark green in colour, with the gall bladder linings being naturally thick. No abnormal discolouring or thickening of this organ was noted in the infected individuals.

Family Torpedinidae

Commonly known as electric rays, members of this family have two large kidney-shaped electric organs in the disc on either side of the head. These organs are capable of generating strong electric shocks (Smith and Heemstra 1986).

***Torpedo fuscomaculata* Peters, 1855 (Fig. 6.9j)**

The black spotted electric ray, *Torpedo fuscomaculata* Peters, 1855 is a round disc-like species, with numerous black spots on the dorsal surface. It is found in western Indian Ocean estuaries and shelf areas. Kidney-shaped electric organs at the base of pectoral fins generate powerful shocks (Branch *et al.* 2002). A single individual of *T. fuscomaculata* was collected during the De Hoop March 1999 survey. Examination of the gall bladder contents revealed a very interesting myxosporean (Fig. 6.8). The huge plasmodia appeared to contain spores similar to those of *Chloromyxum*. The individual spores in each plasmodium were surrounded by what appeared to be a large vacuole (Figs. 6.8e, f).

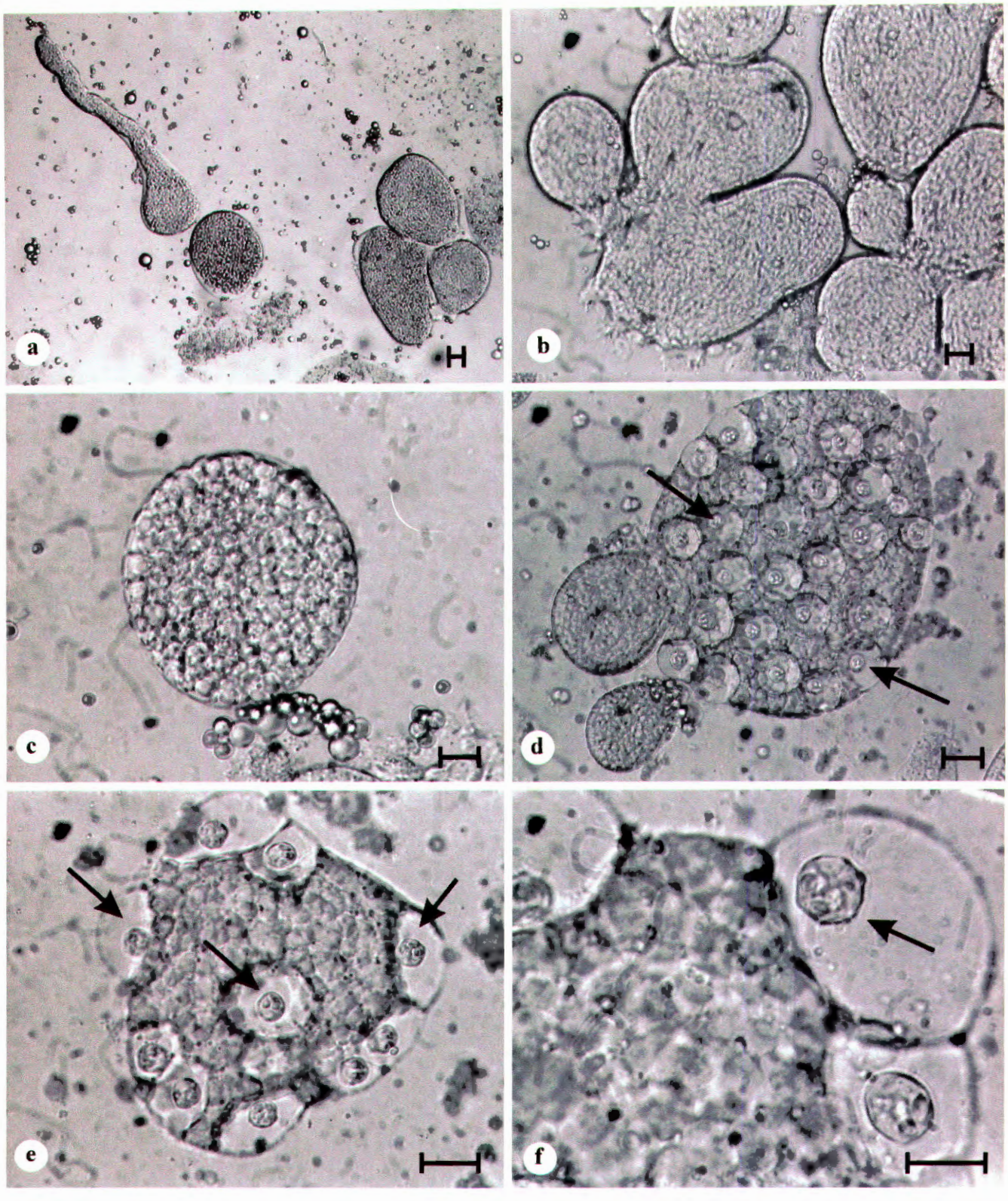


Figure 6.8. Light micrographs (**a-f**) of live plasmodia and spores of a possible *Chloromyxum* Mingazzini, 1890 species in the gall bladder of *Torpedo fuscomaculata* Peters, 1855 collected from the Cape south coast of South Africa. Arrows indicate spores. Scale bars: 10 µm.

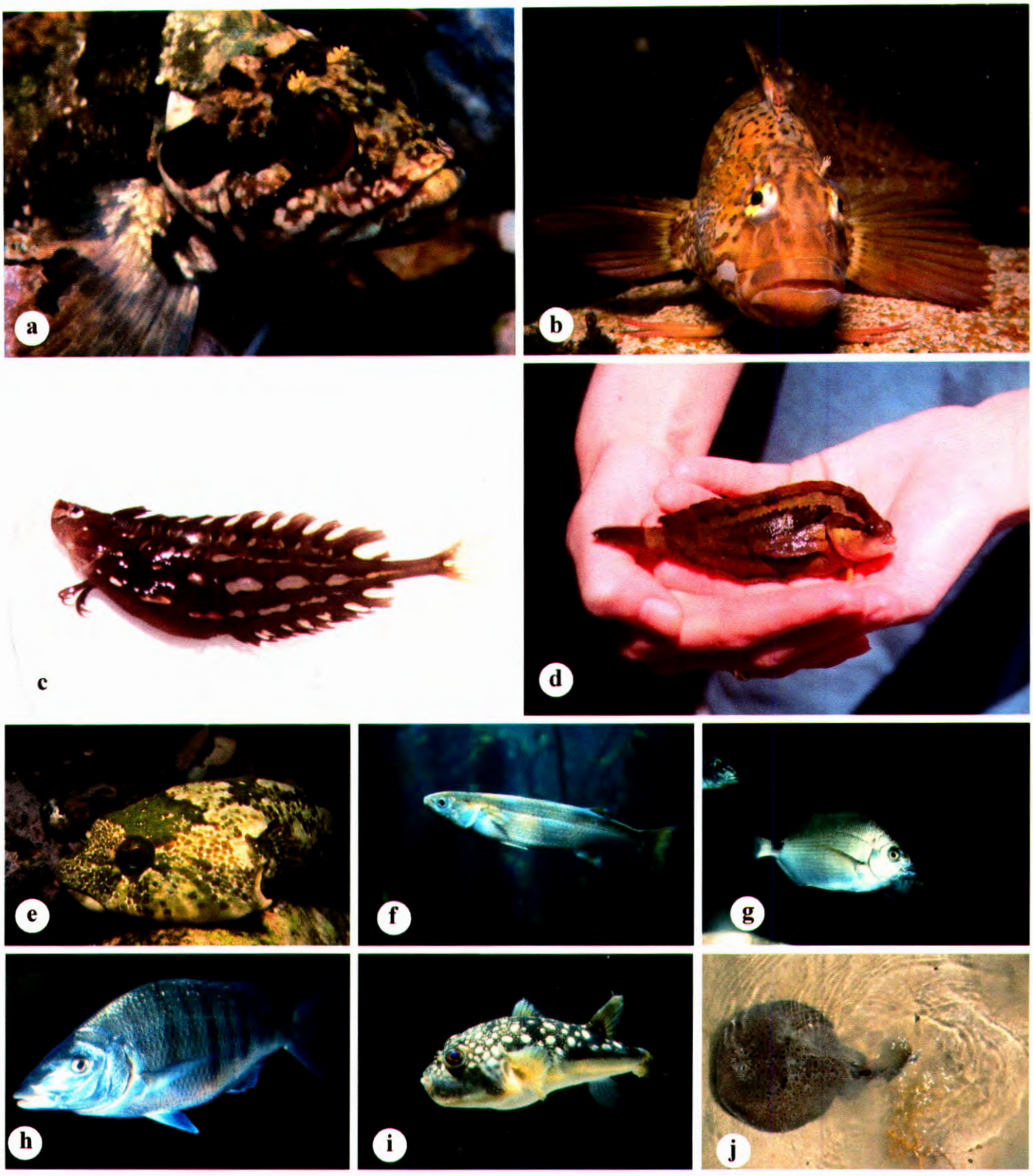


Figure 6.9. a-g. Photographs of fish hosts infected with myxosporean parasites along the Cape south coast of South Africa. **a**. *Clinus cottoides* Valenciennes, 1836. **b**. *C. superciliosus* (Linnaeus, 1758). **c**. *Fucominus mus* Smith, 1946. **d**. *Pavoclinus gaminis* (Gilchrist and Thompson, 1908). **e**. *Chorisochismus dentex* (Pallas, 1769). **f**. *Liza richardsonii* (Smith, 1846). **g**. *Diplodus sargus capensis* (Smith, 1844). **h**. *Lithognathus lithognatus* Cuvier, 1830). **i**. *Amblyrhynchotes honckenii* (Bloch, 1795). **j**. *Torpedo fuscomaculata* (Peters, 1855). Photographs **a, b, e-j** courtesy of Prof. C. L. Griffiths, University of Cape Town.

7. Keys to the Myxosporeans infecting Freshwater, and Marine & Estuarine fishes in Africa

Fomena and Bouix (1997) were the first to propose a key to myxosporeans infecting freshwater fishes in Africa. In this contribution they included all the known freshwater fish infecting African myxosporeans at that time, as well as a list of the different species, hosts and geographical distribution. Using their key as a basis, two keys have been created to include firstly, the freshwater fish-infecting myxosporeans and secondly, the marine and estuarine fish-infecting myxosporeans of Africa. Since some genera are found in both the freshwater and marine habitats, the characteristics of these genera have been repeated for each key. This is simply because the keys are intended to be used separately. Figures of all the freshwater and marine myxosporean species are included at the end of each key, respectively. A list of articles from which these species have been redrawn is included in Table 7.1 and 7.2 in Appendix III.

Key to the myxosporeans infecting freshwater fishes in Africa

Key to the genera

1. Mature spores with only one polar capsule discharging apically and axially……..…..***Thelohanellus* Kudo, 1933.**

2. Spores with more than one polar capsule……....**3**

3a. Spores with two polar capsules (one may be much smaller than the other)……...…...**4**

3b. Spores with four polar capsules ……..…...**9**

4a. Polar capsules discharging at both ends of spore; spores have more or less pointed ends; may be fusiform with pointed ends or ellipsoidal with rounded ends……..…...***Myxidium* Bütschli, 1882.**

4b. Polar capsules discharging at anterior of spore; spores bilaterally symmetrical……**5**

5a. Polar capsules located in plane perpendicular to sutural plane……**6**

5b. Polar capsules located in sutural plane……...**7**

6a. No caudal appendages; spores spherical or almost spherical…… ……...***Sphaerospora* Thélohan, 1892.**

6b. Spores spindle-shaped with a pair of long posterior projections…… …….……***Myxobilatus* Davis, 1944.**

7a. No caudal appendages; sutural line straight……...…***Myxobolus* Bütschli, 1882.**

7b. Caudal appendages present…….**8**

8a. Spores with single caudal appendage …..…….……..***Unicauda*** **Davis, 1944.**

8b. Spores with two appendages, which may be apposed or fused together ……..…..***Henneguya*** **Thélohan, 1892.**

9a. Spores with four shell valves……. ……..…….***Kudoa*** **Meglitsch, 1947.**

9b. Spores subspherical with two shell valves…….....***Chloromyxum*** **Mingazzini, 1890.**

Key to the species

Genus *Chloromyxum* Mingazzini, 1890

Spore valves smooth or ridged, subspherical, occasionally with filamentous projections; four polar capsules located in anterior end of spore. Two pairs of polar capsules may be of unequal size. Binucleate sporoplasm, but uninucleate sporoplasms have been observed. Many species have a similar surface pattern on their spore valves. More than a 100 species worldwide, two in freshwater fish from Africa.

1. Spores spherical, length 6.5-8.5 µm, width 6.5-9 µm. Polar capsules 3-3.5 × 2-3 µm. Plasmodia polysporous, large and circular. Coelozoic in gall bladder of *Barbus aspilus*, *B. martorelli* and *Amphilus longirostris* …….. ***C. birgii*** **Fomena and Bouix, 1994** (Figs. 7.1a, b).

2. Spores subspherical, length 5.9-6.9 µm, width 5.4-6.8 µm. Polar capsules oval, nearly equal 3.1-3.9 × 1.8-2.9 µm. Pseudoplasmodia polysporic, rounded to ellipsoidal, 34 × 42 µm. Coelozoic in gall bladder of *Bagras bayad* …… ……***C. vanasi*** **Ali, 1998** (Fig. 7.2).

Genus *Henneguya* Thélohan, 1892

Spores rounded, ellipsoid, fusiform or spindle-shaped in valvular view, biconvex in sutural view. Each valve extends into a relatively long caudal projection. Shell valves smooth. Two polar capsules, sometimes very elongated. Binucleate sporoplasm with polysaccharide inclusion. Trophozoites large, polysporic with pansporoblast formation. Histozoic in freshwater fishes, rarely in marine fishes.

1. Spore body ovoid …….3

2. Spore body fusiform/spindle-shaped ……..10

3a. Total length of spore ≤ 40 µm ……4

3b. Total length of spores > 40 µm …..9

4a. Caudal appendages equal ……...5

4b. Caudal appendages unequal. Polar capsules unequal, total length of spores 27-32 µm, spore body length 13.5-16 µm, width 4.5-6.5 µm. Larger polar capsule 4-5.5 × 1-1.5 µm, smaller polar capsule 4-4.5 × 1.5-2 µm. Histozoic in gills of *Chrysichthys nigrodigitatus* ……***H. chrysichthyi*** **Obiekezie and Enyenihi, 1988** (Fig. 7.7).

5a. Spore body not very elongate (length/width < 3) ……..6
5b. Spore body elongate (length/width = 3.7) ……9

6a. Anterior of spore rounded ……..7
6b. Anterior of spore pointed ……...8

7a. Spore body not very elongated, total length of spores 12.5-20.5 µm. Spore body length 9-12 µm, width 7-9 µm, anterior end rounded. Polar capsules 5-7 × 3-4 µm with 5-6 coils of per polar filament. Histozoic in kidneys, spleen and gall bladder wall of *Brienomyrus brachyistus* ……***H. ntemensis*** **Fomena and Bouix, 1996** (Fig. 7.20).

7b. Spores ovoid with rounded anterior, short caudal appendages. Total length of spores 17-25 µm. Spore body length 13-17 µm, width 8-10.5 µm. Polar capsules 5-5.5 × 2-3 µm, with 3 oblique coils in polar filament. Histozoic in gills of *Ctenopoma nanum* ……..***H. ctenopomae*** **Fomena and Bouix, 1996** (Fig. 7.9).

7c. Plasmodia ovoid to oval, whitish to grey (1.5 ± 0.23 × 1.4 ± 0.31 mm). Total length of spores approximately 36 µm. Spore body fusiform, length 17.8 µm, width 6.1 µm. Polar capsules elongate fusiform, convergent anteriorly, equal in size, 6.2 × 2.2 µm. Polar filament coils 10-12 times transversely to longitudinal axis of polar capsule. Extruded polar filaments equal in length, 38.1 µm. Two equal caudal processes, 17.9 µm. Sporoplasm in posterior end of spore body with oval nucleus and round iodinophilous vacuole. Histozoic in gills of *Alestes nurse*……..***H. alestes*** **Negm-Eldin, Govedich and Davies, 1999** (Fig. 7.3).

7d. Plasmodia kidney-shaped, whitish in colour (2.3 ± 0.15 × 1.3 ± 0.19 mm). Total length of spores approximately 36 µm. Spore body fusiform, length 17.8 µm and width 6.11 µm. Polar capsules elongate oval, equal in size, occasionally sub-equal, convergent in anterior of spore body, 6.3 × 2.3 µm. Polar filament coiled 10-12 times obliquely to longitudinal axis of polar capsule. Polar filaments equal in length, 35.23 µm. Caudal process extended into two equal processes measuring 17.9 µm.

Sporoplasm restricted to posterior with one or two rounded to ovoid nuclei and large iodinophilous vacuole. Histozoic in gills of *Cyprinus carpio*……***H. cyprini*** **Negm-Eldin, Govedich and Davies, 1999** (Fig. 7.10).

7e. Plasmodia spherical, small (0.5 – 1.0 mm) on primary gill lamellae. Total length of spores 20-23 µm. Spore body oval with rounded anterior and posterior ends. Spore body length 8-9 µm, width 5-6 µm. Polar capsules pyriform, small 2-3 × 1-2 µm. Sporoplasm granular, typically two nuclei. Histozoic in primary gill lamellae of *Lates niloticus*. ……..….***H. massi*** **Kostoïngue, Diebakate, Faye and Toguebaye, 2001** (Fig. 7.17).

7f. Total length of spores 39-42 µm. Spore body ovoid with rounded anterior, length 11-12 µm, width 6-8 µm. Caudal length 28-30 µm. Sporoplasm granular. Histozoic in intestine of *Sarotherodon galilaeus*. ……***H. sarotherodoni*** **Fall, Fomena, Kostoïngue, Diebakate, Faye and Toguebaye, 2000** (Fig. 7.24).

8a. Plasmodia in primary and secondary gill filaments. Total length of spores 13.5-21.5 µm. Spore body ovoid, length 9-11 µm, width 4-5.5 µm. Polar capsules pyriform-shaped 4.5-6.5 × 1-2 µm. Caudal appendages occasionally fused. Histozoic in gills of *Synodontis batesii* and *Eutropius mulitaeniatus*…….. ……..…..***H. camerounensis*** **Fomena and Bouix, 1987** (Fig. 7.6).

8b. Plasmodia small, spherical (0.4 – 0.8 mm). Total spore length 30-34 µm. Spore body oval with pointed anterior end, length 8-9 µm, width 4-5 µm. Polar capsules pyriform, equal in size 3-4 × 1-3 µm. Caudal appendages equal in length, separated from their base 23-25 µm. Histozoic in primary gill lamellae of *Mormyrus cashive*……***H. mormyri*** **Kostoïngue, Diebakate, Faye and Toguebaye, 2001** (Fig. 7.19).

8c. Total spore length 30.5-36.5 µm. Spore body not very elongate, anterior end pointed, length 10-14 µm, width 4.5-6.5 µm. Polar capsules with "neck-like" structure, 5.5-7 × 3 µm. Caudal appendages filiform and separated from base. Histozoic in gills and muscles of *Marcusenius moori*……...***H. nyongensis*** **Fomena and Bouix, 1996** (Fig. 7.21).

8d. Plasmodia large, located at tips of suprabranchial respiratory organs, pale yellow to white, up to 1 mm in diameter. Total length of spores 30.7-43 µm. Spore body elongate-oval in front view, 12.2-14.3 µm in length, with a narrow

anterior end. Posterior end blunt and rounded. Spore body 5.6-6.9 µm wide. Caudal process thin, 18.5-29 µm in length, tapering and not normally separated except at tips. Spores oval to fusiform in side view, 3.9-4.9 µm thick. Polar capsules pyriform, equal, 7-8.1 × 1.8-2.3 µm, or slightly unequal, 6.6-8.1 × 1.8-2.3 µm. Polar filament contains 9-10 filament turns. Histozoic in *Clarias gariepinus*……..***H. suprabranchiae*** **Landsberg, 1987** (Fig. 7.25).

9a. Total spore length 29-36 µm. Spore body elongated, length 13-16 µm, width 3.5-4.5 µm. Caudal appendages equal. Polar capsules 3-5 × 1-1.5 µm. Histozoic in gills of *Marcusenius moorii* ……..……***H. odzai*** **Fomena and Bouix, 1996** (Fig. 7.22).

9b. Plasmodia ovoid, located on primary gill lamellae (0.5 – 1.5mm). Total spore length 33-37 µm. Spore body oval with attenuated anterior end, 11-13 µm in length, width 3-4 µm. Caudal appendage 20-25 µm. Polar capsules pyriform, unequal. Larger polar capsules 3-4 × 1-2 µm, smaller polar capsules 2-3 × 1-2 µm. Sporoplasm finely granular. Histozoic in *Citharinus citharus*……..…***H. logonensis*** **Kostoingue, Diebakate, Faye and Toguebaye, 2001** (Fig. 7.14).

9c. Polysporous plasmodia oval to oblong in primary gill filaments, 2-5 mm long. Spore body elongate to oval, 12.3-15 µm in length, width 5-7 µm. Total length of spores 47-53 µm. Caudal appendages filiform and narrow, separated from base, 34.7-35.3 µm. Polar capsules pyriform, 5-6 × 1.3-1.9 µm. Polar filament with eight coils. Histozoic in *Clarias gariepinus*…… ……***H. samochimensis*** **Reed, Basson and Van As, 2003** (Fig. 7.23).

10a. Caudal appendages separated from base……...…11

10b. Caudal appendages fused…..…..12

10c. Caudal appendages fused half way along their length……..……13

11a. Polar capsules both discharging anteriorly……..……14

11b. One polar capsule discharging laterally……15

12a. Total length of spores 45-107 µm. Spore body length 17.5-28.5 µm, width 5.5-8.5 µm. Polar capsules 5-13.5 × 2.5-3.5 µm. Histozoic in gills of *Clarias lazera*…….……..……***H. clariae*** Abolarin, 1971 (Fig. 7.8).

12b. Plasmodia ovoid measuring 1-1.5 mm, located at base of primary gill

lamellae. Spore body lanceolate and elongate, 11-13 × 3-4 µm. Caudal appendages fused, 37-40 µm. Total length of spores 52-58 µm. Polar capsules pyriform, elongate and equal in size, 6-7 × 2-3 µm. Polar filament not apparent. Sporoplasm finely granular. Histozoic in *Auchenoglanis occidentalis*. ……..……***H. auchenoglanii* Kostoingue, Diebakate, Faye and Toguebaye, 2001** (Fig. 7.4).

13. Total length of spores 48.1-66.5 µm. Spore body oval with a rounded anterior end, 11.8-14 µm long, 6.9-7.9 µm wide. Characteristic thickening at the base of the long caudal process. Relatively long CP run adherent to each other then, bifurcates 2/3 of their length to very fine processes, 36.3-53 µm long. PC equal, pyriform, occupying half the spore body 4.8-5.9 × 2.8-3.9 µm. Polar filaments oblique to the longitudinal axis with 4-5 coils. Histozoic in the intestine, pyloric caeca and gill filaments, gill arches and gill rakers of *Lates niloticus* …… ……...***H. ghaffari* Ali, 1999** (Fig. 7.12).

14a. Rounded plasmodia in secondary gill lamellae of host (192–450 × 116–303 µm). Total length of spores 41-48 µm. Spore body ovoid, length 15-19 µm, width 5.5-7 µm. Two long caudal appendages separated from their base. Polar capsules equal 7-9 × 1.5-2.5 µm, with 7-9 coils in polar filament. Histozoic in *Chrysichthys nigrodigitatus* ……..…….....***H. bopeleti* Fomena and Bouix, 1987** (Fig. 7.5).

14b. Plasmodia ovoid, whitish (0.25 – 2.5 mm). Total length of spores 59-61 µm. Spores fusiform in shape, length 29-33 µm and width 5-7 µm. Polar capsules equal, pyriform, located one behind the other 5-6 × 3-4 µm with 5-6 coils per filament. Caudal appendage equal in length, divergent, curving outwards. Histozoic in the gills of *Clarias anguillaris*…….***H. fusiformis* Kostoingue, Fall, Faye and Toguebaye, 1999** (Fig. 7.11).

14c. Anterior end of spore rounded. A bulge at the base of the caudal appendages is present. Total length of spores 42-53 µm. Spore body length 14-18 µm, width 8.5-11 µm. Polar capsules 5-7.5 × 3-4 µm, with 4-5 coils of filament. Histozoic in the skin and muscles of *Malapterurus electricus* ……..…***H. malapteruri* Fomena and Bouix, 1996** (Fig. 7.16).

14d. Plasmodia ovoid, fixed on primary gill lamellae. Total length of spores 58-63 µm. Spore body lanceolate and

elongated, length 15-18 µm, width 5-6 µm. Caudal appendages equal, separated from base, 41-46 µm. Polar capsules pyriform, equal 5-7 × 2-3 µm. Histozoic in *Mormyrus cashive*…...***H. mailaoensis*** **Kostoingue, Diebakate, Faye and Toguebaye, 2001** (Fig. 7.15).

14e. Plasmodia whitish, ovoid, subspherical, parallel to the long axis of the primary gill filaments (120–140 × 60–230 µm), polysporous. Total length of spores 51.5-69.2 µm. Spores long, ovoid or subspherical, 10-12 µm long and 7-9 µm wide. Side view spores are fusiform with a thickness of 4.8-5.2 µm. Caudal process thin, equal and separated along entire length, extremely long (4/5 of entire spore length) 40.5-59 µm. Polar capsules are pyriform, convergent and equal, filling more than 1/3 of spore cavity, 3.5-4.7 × 2-3 µm. Polar filaments lie perpendicular to long axis of polar capsule with 4-5 filament turns. Histozoic in *Lates niloticus* ……..…. ……..……***H. mbakaouensis*** **Fomena and Bouix, 2000** (Fig. 7.18).

15. Anterior of spore pointed. One polar capsule discharging laterally. Total length of spores 29-36 µm. Spore body length 14-16 µm, width 3.5-5.5 µm. Polar capsules 4-5.5 × 2-3µm, with 5-6 oblique coils. Histozoic in gills of *Clarias lazera*……...***H. laterocapsulata*** Landsberg, 1987 (Fig. 7.13)

Genus *Kudoa* Meglitsch, 1947

Spores stellate, quadrate or rounded quadrate in apical view. Four pyriform polar capsules. Two uninucleate sporoplasms, one enveloping the other. Trophozoites small, producing one to seven spores or large and polysporic. Histozoic mostly intracellular in muscles, exceptionally coelozoic in marine fishes. Approximately 40 species world wide, with one from freshwater fish in Africa.

1. Polar capsules forming a cross-shaped figure. Shell valves thick (1.5 µm). Length of spores 8 µm. Length of polar capsules 1.5 µm. Histozoic in gills of *Eleostris kribensis*……...***K. eleotrici*** **Siau, 1971** (Figs. 7.26a, b).

Genus *Myxidium* Bütschli, 1882

Spores as a rule fusiform, straight or slightly crescentic or sigmoid, with more or less pointed ends. Shell valves smooth or with ridges. Sutural line bisecting the spore. Two mostly pyriform or spherical polar capsules situated one at each end of the spore. Capsula foramina lie in a sutural plane, or near the end of the spore, opening in opposite directions. One binucleate

sporoplasm located between the polar capsules. Typically coelozoic with small to large trophozoites being mono-, di- and polysporic. More than 100 species known throughout the world, 12 known from freshwater fishes in Africa.

1. Spores fusiform with pointed ends…3
2. Spores ellipsoidal, with rounded ends. Polar capsules spherical or nearly so….8

3a. Polar capsules pyriform……...4
3b. Polar capsules spherical……..5

4a. Large plasmodia of varied form and size……..6
4b. Spores diffuse……..7

5. Plasmodia not yet found. Spores oval with pointed extremities, length 15-16 µm, width 8-9 µm. Polar capsules spherical, 3-3.5 µm in diameter. Surface of spore longitudinally striated. Coelozoic in gall bladder of *Lates niloticus*……..……..***M. latesi*** **Kostoïngue, Faye and Toguebaye, 1998** (Fig. 7.32).

6a. Circular plasmodia, approximately 2 µm in diameter or longer. One to three per host. Spores sometimes curved, length 21.5-27 µm, width 6.5-10 µm. Polar capsules 8.5-11.5 × 4-5 µm. Coelozoic in gall bladder of *Petrocephalus simus…**M. petrocephali*** **Fomena and Bouix, 1986** (Fig. 7.35a, b).

6b. Plasmodia elongate, approximately 2mm long, ectoplasm bearing denticles regularly spaced. Spores fusiform, length 17.5-22.5 µm, width 7-11 µm. Polar capsules 7-9 × 2.5-5 µm. Coelozoic in gall bladder of *Aphyosemion splendopleure*…...***M. birgi*** **Fomena and Bouix, 1986** (Fig. 7.27a, b).

6c. Filiform budding plasmodia (up to 10 per infected host), 2.27 mm long × 0.11 mm wide. Length of spores 19-22.5 µm, width 5-8.5 µm. Polar capsules 7-11 × 3-4 µm. Coelozoic in gall bladder of *Neolebias ansorgi*.....***M. camerounensis*** **Fomena and Bouix, 1986** (Fig. 7.30a, b, c).

7a. Plasmodia not yet found. Length of spores 14 µm, width 4 µm. Polar capsules 1.5 × 2.5 µm. Coelozoic in gall bladder of *Synodontis ansorgii*…….. ……..…….***M. bouixi*** **Siau, 1971** (Figs. 7.28a, b).

7b. Plasmodia not seen. Spores oval with pointed extremities, length 16-17 µm, width, 6-7 µm. Polar capsules pyriform, situated in extremities of

spore, 4.5-5.5 × 3-3.5 µm. Longitudinal striations on surface of spore. Coelozoic in gall bladder of *Distichodus engycephalus*……..***M. distichodi* Kostoïngue, Faye and Toguebaye, 1998** (Fig. 7.31).

7c. Plasmodia not yet found. Length of spores 11-12.5 µm, width 4.5-6.5 µm. Polar capsules 2.5-3.5 × 1.5-2 µm, with 4-5 coils in the polar filament. Coelozoic in gall bladder of *Synodontis schall*……..…***M. schalli* Ghaffar, El-Shahawi and Naas, 1995** (Fig. 7.36).

7d. Plasmodia not yet found. Spores with slightly blunt ends, length 8-13 × 3-5 µm. Polar capsules 2.5-4.5 × 2-3 µm. Spores diffuse in kidneys of *Barbus guirali* and *B. mortelli*….***M. mendehei* Fomena and Bouix, 1994** (Fig. 7.33a, b).

8a. Plasmodia elongate to circular, 0.7-1.85 mm × 0.28-0.6 mm (one to three per infected host). Ventral region of spores not enlarged. Length of spores 12-16 µm, width 5.5-9 µm. Diameter of polar capsules 3.5-5 µm. Coelozoic in gall bladder of *Brienomyrus brachyistus*……*M. brienomyri* **Fomena and Bouix, 1986** (Fig. 7.29a, b).

8b. Plasmodia large and circular (155 per host). Spores with ventral region enlarged, length 11-14.5 µm, width 4.5-9.5 µm. Diameter of polar capsules 2-4.5 µm. Coelozoic in gall bladders of various *Barbus* sp.…….***M. nyongensis* Fomena and Bouix, 1986** (Figs. 7.34a, b).

8c. Disporic pseudoplasmodia in bile. Spores spindle-shaped with rounded ends, length 12.7-14.9 µm, width 4.9-6.1 µm. Polar capsules equally round, 3-4.9 × 2-3.4 µm. Four coils per polar filament. Longitudinal striations on the surface of the spore. Coelozoic in gall bladder of *Schilbe mystus*……. ……..…..… ***M. schilba* Ali, Sakran and Abdel-Baki, 1999** (Fig. 7.37).

8d. Spores spindle-shaped with rounded ends, length 14.8-16.8 µm, width 5.6-7.2 µm. Polar capsules almost spherical, 3.8-4.4 × 3.6-4.0 µm. Polar filament contains six coils slightly angled to the longitudinal axis of the polar capsule. Ten longitudinal striations on the surface of the spores. Spores diffuse within renal tubules of *Labeo niloticus* ……***M. shamama* Ali, Sakran and Abdel-Baki, 1999** (Fig. 7.38).

Genus *Myxobilatus* Davis, 1944

Spores elongate and anteriorly pointed. Shell valves often with fine ridges, extend posteriorly into two caudal appendages. Polar capsules pyriform in a plane perpendicular to the suture. Binucleate sporoplasm may contain an iodinophilous vacuole. Trophozoites small to large, disporic to polysporic, coelozoic in the excretory system, from the kidney tubules down to the urinary bladder. Rarely histozoic. More than 24 species known from freshwater and marine fishes around the world. Two species known from freshwater fish in Africa.

1a. Caudal appendages separated from their base. Total length of spores 30-33 µm, spore body length 11-12.5 µm, width 4.5 µm. Polar capsules unequal. Larger polar capsule 5.5-6 × 1.5 µm, smaller polar capsule 4-5 × 1.5-2 µm. Histozoic in accessory breathing organ of *Heterobranchus bidorsalis*. ……....***M. accessobranchialis* Obiekezie and Okaeme, 1987** (Fig. 7.39).

1b. Single caudal appendage. Length of spores 20-25 µm, width 5 µm. Polar capsules equal. Histozoic in gills of *Synodontis ansorgii*…...…***M. synodontis* Siau, 1971** (Fig. 7.40a, b, c).

Remark. According to Fomena and Bouix (1997), the representatives of this genus *Myxobilatus* are generally more coelozoic so the above two species are possibly based on erroneous descriptions and probably correspond to *Henneguya* sp. Further studies are needed to justify their transfer to the latter genus (Fomena and Bouix 1997).

Genus *Myxobolus* Bütschli, 1882

Spores ellipsoidal, ovoid or rounded in valvular view, biconvex in sutural view. Shell valves smooth. Two mostly pyriform polar capsules situated in anterior end of spore, parallel to the sutural plane. Posteriorly sutural ridge may extend into a crescentic ledge. Binucleate sporoplasm, often with an iodinophilous vacuole. Plasmodia large, polysporic with pansporoblast formation. Histozoic in freshwater fishes, occasionally, some in marine (mostly estuarine) fishes. More than 450 species throughout the world, 50 species from freshwater fishes in Africa.

1. Length of spores greater or equal to width……3
2. Length of spores less than width...33

3a. Spores spherical or subspherical ($1 \leq$ length/width < 1.4)……..4

3b. Spores elongate (1.4 ≤ length / width ≤ 2)……...17

3c. Spores very elongate (length / width > 2)……...30

4a. Intercapsular process present……..5

4b. Intercapsular process absent……..10

5a. Polar capsules equal……6

5b. Polar capsules unequal……9

6a. Intercapsular process indistinct…...7

6b. Intercapsular process developed….8

7a. Spores ovoid, smooth and slightly thicker at anterior point where the discharging ducts emerge. Lemon-shaped in side view with a thin indistinct sutural ridge. Length of spores 10-11.5 µm, width 7.5-9 µm. Polar capsules pyriform, 6-7.5 × 3-4 µm with 10-11 coils per polar filament. Spores diffuse in melanomacrophage centers of kidneys and spleen of *Oreochromis niloticus* and *O. niloticus vulcani*…… ……***M. agolus*** **Landsberg, 1985** (syn. *M. melenensis*) (Fig. 7.42).

Remark. Fomena and Bouix (1997) synonomised *M. melenensis* Fomena, Bouix and Birgi, 1985, a parasite of *Hemichromis fasciatus*, with *M. agolus*, since the morphometric characteristics of the two species are not significantly different.

7b. Anterior end of spores slightly pointed. Sutural edge with 6 markings. Length of spores 8-9 µm, width 6-7 µm. Histozoic in skin and gills of *Abramis brama*, *Mugil capito* and *M. chelo* ……..…….***M. exiguus*** **Thélohan, 1895** (Fig. 7.60).

7c. In frontal view spores are ovoid to pyriform with the anterior end narrower and slightly pointed than the posterior end. Shell valves are smooth and slightly thicker at the anterior point where the discharging ducts emerge. Length of spores 11.5-14 µm, width 7.5-10 µm. In side view the spores are lenticular with an indistinct sutural ridge and a thin sutural line. Polar capsules are flask-shaped, of equal size and converge in the anterior end of the spore, 7-8.5 × 3-4 µm. Polar filament with 7-8 coils. Spores diffuse in kidneys and spleen of hybrid *O. niloticus* × *O. aureus*, *Sarotherodon galilaeus* and *O. niloticus vulcani*……***M. israelensis*** **Landsberg, 1985** (Fig. 7.68).

8a. Plasmodia spherical to ovoid, 60-290 µm × 75-265 µm. Spores almost spherical with a truncate anterior end. Length of spores 14-20 µm, width 11.5-

18.5 µm. Polar capsules large, 6.5-9 × 3.5-5.5 µm. Histozoic in gills of *Barbus* sp……..……***M. njinei* Fomena, Bouix and Birgi, 1985** (Fig. 7.76).

8b. Spores subspherical with a flattened anterior end, which is wider than the posterior end. Length of spores 13-15 µ, width 11.5-14 µm. A triangular and well developed intercapsular process present, made up of two symmetric triangular appendages which are not completely fused so that one can see a space between the two polar capsules ovoid, not convergent, 5-6.5 × 4-5 µm. Polar filament with 4-5 coils. Spores diffuse in kidneys and spleen of *Sarotherodon galileaus* and *Tilapia mariae* ……...……..…...***M. nouensis* Fomena and Bouix, 2000** (Fig. 7.79).

8c. Ovoid to spherical plasmodia in secondary gill filaments. Spores have a pointed anterior end and rounded posterior end, length 8-11 µm, and width 6-8 µm. Intercapsular process is present. Two pyriform-shaped polar capsules that do not converge are situated in anterior end of spore, 4-6 × 2-3 µm. Histozoic in *Tilapia zillii*……***M. zillei* Sakiti, Blanc, Marques and Bouix, 1991** (syn. *M. latesi*) (Fig. 7.90).

Remark. Myxobolus latesi Kostoïngue and Toguebaye, 1994, a parasite of *Lates niloticus*, is synonymised with *M. zillii* by Fomena and Bouix (1997) because the criterion used to distinguish the two is insignificant.

9a. Length of spores 14-17 µm, width, 11.5-14.5 µm. Anterior end slightly truncated. Larger polar capsule 6.5-8 × 4-6 µm. Polar filament with 9-10 coils. Smaller polar capsule 4-6.5 × 3-4 µm. Polar filament with 6-7 coils. Histozoic in gills and fins of *Labeo* sp… ……..……***M. bilongi* Fomena, Marques, Bouix and Njiné, 1994** (Fig. 7.46).

9b. Shell valves thick. Length of spores 11-13 µm. width 7-9 µm. Larger polar capsule 6-7 × 3-4 µm with 5 coils of filament. Smaller polar capsule 4-5 × 2-3 µm, with 3 coils of filament. Histozoic in gills and fins of *Labeo coubie*… ……..…..……..…….***M. burkinei* Kabré, Sakiti, Marqués and Sawadago, 1995** (Fig. 7.48).

9c. Length of spores 8.5-11 µm, width 8-10.5 µm. Larger polar capsule 4.5-6.5 × 2.5-5 µm, 7-9 coils per filament. Smaller polar capsule 3-5.5 × 2-3.5 µm, 5-6 coils of filament. Histozoic in gills of *Tilapia zillii*, *Hemichromis fasciatus*

and *O. mossambica* × *O. niloticus*……..……..…***M. dossoui* Sakiti, Blanc, Marqué and Bouix, 1991** (Fig. 7.57).

10a. Polar capsules equal……..11
10b. Polar capsules unequal……16

11a. Length of polar capsule < 1/3 length of spore……..12
11b. Length of polar capsule > 1/3 of spore length……..15

12a. Sutural line with markings……..13
12b. Sutural line without markings….14

13a. Spores ovoid, anterior end as large as posterior end with 11-12 notches on sutural line. Length of spores 10.5-13 µm, width 8-10 µm. Polar capsules equal and ovoid, not convergent 3-4 × 2.5-3 µm, with 4-5 oblique coils. Infecting kidneys and spleen of *Saratherodon galilaeus*….***M. galilaeus* Landsberg, 1985** (Fig. 7.62).

13b. Spores almost spherical in frontal view and contain 8 notches in the sutural edge. Length of spores 8-10 µm and width 6.5 µm. Two small pyriform shaped polar capsules are present in the anterior end of spore, 2-2.5 × 1-1.5 µm. Each contains three oblique coils in polar filaments. Histozoic in ovaries of *Haplochromis angustifrons* and *H. elegans*……***M. kainjae* Obiekezie and Okaeme, 1987** (syn. *M. ovariae* nom. nud.) (Fig. 7.69).

Remark. Paperna (1973) created *Myxobolus ovariae* for a parasite from the gonads of *Haplochromis angustifrons* and *H. elegans*, in Lake George (Uganda) without any description. Obiekezie and Okaeme (1990) provided a full description and consequently renamed it.

14a. Polysporic, spherical plasmodia of variable sizes occur in fatty tissue overlying the extremity of gill arches (215 - 432 × 190 – 410 µm). Spores globoid without an intercapsular process, length 13.5-16 µm, and width 10-14 µm. Polar capsules sub oval, 4-5 × 3-4.5 µm. Histozoic in gills of *Oreochromis niloticus*……***M. fotoi* Fomena, Marqués and Bouix, 1993** (Fig. 7.61).

14b. Spores triangular in shape with anterior broader than posterior, length 10-12 µm and width 9-12 µm. Polar capsules spherical, 3-5 µm in diameter. Sporoplasm granular. Histozoic in kidneys of *Tilapia guinensis* ……..……...***M. gandiolensis* Fall, Fomena, Kostoïngue, Diebakate, Faye and Toguebaye, 2000** (Fig. 7.64).

14c. Spores ovoid in frontal view with anterior end tapering to a blunt point and posterior end rounded. Length of spores 9-13 µm and width 7.5-10 µm. Two small-pyriform shaped polar capsules are situated in the anterior end of the spore and fill approximately one fourth of the spore cavity, 2-4 × 2-3 µm. Histozoic in gills of *Sarotherodon melanotheron* ……..***M. sarotherodoni* Sakiti, Blanc, Marqués and Bouix, 1991** (Fig. 7. 85).

15a. Spores almost spherical, length 9-12 µm, width 7.5-10 µm. Polar capsules ovoid, 3.5-5 × 2-2.5 µm. Parasites of testes of *Clarias lazera*……..***M. clarii* Mandour, Galal and Abed, 1993** (Fig. 7.53).

15b. Spores almost spherical, anterior slightly pointed, length 10-12 µm, width 8-9 µm. Polar capsules large and pyriform, 4-5 × 2.5-3 µm. Histozoic in gills of *Clarias anguillaris* ……. ……***M. comoei* Kabré, Sakiti, Marqués and Sawadago, 1995** (Fig. 7.54).

15c. Spores almost spherical in frontal view and lenticular in side view, length 8-11 µm, width 7-11 µm. Both polar capsules are subspherical, volumous and of equal sizes, 3.5-5.5 × 2-3.5 µm. Some tetralogical forms presenting 3 polar capsules have been observed. Sutural line is straight and prominent and a reduced sporoplasm fills rest of spore. Histozoic in gills of *Barbus jae*……. ……..…..***M. nkolyaensis* Fomena and Bouix, 1994** (Fig. 7.77a, b).

15d. Spores are ovoid in frontal view with a flattened anterior end that is as wide as posterior end. Two smooth shell valves are present and in side view the spores are lenticular in shape with an indistinct sutural line. Length 10-13 µm and width 8-9.5 µm. Two ovoid to pyriform polar capsules, 4-5 × 3-4 µm. Capsules are non-convergent and contain 4-5 loosely arranged coils in the polar filament. Histozoic in kidneys and spleen of various ciclids……...***M. sarigi* (Landsberg, 1985)** (Fig. 7.84).

15e. Polysporic plasmodia in ovaries, spherical, 2-3 mm in diameter. Spore body ovoid to spherical, 13.7-15 µm long × 10-11.2 µm wide. Shell valves smooth. Polar capsules pyriform, 6-6.2 × 3-3.7 µm. Histozoic in *Clarias gariepinus*……..***M. gariepinus* Reed, Basson and Van As, 2003** (Fig. 7.63).

16a. Oval to spherical plasmodia are found in the infected organs. The spores are of variable size and are ovoid in front view and lenticular in side view. Anterior ends of the spores are slightly fusiform. Length 6.5-11.5 µm, width 5-9.5 µm. Two unequal polar capsules. Larger polar capsule, 4-7 × 2-3 µm with 4-5 coils in filament. Smaller polar capsule, 2-4 × 1.5-2.5 µm with 3 coils in filament. Histozoic in gills, kidneys and heart of *Barbus* sp……..……***M. oloi*** **Fomena and Bouix, 1994** (Fig. 7.81).

17a. Spores ovoid. Anterior end more or less attenuated……18
17b. Spores ellipsoidal with rounded anterior……25

18a. Polar capsules unequal……19
18b. Polar capsules equal……20

19a. Spores pyriform, length 13-15 µm, width. Shell valves smooth and slightly thicker at anterior point where discharging ducts emerge. Side view of spores are lenticular to flattened with an indistinct sutural ridge. Polar capsules ovoid to pyriform, unequal and situated equatorially. Larger polar capsule, 4-5 × 3-4 µm. Smaller polar capsule 3-4 × 2.5-3 µm. The anterior of each polar capsule appears to have an extremely elongated neck region with discharging ducts running inwards from the anterior end of the spore. Histozoic in the spleen of *Oreochromis* species…… ……***M. equatorialis*** **(Landsberg, 1985)** (Fig. 7.58).

19b. Spores ovoid with pointed anterior end, length 9-11 µm, width 5-6 µm. Sutural edge with markings. Polar capsules ovoid and unequal. Larger polar capsule 4-5 × 2-3 µm. Smaller polar capsule 3-3.5 × 2-3 µm. Histozoic in gills of *Citharinus citharinus*…… ……..……***M. maraensis*** **Kostoïngue, Faye and Toguebaye, 1998** (Fig. 7.73).

19c. Spores oval, length 10-12 µm, width 6.5-8 µm. Polar capsules unequal. Larger polar capsule 5-7 × 2.5-3.5 µm. Smaller polar capsule 2.5-4.5 × 1.5-2 µm. Each individual spore is surrounded by a thick refractile wall. Histozoic in fins of *Labeo niloticus*…….. ……***M. niloticus*** **Fahmy, Mandour and El-Naffar, 1971** (No figure in original description).

20a. Polar capsules ovoid……21
20b. Polar capsules pyriform and elongate……22

21a. Spores ovoid with narrow anterior end and rounded posterior end, length

14-22 µm, width 10-16 µm. Shell valves smooth and thin. Polar capsules 6-8 × 2.5-5 µm, with 6-7 coils per filament. Histozoic in gills, eyes and muscles of *Oreochromis niloticus*……..…… …….....***M. camerounensis*** **Fomena, Marqués and Bouix, 1993** (Fig. 7.49).

21b. Plasmodia associated with diffuse yellowish pigment among muscle fibers, elevated (1-2 mm). Spores ovoid, anterior slightly narrower than posterior, length 13.5-17 µm, width 8.5-11 µm. Polar capsules large, 4-6 × 2-4 µm. Histozoic in muscles of *Tilapia esculenta* and *T. variabilis*…….. ……..***M. homeosporus*** **(Baker, 1963)** (Fig. 7.66).

21c. Spores ovoid with anterior and posterior equally rounded, length 13-14 µm, width 10-11 µm. Polar capsules ovoid and equal, 5-6 × 4-5 µm. Histozoic in the kidneys *of Citharinus citharinus*…….***M. ndjamenaeansis*** **Kostoingue, Faye and Toguebaye, 1998** (Fig. 7.74).

22a. Ratio of polar capsule length / width = 2……23

22b. Ratio of polar capsule length / width = 3……24

23a. Plasmodia oval, whitish in shape (1.2 ± 0.05 × 0.9 ± 0.23 mm). Spores oval, length 8.51 µm, width 5.35 µm. Polar capsules elongated, convergent anteriorly and equal, 6.11 × 3.91 µm. Polar filament coiled 10-12 times at oblique angle to longitudinal axis of polar capsules. Histozoic in gills of *Bagrad bayad*……***M. bagri*** **Negm-Eldin, Govedich and Davies, 1999** (Fig. 7.44).

23b. Plasmodia sausage or rod-shaped, whitish (1.2 × 0.4). Spores ovoid to oval with seven to nine sutural ridge makings. Length 10.21 µm, width 6.11 µm. Distinct triangular intercapsular process. Polar capsules elongated to oval, convergent anteriorly and equal in size, 4.61 × 2.41 µm. Polar filament coiled 8-11 times perpendicular to longitudinal axis of polar capsules. Histozoic in the gills of *Chrysichthys auratus*…… ……...***M. chrysichtyi*** **Negm-Eldin, Govedich and Davies, 1999** (Fig. 7.51).

23c. Spores ovoid with sutural edge markings, length 9-11 µm, width 5-7 µm. Polar capsules pyriform, 4-5 × 1-2.5 µm. Histozoic in gills of *Citharinops distichoides*…….……***M. citharinopsi*** **Kostoingue, Faye and Toguebaye, 1998** (Fig. 7.52).

23d. Spores roughly ovoid or ellipsoidal, but very variable in shape. Length of spores 8.5-17 µm, width 6.5-11 µm. Polar capsules 2-9.5 × 1.5-3.5 µm. Histozoic in liver, kidneys and spleen of *Tilapia esculenta*, *T. variablis* and *Oreochromis niloticus*…..…….. ……***M. heterosporus*** **(Baker, 1963)** (Figs. 7.65a, b, c)

Remark. As described by Baker (1963) the spores of *M. heterosporus* fall into three main categories:

M. heterosporus type 1: Occasionally small, intercapsular appendage. Length of spores 8.5-17 µm. width 6.5-11 µm. Polar capsules 2-5.5 × 1.5-3.5 µm (Fig. 7.65a).

M. heterosporus type 2: Spores with pointed anterior end. Polar capsules about half the spore length. Length of spores 9-15 µm, width 6.5-10.5 µm. Polar capsules 3-7 × 1.5-3 µm (Fig. 7.65b).

M. heterosporus type 3: Polar capsules sometimes curved, more than half the spore length. Length of spores 10-14.5 µm, width 6.5-8 µm. Polar capsules 5.5 × 2.3 µm (Fig. 7.65c).

23e. Spores ellipsoidal, length 13-14 µm, width 8-10 µm. Polar capsules elongated, 4-5 × 2-3 µm. Histozoic in gills of *Hydrocynus forskali* ……. ……....***M. hydrocyni*** **Kostoïngue and Toguebaye, 1994** (Fig. 7.67).

23f. Plasmodia ovoid and white (1.4 × 1.3 mm). Spores ovoid to oval, length 10.5 µm, width 6.25 µm. Polar capsules fusiform, convergent anteriorly and of equal size, 5.2 × 2.1 µm. Polar filament oblique to longitudinal axis of polar capsule with 7-10 coils. Histozoic in gills of *Synodontis schall*…….. ……...***M. synodontis*** **Negm-Eldin, Govedich and Davies, 1999** (Fig. 7.88).

24a. Spores ovoid, pointed anterior, length of spores 10.5-14 µm, width 5.5-9 µm. Polar capsules take up more than half of spore length, 6-8 × 1.5-3 µm, with 8-10 coils of filament. Histozoic in the of *Sarotherodon melanotheron*…… ……...***M. beninensis*** **Sakiti, Blanc, Marqués and Bouix, 1991** (Fig. 7.45).

24b. Spores ovoid with triangular markings along the sutural edge. Length of spores 9-11 µm and width 5-6 µm. Polar capsules pyriform and equal, 2-3 × 1-2 µm. Histozoic in gills of *Brycinus macrolepidotus*……..***M. chariensis*** **Kostoïngue, Faye and Toguebaye, 1998** (Fig. 7.50).

24c. Spores ovoid to pyriform, length 12 µm and width 6 µm. Polar capsules 4-5 × 2-3 µm, with 4-5 coils per filament. Histozoic in ovaries of *Synodontis ansorgii*……....***M. dahomeyensis* (Siau, 1971)** (Fig. 7.55).

24d. Spores ovoid and elongated, with anterior much narrower than posterior, length 13-15 µm, and width 8-9 µm. Polar capsules pyriform and elongated, 6-7 × 2-3 µm. Parasitising kidneys of *Synodontis gambiensis*…….. ……..…….***M. mailaoensis* Kostoïngue, Faye and Toguebaye, 1998** (Fig. 7.72).

24e. Spores ovoid in frontal view with anterior end tapering to a blunt point and posterior end rounded, length 7.5-13 µm, width 5-7 µm. Polar capsules pyriform, 5-7 × 1.5-2.5 µm with 6-9 coils in polar filament. Histozoic in gills of *Barbus* sp……....***M. nyongana* (Fomena, Bouix and Birgi, 1985)** (Fig. 7.80).

Remark. *Myxobolus barbi* Fomena, Bouix and Birgi, 1985 is renamed *M. nyongana* by Fomena and Bouix (1997) after the Nyong Basin, where the hosts were captured. Tripathi (1953) already attributed the name *M. barbi* to a different species parasitising *Barbus ticto.*

25a. Length of polar capsules ≤ 1/3 of spore length……26

25b. Length of polar capsules ≥ 1/3 of spore length……27

26a. Spores ellipsoidal with a thick wall and ten to 13 triangular sutural markings. Length of spores 21.1 µm and width 17.2 µm. Polar capsules round to ovoid, convergent and non-convergent, 6.2 × 5.3 µm. Histozoic in gills of *Lates niloticus*……..…….***M. lates* Negm-Eldin, Govedich and Davies, 1999** (Fig. 7.71).

26b. Spores ovoid, length 8-11 µm, and width 5-7 µm. Intercapsular process present. Polar capsules 2.5-4 × 1.5-2.5 µm, with 5-6 coils per filament. Histozoic in the gills of *Sarotherodon melanotheron*……..***M. nokoueensis* Sakiti, Blanc, Marqués and Bouix, 1991** (Fig. 7.78).

26c. Spores ellipsoidal to elongate, with the posterior end slightly wider than the anterior end, length 12-14.5 µm, width 5.5-10 µm. Shell valves thick (1.5 µm). Two small polar capsules are situated in the anterior end of the spore, 3.5-4.5 × 1.5-2.5 µm, with 4-5 coils of filament. Histozoic in gills of *Polycentropsi abbreviata*…….***M. polycentropsi***

Fomena, Bouix and Birgi, 1985 (syn. *M. microcapsularis*) (Fig. 7.83).

Remark. Myxobolus microcapsularis Sakiti, Blanc, Marqués and Bouix, 1991, a parasite of *Tilapia zillei* was synonymised with *M. polycentropsi* since the morphometric characteristics of the two species are alike and the host fish is not a criterion for recognising species (Fomena and Bouix 1997).

26d. Spores variable in shape, but are mostly rectangular with blunt corners, length 12-20 µm, width 7.5-11 µm. Some may be oblong showing a pointed anterior end, while others are symmetrically oval. Polar capsules ovoid. Length of polar capsules ¼ of spore length, 2-3.5 × 2-2.5 µm. Histozoic in gills and fins of *Tilapia zillii*, *Sarotherodon galilaeus* and *Oreochromis niloticus*…….***M. tilapiae*** **Abolarin, 1974** (Figs. 7.89a, b).

27a. Length of polar capsules less than half of spore length……...28

27b. Length of polar capsules greater than half of spore length……...29

28a. Spores ellipsoidal to elongate, length 10-11 µm, width 5-6 µm. Polar capsules relatively small, 4-5 × 1.5-2 µm. Histozoic in gills, liver and intestine of *Distichodus engycephalus*…. ……..…….*M. distichodi* **Kostoïngue and Toguebaye, 1994** (Fig. 7.56).

28b. Spores ovoid in frontal view with an anterior end that is broader and more rounded than the narrower posterior end. Length of spores 11-12.5 µm, width 7.5-8.5 µm. Polar capsules pyriform, not convergent, 5-5.5 × 3-3.5 µm. Histozoic in gills of *Synodontis schall*…….. ……..***M. stenosus*** **Paperna, 1973** (Fig. 7.86).

29a. Spores pyriform, length 11.5-16 µm, width 5.5-8.5 µm. Polar capsules pyriform and very elongate (ratio length/width = 4), reaching 2/3 spore length, 6-10 × 1.5-2.5 µm, with 3 oblique coils. Histozoic in gills, eyes and muscles of *Ctenopoma nanum*…….. ……..***M. amieti*** **Fomena, Bouix and Birgi, 1985** (Fig. 7.43).

29b. Spores ovoid to spherical, length 11.5-12.5 µm, width 7.5-8.5 µm. Polar capsules flask-shaped, 7-8 × 3-3.5 µm, with 5-6 coils located at an oblique angle to the longitudinal axis of the polar capsule. Histozoic in gills, skin, eyes, kidneys and pancreas of *Oreochromis niloticus*……...***M. nilei***

(Faisal and Shalaby, 1987) (syn. *Myxosoma tilapiae*) (Fig. 7.75).

Remark. Fomena and Bouix (1997) renamed *Myxosoma tilapiae*, a parasite of *O. niloticus* due to the fact that the genus *Myxosoma* Thélohan, 1892 is a junior synonym of *Myxobolus*. On transfer to *Myxobolus*, *M. tilapiae* would have become a secondary homonym and thus required renaming since it was pre-occupied by *Myxobolus tilapiae* (Abolarin, 1974) (Fomena and Bouix 1997).

29c. Spores pyriform to ovoid with anterior tapering to blunt point and posterior rounded, length 11.2-10 µm, width 7.5-10 µm. Polar capsules 5-6.8 × 2-2.5 µm, with 6-7 coils per filament. Histozoic in gills of *Barbus paludinosus* ……..……***M. paludinosus* Reed, Basson and Van As, 2002** (Fig. 7.82).

30a. Polar capsules unequal……31
30b. Polar capsules equal……32

31a. Spores extremely elongated, pyriform to teardrop, anterior end tapering to a blunt point posterior rounded, length 12.8-15 µm, width, 6.2-8 µm. Sutural ridge slightly broader at posterior end of spore. Polar capsules extremely elongated, pyriform, unequal. Larger polar capsule 7-8 × 1.2-2.5 µm. Histozoic in gills of *Barbus etsatsaensis* ……..***M. etsatsaensis* Reed, Basson and Van As, 2002** (Fig. 7.59).

31b. Spores relatively large, ovoid and elongated, with the anterior end narrower than the rounder, larger posterior end. Length of spores 20-23 µm, width 9-10 µm. Polar capsules pyriform and unequal. Larger polar capsules 14.5-17.5 × 3-4 µm, with 19-28 coils per filament. Smaller polar capsules 13.5-17 × 3-4 µm. Histozoic in skin, eyes and kidneys of *Brycinus longipinnis*…… ……..……..***M. kribiensis* Fomena and Bouix, 1994** (Fig. 7.70).

32a. Spores ovoid with pointed anterior end, length 13.5-17.5 µm, width 5.5-9 µm. Polar capsules equal with one discharging laterally, 5.5-9.5 × 1.5-3.5 µm, with 5-6 coils perpendicular to longitudinal axis. Histozoic in skin, fins and gills of *Hepsetus odoe*…… ……..……....***M. africanus* Fomena, Bouix and Birgi, 1985** (Fig. 7.41).

32b. Spores ellipsoid or oval, anterior end rounded. Length of spores 12-15 µm, width 6-7 µm. Polar capsules pyriform, 5.5-7 × 1.5-2.5 µm. Histozoic

in stomach wall of *Synodontis batesii*……..…….……***M. synodonti* Fomena, Bouix and Birgi, 1985** (Fig. 7.87).

33. Spores ellipsoid, length 7-7.5 µm, width 12-13.5 µm. Polar capsules rounded or ellipsoidal, equal or unequal, 2.5-4 × 2.5 µm. Parasites of various cichlids……...…..***M. brachysporus* (Baker, 1963)** (syn. *Myxosoma brachyspora* Baker, 1963) (Fig. 7.47).

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. Sutural ridge often prominent. Polar capsules subspherical or pyriform. Two uninucleate sporoplasms. Mono- or disporic trophozoites usually coelozoic in urinary system of freshwater and marine fishes, some are histozoic. Often with intracellular stages and with presporogonic development cycles in various body organs. Coelozoic species from the urinary system seem to be host specific and have extrasporogonic stages in blood and also some in other tissues. Approximately 50 species throughout the world, three known from freshwater fishes in Africa.

1. Shell valves smooth……...3
2. Shell valves striated……...4

3a. Spores briefly pyriform with tubercles in posterior region. Length of spores 9-10 µm, width 7.5-9.5 µm. Polar capsules 3-4.5 µm × 2.5-4 µm. Spores grouped in kidneys of *Oreochromis niloticus*…...***S. melenensis* Fomena, Marqués and Bouix, 1993** (Figs. 7.91a, b).

3b. Spores slightly pyriform, sutural line prominent. Length of spores 8-9 µm, width 6.5-9 µm. Polar capsules 2.5-4 × 2-3 µm. Coelozoic in kidneys of *Brienomyrus brachyistus* and *Hepsetus odoe*……..***S. sangmelimaensis* Fomena and Bouix, 1994** (Figs. 7.92a, b).

4. Spores spherical, length 7-8.5 µm. width 7-8.5 µm. Diameter of polar capsules 2.5-3.5 µm. Spores grouped in kidneys and rarely in spleen of *Oreochromis niloticus*…….***S. tilapiae* Fomena, Marqués and Bouix, 1993** (Figs. 7.93a, b).

Genus *Thelohanellus* Kudo, 1933

Spores pyriform, tear-shaped or ellipsoid in valvular view. Tear-shaped or pyriform in sutural view. Valves smooth. A single pyriform, tear-shaped or subspherical polar capsule in anterior end of spore. Binucleate sporoplasm mostly with a spherical polysaccharide inclusion. Trophozoites large and polysporic with pansporoblast formation. Histozoic in freshwater fishes. More than 40 species throughout the world, six known from freshwater fishes in Africa.

1. Spores pyriform. Polar capsules lying parallel to the long axis of spore……...3
2. Spores ovoid. Polar capsules lying obliquely with regard too long axis of spore……...6

3a. Spores elongate: length/width ration >.5……..5
3b. Length of spore less than twice the width……4

4a Spores pyriform, anterior end slightly truncated. Length of spores 9-12 µm, width 5-7 µm. Polar capsule 6-9 × 2-3.5 µm. Polar filament contains 5-6 coils. Histozoic in gills and fins of *Labeo* sp……..…***T. assambai* Fomena, Marqués, Bouix and Njiné, 1994** (Fig. 7.94).

4b. Plasmodia ovoid and whitish up to 1.5 mm. Spores elongate and slightly curved with blunted anterior and broadly rounded posterior. Histozoic in heart of *Citharinus citharinus*……***T. citharini* Kostoingue, Fall, Faye and Toguebaye, 1999** (Fig. 7.95).

5. Length of spores 11-13 µm, width 4-5 µm. Polar capsule 5.5-7 × 2-3 µm with 6-8 coils per filament. Histozoic in gills of *Barbus jae* and *B. aspilus*……. ……...***T. valeti* Fomena and Bouix, 1987** (Figs. 7.98a, b, c).

6a. Plasmodia variable, up to 2.5 mm. Spores ovoid with posterior end usually wider than anterior. Length of spores 10-11 µm, width 7-8 µm. Polar capsules pyriform 4-5 × 3-5 µm with 4-5 coils per filament. Histozoic in gills of *Labeo parvus*……..***T. ndjamenaensis* Kostoïngue, Fall, Faye and Toguebaye, 1999** (Figs. 7.96).

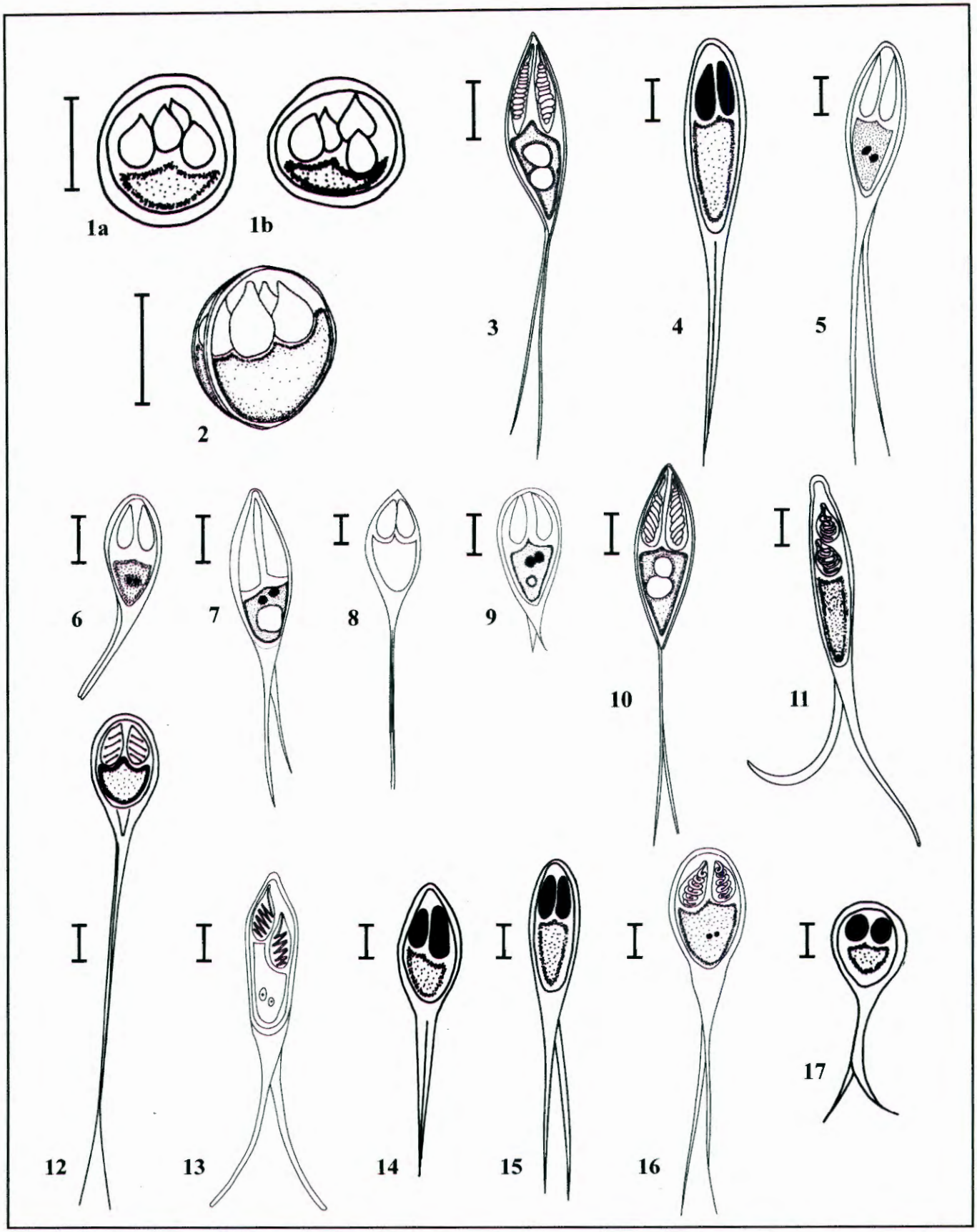
6b. Spores ovoid, 5 µm in length and 3.5 µm in width. Polar capsules oblique to longitudinal axis of the spore. Histozoic in head skin of *Labeo niloticus* ……..…***T. niloticus* (Gurley, 1893)** (No figure available).

6c. Anterior of spores slightly truncate, length 10.5-13.5 µm, width 8-10.5 µm. Polar capsule 5-6.5 × 3-4 µm with 9-11 coils of filament. Histozoic in *Labeo* sp. ……..……..……..***T. sanagaensis*** **Fomena, Marqués, Bouix and Njiné, 1994** (Figs. 7.97a, b).

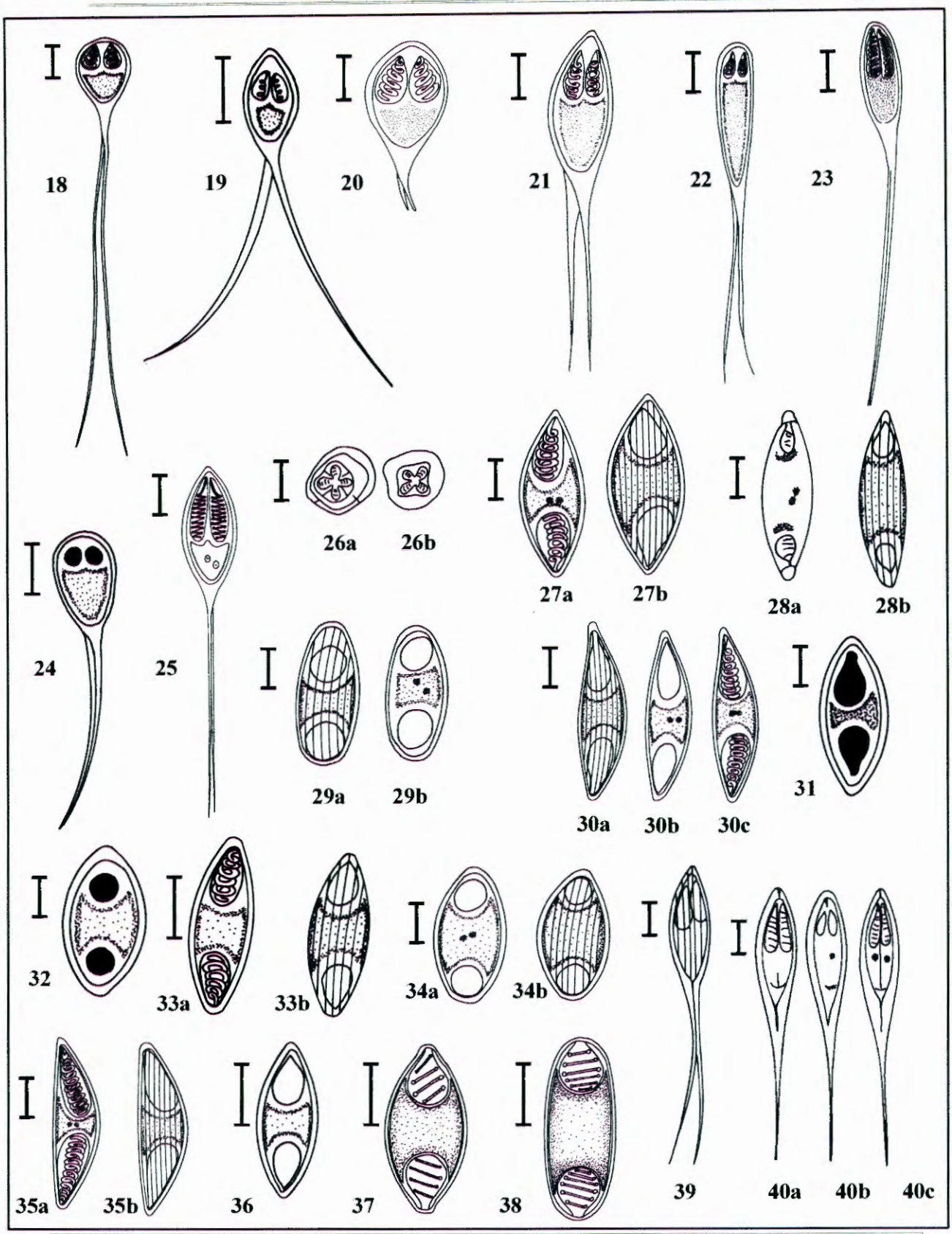
Genus *Unicauda* Davis, 1944

Spores similar to *Myxobolus*, but have a single caudal appendage which, unlike *Henneguya*, is not a continuation of the smooth shell valves, but is a structure made up from a different material, adhering to the shell valves along a distinct boundary. Strictly histozoic in freshwater fishes. Only nine species known throughout the world, one found in Africa.

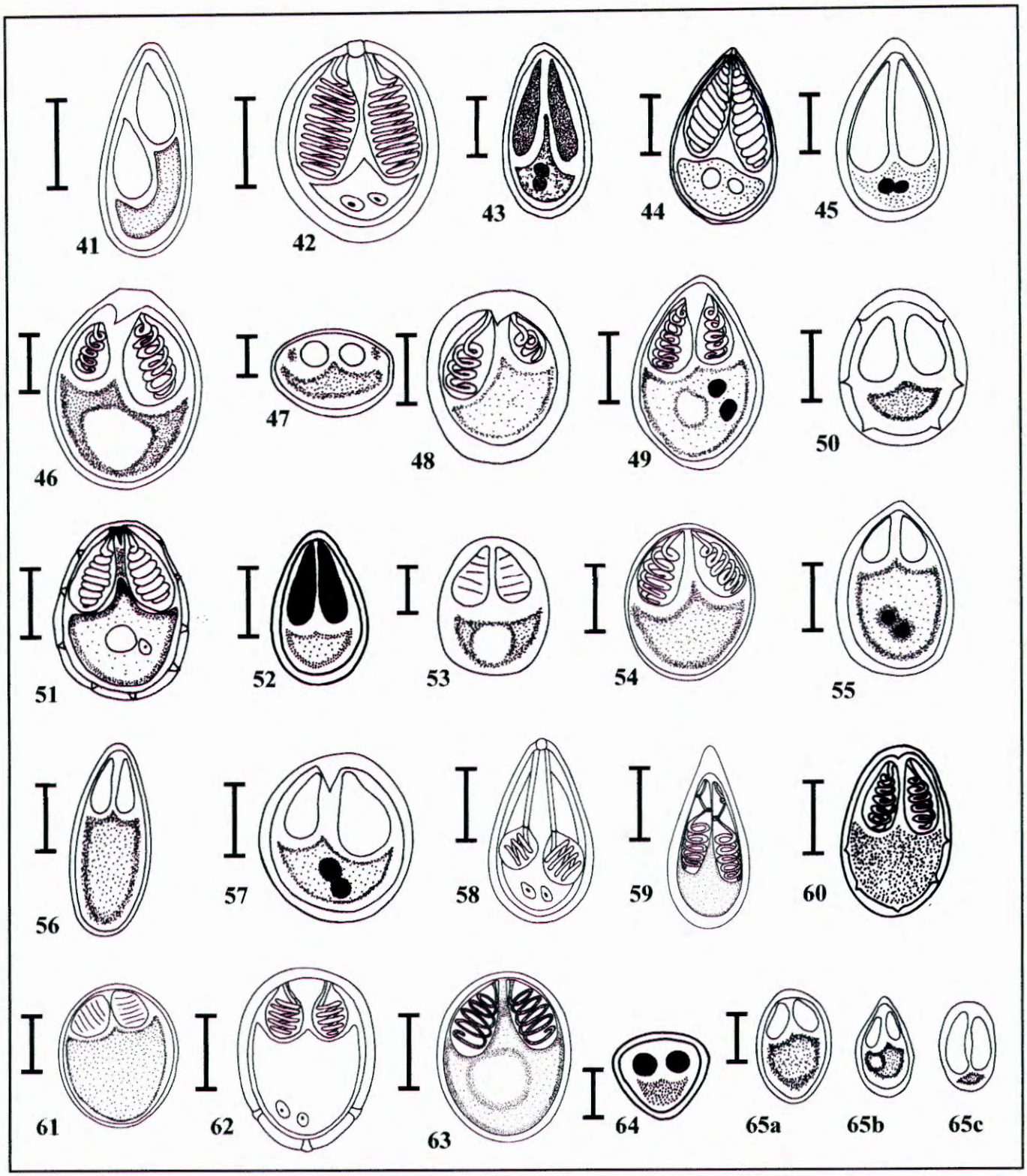
1. Spore body length 9 µm, width 5.5 µm. Histozoic in *Synodontis schall*….. ……..….***U. strongylura*** **(Gurley, 1893)** (syn. *Henneguya strongylura* (Gurley, 1893) Labbé, 1899) (Figs. 7.99a, b).



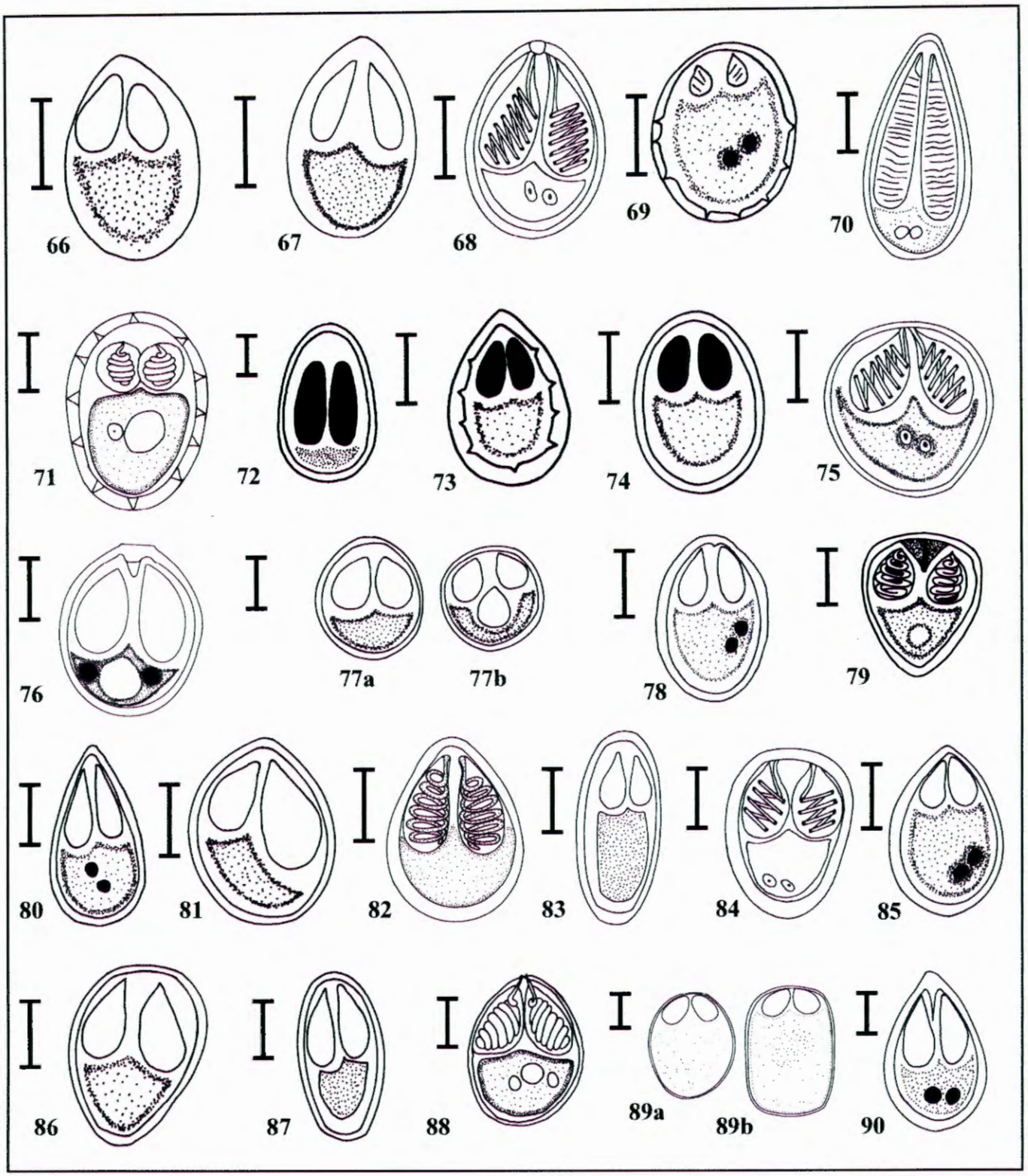
Figures 7.1-7.17: Spores. 1a, b. *Chloromyxum birgii* Fomena and Bouix, 1994. **2.** *C. vanasi* Ali, 1998. **3.** *Henneguya alestes* Negm-Eldin,Govedich and Davies, 1999. **4.** *H. auchenoglanii* Kostoïngue, Diebakate, Faye and Toguebaye, 2001. **5.** *H. bopeleti* Fomena and Bouix, 1987. **6.** *H. camerounensis* Fomena and Bouix, 1987. **7.** *H. chrysichthyi* Obiekezie and Enyenihi, 1988. 8. *H. clariae* Abolarin, 1971. **9.** *H. ctenopomae* Fomena and Bouix, 1996. **10.** *H. cyprini* Negm-Eldin,Govedich and Davies, 1999. **11.** *H. fusiformis* Kostoïngue, Fall, Faye and Toguebaye, 1999. **12.** *H. ghaffari* Ali, 1999. **13.** *H. laterocapsulata* Landsberg, 1987. **14.** *H. logonensis* Kostoïngue, Diebakate, Faye and Toguebaye, 2001.**15.** *H. mailaoensis* Kostoïngue, Diebakate, Faye and Toguebaye, 2001. **16.** *H. malapteruri* Fomena and Bouix, 1986. **17.** *H. massi* Kostoïngue, Diebakate, Faye and Toguebaye, 2001. Scale bars: 5µm. Figures drawn from original descriptions.



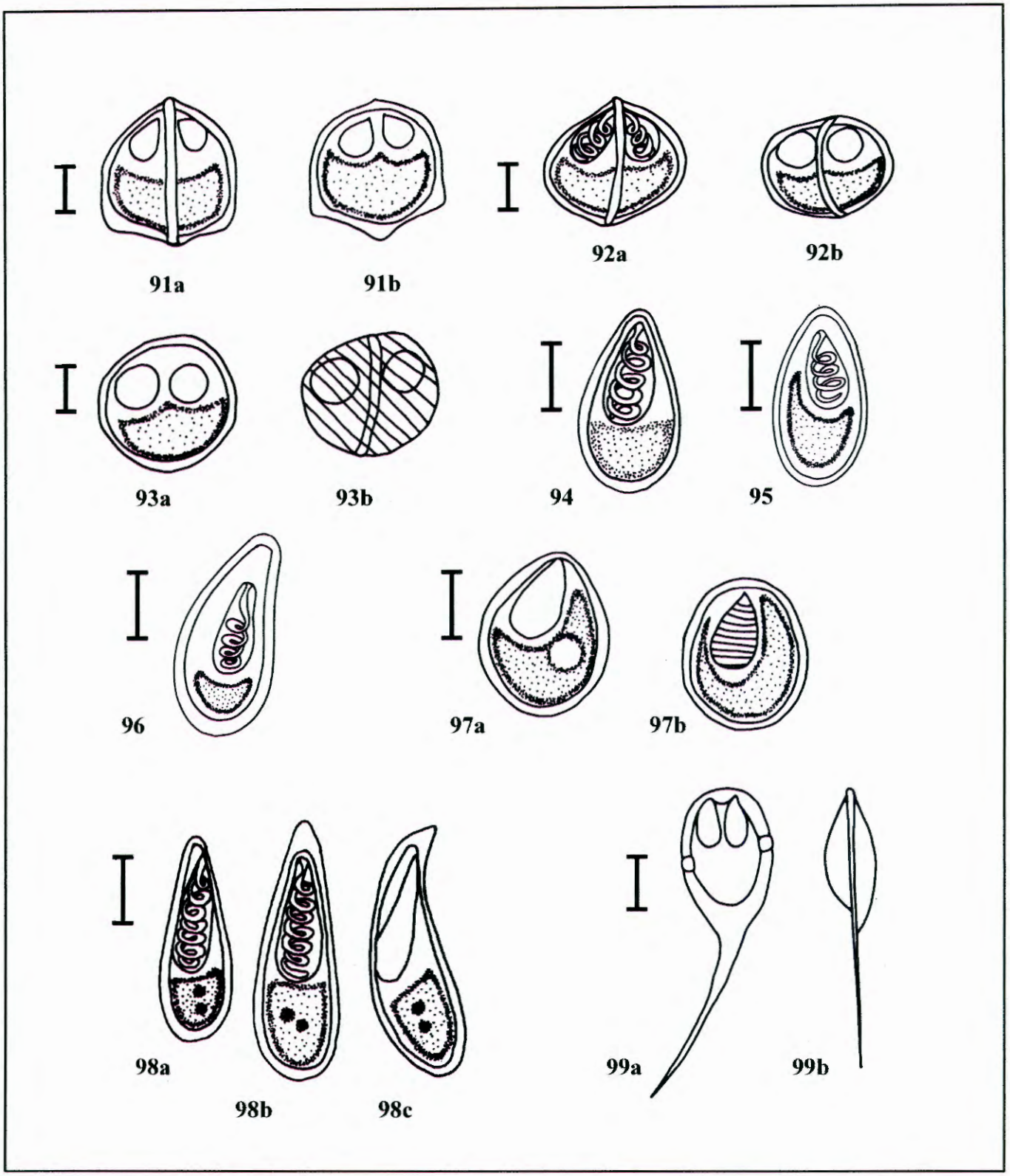
Figures 7.18-7.40: Spores. **18.** *Henneguya mbakaouensis* Fomena and Bouix, 2000. **19.** *H. mormyri* Kostoïngue, Diebakate, Faye and Toguebaye, 2001. **20.** *H. ntemensis* Fomena and Bouix, 1996. **21.** *H. nyongensis* Fomena and Bouix, 1996. **22.** *H. odzai* Fomena and Bouix, 1996. **23.** *H. samochimensis* Reed, Basson and Van As, 2003. **24.** *H. sarotherodoni* Fall, Fomena, Kostoïngue, Diebakate, Faye and Toguebaye, 2000. **25.** *H. suprabranchiae* Landsberg, 1987. **26a, b.** *Kudoa eleotrici* Siau, 1971. **27a, b.** *Myxidium birgi* Fomena and Bouix, 1986. **28a, b.** *M. bouixi* Siau, 1971. **29a, b.** *M. brienomyri* Fomena and Bouix, 1986. **30a, b, c.** *M. camerounensis* Fomena and Bouix, 1986. **31.** *M. distichodi* Kostoïngue, Faye and Toguebaye, 1998. **32.** *M. latesi* Kostoïngue, Faye and Toguebaye, 1998. **33a, b.** *M. mendehei* Fomena and Bouix, 1994. **34a, b.** *M. nyongensis* Fomena and Bouix, 1986. **35a, b.** *M. petrocephali* Fomena and Bouix, 1986. **36.** *M. schalli* Ghaffer, Shahawi and Naas, 1995. **37.** *M. schilba* Ali, Sakran and Abdel-Baki, 1999. **38.** *M. shamama* Ali, Sakran and Abdel-Baki, 1999. **39.** *Myxobilatus accessobranchialis* Obiekezie and Okaeme,



Figures 7.41-7.65: Spores. 41. *Myxobolus africanus* Fomena, Bouix and Birgi, 1985. **42.** *M. agolus* Landsberg, 1985. **43.** *M. amieti* Fomena, Bouix and Birgi, 1985. **44.** *M. bagri* Negm-Eldin, Govedich and Davies, 1999. **45.** *M. beninensis* Sakiti, Blanc, Marques and Bouix, 1991. **46.** *M. bilongi* Fomena, Marques, Bouix and Njiné, 1994. **47.** *M. brachysporus* (Baker, 1963). **48.** *M. burkinei* Kabre, Sakiti, Marques and Sawadago, 1995. **49.** *M. camerounensis* Fomena, Marques and Bouix, 1993. **50.** *M. chariensis* Kostoïngue, Faye and Toguebaye, 1998. **51.** *M. chrysichthyi* Negm-Eldin, Govedich and Davies, 1999. **52.** *M. citharinopsi* Kostoïngue, Faye and Toguebaye, 1998. **53.** *M. clarii* Mandour, Galal and Abed, 1993. **54.** *M. comoei* Kabre, Sakiti, Marques and Sawadago, 1995. **55.** *M. dahomeyensis* Siau, 1971. **56.** *M. distichodi* Kostoïngue, and Toguebaye, 1994. **57.** *M. dossoui* Sakiti, Blanc, Marques and Bouix, 1991. **58.** *M. equatorialis* Landsberg, 1985. **59.** *M. etsatsaensis* Reed, Basson and Van As, 2002. **60.** *M. exiguus* Thélohan, 1895. **61.** *M. fotoi* Fomena, Marques and Bouix, 1993. **62.** *M. galilaeus* Landsberg, 1985. **63.** *M. gariepinus* Reed, Basson and Van As, 2003. **64.** *M. gandiolensis* Fall, Fomena, Kostoïngue, Diebakate, Faye and Toguebaye, 2000. **65a, b, c.** *M. heterosporus* (Baker, 1963), types I-III. Scale bars: 5µm. Figure 60 redrawn from Fomena and Bouix (1997), all other figures redrawn from original descriptions.



Figures 7.66-7.90: Spores. **66.** *Myxobolus homeosporus* Baker, 1963. **67.** *M. hydrocyni* Kostoïngue and Toguebaye, 1994. **68.** *M. israelensis* Landsberg, 1985. **69.** *M. kainjiae* Paperna, 1973. **70.** *M. kriebiensis* Fomena and Bouix, 1994. **71.** *M. lates* Negm-Eldin, Govedich and Davies, 1999. **72.** *M. mailaoensis* Kostoïngue, Faye and Toguebaye, 1998. **73.** *M. maraensis* Kostoïngue, Faye and Toguebaye, 1998. **74.** *M. ndjamenaensis* Kostoïngue, Faye and Toguebaye, 1998. **75.** *M. nilei* Faisal and Shalaby, 1987. **76.** *M. njinei* Fomena, Bouix and Birgi, 1985. **77a, b.** *M. nkolyaensis* Fomena and Bouix, 1994. **78.** *M. nokoueensis* Sakiti, Blanc, Marques and Bouix, 1991. **79.** *M. nouensis* Fomena and Bouix, 2000. **80.** *M. nyongana* Fomena, Bouix and Birgi, 1985. **81.** *M. oloi* Fomena and Bouix, 1994. **82.** *M. paludinosus* Reed, Basson and Van As, 2002. **83.** *M. polycentropsi* Fomena, Bouix and Birgi, 1985. **84.** *M. sarigi* Landsberg, 1985. **85.** *M. sarotherodoni* Sakiti, Blanc, Marques and Bouix, 1991. **86.** *M. stenosus* Paperna, 1973. **87.** *M. synodonti* Fomena, Bouix and Birgi, 1985. **88.** *M. synodontis* Negm-Eldin, Govedich and Davies, 1999. **89a, b.** *M. tilapiae* Abolarin, 1974. **90.** *M. zillei* Sakiti, Blanc, Marques and Bouix, 1991. Scale bars: 5µm. Figures redrawn from original descriptions.



Figures 7.91-7.99: Spores. 91a, b. *Sphaerospora melenensis* Fomena, Marques and Bouix, 1993. **92a, b.** *S. sangmelimaensis* Fomena and Bouix, 1994. **93a, b.** *S. tilapiae* Fomena, Marques and Bouix, 1993. **94a, b.** *Thellohanellus assambai* Fomena, Marques, Bouix and Njinei, 1994. **95.** *T. citharini* Kostoïngue, Fall, Faye and Toguebaye, 1999. **96.** *T. ndjamenaensis* Kostoïngue, Fall, Faye and Toguebaye, 1999. **97a, b.** *T. sanagaensis* Fomena, Marques, Bouix and Njiné, 1994. **98a, b, c.** *T. valeti* Fomena and Bouix, 1987. **99a, b.** *Unicauda strongilura* (Gurley, 1893). Scale bars: 5µm. Figure 99a, b redrawn from Fomena and Bouix (1997), all other figures redrawn from original descriptions.

Key to the Marine and Estuarine fish-infecting myxosporeans of Africa

Key to the genera

1a. Mature spores with only one polar capsule. Spores more or less spherical with sutural line difficult to see. Three valves (one small, two large), exclusively histozoic……..***Unicapsula*** **Davis, 1924.**

1b. Two polar capsules per spore…...**2**

1c. Four polar capsules per spore. Four shell valves……..…….***Kudoa*** **Meglitsch, 1947.**

2a. Polar capsules located separately in the ends of a spindle-shaped or elongated spore……..…**3**

2b. Polar capsules not terminally in opposing ends, but also not close together…….….**5**

2c. Polar capsules close together..……**8**

3a. Polar filament is a thin spirally wound tube of about the same thickness all along its length……**4**

3b. Polar filament strongly tapered from base to tip. Polar filament does not form a regular coil, but is folded and bent over several times……..***Sphaeromyxa*** **Thélohan, 1892.**

4a. Spores with more or less pointed ends……..***Myxidium*** **Bütschli, 1882.**

4b. Spores usually ellipsoidal, with rounded or bluntly pointed ends and almost spherical polar capsules. ……..……...***Zschokkella*** **Auerbach, 1910.**

5a. Rounded or ovoid spores with polar capsules set wide apart in the sutural plane……**6**

5b. Spherical, rounded or pyramidal spores with polar capsules in a plane perpendicular to sutural line which is mostly sinuous……**7**

6. Spores spherical or subspherical. Infecting marine fishes……...***Ortholinea*** **Shulman, 1962.**

7a. Spores spherical, each shell valve bears a hollow, usually horn-like projection approximately at its centre ……..…….…….***Davisia*** **Laird, 1953.**

7b. Spores inversely pyramidal with tapering end extending backwards. Wing-like projection attached to anterior surface of each valve……..….***Bipteria*** **Kovaleva, Zubchenko and Krasin, 1983.**

8a. Spores bilaterally symmetrical. Polar capsules set in a plane, essentially perpendicular to plane of the sutural line……**9**

8b. Spores bilaterally symmetrical. Polar capsules in apex of spore set in sutural plane……**12**

9a. Polar capsules more or less close to apex of spore. Spores without projections or veils……...**10**

9b. Polar capsules more or less close to apex of spore. Spores with projections or veils……..……**11**

10a. Spores elongated in the direction perpendicular to the sutural plane, sometimes arcuate. Depth of shell valve may reach dimensions of sutural diameter…….……***Leptotheca* Thélohan, 1895.**

10b. Spores crescent-shaped, extremely elongated in direction perpendicular to the sutural line……..***Ceratomyxa* Thélohan, 1892.**

11a. Subspherical spores enveloped in large membranous veil……..***Palliatus* Kovaleva and Dubina, 1979.**

11b. Triangular spores laterally drawn into wing-like membranous projections ……..…….……***Alatospora* Shulman, Kovaleva and Dubina, 1979.**

12a. Spores without projections. Sutural line straight…….***Myxobolus* Bütschli, 1882.**

12b. Spores two caudal, often slightly divergent projections…..…..***Henneguya* Thélohan, 1892.**

Key to the species

Genus *Alatospora* Shulman, Kovaleva and Dubina, 1979

Spores extremely elongated in the plane perpendicular to the central straight sutural line. Shell valves bear wing-like membranous projections adhering along their posterior half. Two small pyriform polar capsules. Trophozoites disporic and coelozoic in gall bladders of marine fishes. Only 10 species known throughout the world, with five described from Africa. All African species from this genus were described in a single article by Shulman, Kovaleva and Dubina (1979). This article is in Russian and unfortunately was not translated in time for use in this key. The following five species were described.

1. ***A. africana* Shulman, Kovaleva and Dubina, 1979** (Figs. 7.100a, b).

2. ***A. dracoidea* Shulman, Kovaleva and Dubina, 1979** (Figs. 7.101a-d).

3. ***A. contrariocapsularia* Shulman, Kovaleva and Dubina, 1979** (Figs. 7.102a-g).

4. ***A. parvicapsula* Shulman, Kovaleva and Dubina, 1979** (Figs. 7.103a-c).

5. ***A. samaroidea* Shulman, Kovaleva and Dubina, 1979** (Figs. 7.104a-e).

Genus *Bibteria* Kovaleva, Zubchenko and Krasin, 1983

Spores inversely pyramidal in sutural view with a pointed end extending backwards. Sinuous sutural line. Anterior end of each shell valve extends into wing-like projections containing parts of valvogenic nucleus. Spores ellipsoid in transverse section. Polar

capsules spherical. A single sporoplasm exists. Trophozoites are di- and polysporic. Only five species are known throughout the world, one from Africa.

1. Flat plasmodia up to 50 µm. Spores anteriorly rounded with wing-like projections 13 µm long. Length of spores 12.2 µm, width 11 µm. Polar capsules spherical, 4 µm in diameter with 4-5 coils per filament. Parasitising kidneys of *Spondyliliosoma canthurus* ……..…….***B. admiranda*** **Kovaljova, Zubchenko and Krasin, 1983** (Fig. 7.105).

Genus *Ceratomyxa* Thélohan, 1892

Elongated, crescent shaped or arcuate spores. Shell valves often conical, exceeding in length the axial diameter of the spore. Subspherical polar capsules have capsular foramina near sutural line at anterior pole of spore. Binucleate sporoplasm does not completely fill spore cavity. Trophozoites may be mono-, di- and polysporic. Usually disporic and coelozoic in marine fishes. More than 140 species known throughout the world with nine known from marine fish in Africa.

1a. Spores arcuate……2
1b. Spores ovoid……..5

2a. Spores slightly arched…….3
2b. Spores extremely arched…….4

3a. Spores broadly arched, length 4-5.3 µm, width 13.3-15 µm. Polar capsules pyriform, 2-2.6 × 1.3 µm. Coelozoic in gall bladder of *Trachurus trachurus capensis*…….……***C. australis*** **Gaevskaya and Kovaleva, 1976** (Fig. 7.107).

3b. Pansporoblasts ovoid, disporic and variable. Spores arcuate with elongated extremities, length 10-12 µm and width 38.8-40 µm. Polar capsules spherical, 4.5-5.5 µm in diameter. Some polar capsules pyriform 4.5-6 × 4-5.5 µm. Coelozoic in gall bladder of *Fistularia petimba*……...***C. fistulariae*** **Kpatcha, Diebakate, Faye and Toguebaye, 1996** (Fig. 7.108).

3c. Spores broadly ovoid to slightly arched. Length of spores 9-10.5 µm and width 20-22.5 µm. Polar capsules spherical and equal situated on either side of the suture line, 3.5-4.5 in diameter. Coelozoic in gall bladder of *Lagocephalus laevigaus*……..……
……...***C. lagocephali*** **Kpatcha, Diebakate, Faye and Toguebaye, 1996** (Fig. 7.109).

3d. Pansporoblasts ellipsoid and di-sporic. Spores slightly arched with right side of spore more pointed than rounded left side of spore. Length of spores 9-9.5 µm and width 9-9.5 µm. Polar capsules spherical 1.5-2.0 µm in diameter. Coelozoic in gall bladder of *Syacium micrurm*……..……***C. syacii*** **Kpatcha, Diebakte, Faye and Toguebaye, 1996** (Fig. 7.111).

3e. Spores elongated, slender and slightly arched. Length of spores 5-7 µm and width 25.5-27 µm. Polar capsules spherical 2-2.25 µm in diameter. Coelozoic in gall bladder of *Sardinella maderensis* and *S. aurita*. ……...***C. truncata*** **Thélohan, 1892** (Fig. 7.114).

4a. Spores elongated and extremely arched. Length 10-12 µm and width 48-50 µm. Polar capsules spherical, 2-3 µm in diameter. Coelozoic in gall bladder of *Trachinocephalus myops*……..…… ……..…….***C. trachinocephali*** **Kpatcha, Diebakate, Faye and Toguebaye, 1996** (Fig. 7.112).

4b. Spores extremely arched and elongated length 10-12 µm and width 98-100 µm. Polar capsules spherical and equal, 4.5-5 µm in diameter. Sporoplasm limited to region around suture line. Coelozoic in gall bladder of *Trichiurus lepturus*……....***C. trichiuri*** **Kpatcha, Diebakate, Faye and Toguebaye, 1996** (Fig. 7.113).

5a. Spherical plasmodia that measure 19 x 22 µm in diameter. Spores ovoid, length 10-12 µm, width 16-18 µm. Polar capsules spherical situated on either side of suture line, 2-3.2 µm in diameter. Coelozoic in gall bladder of *Acanthurus monroviae*……***C. acanthuri*** **Kpatcha, Diebakate, Faye and Toguebaye, 1996** (Fig. 7.106).

5b. Plasmodia have fingerlike elongated pseudopodia. Spores semicircular, length 17 µm and width 120 µm. Polar capsules 11 × 10 µm. Coelozoic in gall bladder of *Alepocephalus australis*... ……..***C. shulmani*** **Dubina and Isakov, 1976** (Fig. 7.110).

Remark. This species was described from a deep-sea host that was collected at a depth of 1300-1500m off the coast of South Africa and is amongst the largest of the myxosporeans (Lom and Dyková 1992).

Genus *Davisia* Laird, 1953

Spherical or subspherical spores with a straight or sinuous sutural line. Shell valves bear a long, hollow lateral appendage. Polar capsules situated

anteriorly at a certain distance from each other. Trophozoites mono-, di- and polysporic. Fifteen species known throughout the world, only one from marine fish in Africa.

1. Oval plasmodia up to 26 µm. Spore body rounded, lateral appendages about 35 µm long then continue for about 10 µm as thin threads. Length of spores 11 µm, width 10 µm. Polar capsules 4.5 × 4 µm with 5 coils per filament. Coelozoic in gall bladder of *Trachurus trachurus capensis*…….……***D. donecae*** **Gaevskaya and Kovaleva, 1979** (Figs. 7.115a, b).

Genus *Henneguya* Thélohan, 1892

Spores rounded, ellipsoid, fusiform or spindle-shaped in valvular view, biconvex in sutural view. Each valve contains a relatively long caudal projection. Shell valves smooth. Two polar capsules, sometimes very elongated. Binucleate sporoplasm with polysaccharide inclusion. Trophozoites large, polysporic with pansporoblast. Histozoic in freshwater fishes, rarely in marine fishes. Eight species known from marine fishes in Africa.

1a. Total length of spores ≤ 40 µm…...2
1b. Total length of spores > 40 µm…...4

2a. Caudal process elongate……..…3
2b. Caudal process short. Spores oval. Total spore length 16-24 µm, spore body length 9-13 µm and spore body width 5-9 µm. Polar capsules ovoid and equal, 3-4 × 2-3 µm. Caudal appendages short, 6-14 µm. Histozoic in the gills and heart of *Mugil cephalus*……***H. oukamensis*** **Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997** (Fig. 7.121).

3a. Spores ovoid with rounded anterior. Total length of spores 36-41 µm, spore body length 10-12 µm, width 7-9 µm. Polar capsules equal and pyriform, 4-5 × 2-3 µm. Caudal process equal and separated from base, 26-29 µm. Histozoic in heart of *Brachydeuterus auritus*……..***H. brachideuteri*** **Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997** (Fig. 7.116).

3b. Spores body ovoid. Total length of spores 28-33 µm, spore body length 10-11 µm and spore body width 20-22.5 µm. Polar capsules ovoid and equal, 6.5-9 × 3.5-5 µm. Caudal appendage filiform and long, 20-22.5 µm. Histozoic in kidneys of *Dentex canariensis*……..….***H. mbourensis*** **Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997** (Fig. 7.120).

3c. Spores ovoid. Total length of spores 36-41 µm, spore body length 9-9.5 µm and spore body width 6.5-8 µm. Polar capsules ovoid, 2-2.5 × 1-2 µm. Caudal appendage filiform and elongate, 22.5-31.5 µm. Histozoic in gills of *Pricanthus arenatus*……...***H. priacanthi*** **Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997** (Fig. 7.122).

4a. Caudal appendages separated from base……5

4b. Caudal appendages fused. Spores ovoid. Total length of spores 44.5-45 µm, spore body length 8.5-9 µm and spore body width 6-7 µm. Polar capsules pyriform and unequal in size. Larger polar capsules 4.5-5.5 × 2.5-3 µm. Smaller polar capsules 3.5-4.5 × 1.8-2 µm. Caudal filiform and fused, 34-36 µm. Histozoic in kidneys of *Cephalopholis taeniops*…....***H. joalensis*** **Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997** (Fig. 7.117).

5a. Spores ovoid with rounded anterior. Total length of spores 52-56 µm, spore body length 7-9 µm and spore body width 6-7 µm. In profile, spores lenticular. Polar capsules pyriform and equal, 4-5 × 2.25-2.5 µm. Caudal appendages equal, separated from base, 45-47.5 µm. Histozoic in liver of *Galeodies decadactylus*….***H. kayarensis*** **Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997** (Fig. 7.118).

5b. Spore body ovoid. Total length of spores 47.25-50.4 µm, spore body length 11.25-13 µm and spore body width 6-8 µm. Polar capsules pyriform and equal, 3-4.5 × 2.25-3.5 µm. Caudal appendages equal and separated from base, 36-38.25 µm. Plasmodia (0.8 – 1.8 mm) in gills of *Lutjanus agennes*… ……..***H. lutjani*** **Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997** (Fig. 7.119).

5c. Spores ovoid. Total length of spores 37-50 µm, spore body length 12-15 µm and spore body width 8-11 µm. Polar capsules ovoid, 3-4 × 2-3 µm. Extremely elongated caudal appendage, 24-36 µm. Histozoic in gills and heart of *Sparus caeruleosticus* ……***H. yoffensis*** **Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997** (Fig. 7.123).

Genus *Kudoa* Meglitsch, 1947

Spores stellate, quadrate or rounded quadrate in apical view. Four pyriform polar capsules. Two uninucleate sporoplasms, one enveloping the other. Trophozoites small, producing one to seven spores, or large and polysporic. Histozoic mostly intracellular in muscles, exceptionally coelozoic in

marine fishes. Approximately 40 species world wide, with two from marine fishes in Africa.

1a. Plasmodia whitish, ellipsoidal at base of gill filaments (0.5 – 1.5 mm). In apical view, spores rounded to quadrate. In lateral view spores ellipsoidal. Spore dimensions 4-6 × 8-1 µm, thickness 7-8 µm. Suture lines well visible. Four equal polar capsules 2-4 × 1-2 µm, with 2-3 coils per filament. Histozoic in gills of *Boops boops*……..***K. boopsi*** **Kpatcha, Diebakate, Faye and Toguebaye, 1999** (No figure in original description).

1b. Spores stellate, measuring 7.1 µm long × by 16.6 µm wide. Four unequal polar capsules, one small, one large, two intermediate. Histozoic in muscles of *Thyristes atun* and *Merluccius capensis* ……..……***K. thyristes*** **(Gilchrist, 1924)** (Figs. 7.124a, b).

Genus *Leptotheca* Thélohan, 1895

Spores are oval, ellipsoidal and 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 (differentiating it from *Ceratomyxa*) but significantly exceeds one half of this diameter (at variance with Sphaerospora). Capsular foramina near the sutural plane. Sporoplasm often fills entire spore cavity. Usually one binucleate but occasionally two uninucleate sporoplasms. Trophozoites as a rule disporic and coelozoic in the gall bladder and urinary system of marine fishes. Approximately 44 species throughout the world, three known from marine fishes in Africa.

1a. Spores ovoid……2

1b. Spores small, oval to subspherical. Length of spores 6.7-10.1 µm, width 4.5-7.6 µm. Polar capsules spherical and small, situated in centre of spore, 2-2.5 µm in diameter. Infecting the kidneys of *Lutjanus fulgens*……..***L. lutjani*** **Kpatcha, Diebakate and Toguebaye, 1996** (Fig. 7.126).

2a. Spores ovoid, length 13.5-14.4 µm, width 9.9-10.35 µm. Polar capsules spherical 2.7-3.15 µm in diameter. Coelozoic in gall bladder of *Merluccius senegalensis*……...***L. elongata*** **Thélohan, 1895** (Fig. 7.125).

2b. Spores ovoid with rounded extremities. Length of spores 11.25-13.5 µm and width 6.7-9 µm. Polar capsules spherical situated in broadest part of spore, 3.6-4.5 µm in diameter.

Coelozoic in gall bladder of *Pegusa lascaris*……..….***L. pegusae*** **Kpatcha, Diebakate and Toguebaye, 1996** (Fig. 7.127).

Genus *Myxidium* Bütschli, 1882

Spores as a rule fusiform, straight or slightly crescentic or sigmoid, with more or less pointed ends. Shell valves smooth or with ridges. Sutural line bisecting the spore. Two mostly pyriform or spherical polar capsules situated one at each end of the spore. Capsula foramina lie in a sutural plane, or near the end of the spore, opening in opposite directions. One binucleate sporoplasm located between the polar capsules. Typically coelozoic with small to large trophozoites being mono-, di- and polysporic. More than 100 species known throughout the world, four known from marine fishes in Africa.

1a. Length of spores ≤ 20 µm……..2
1b. Length of spores > 20 µm……..3

2a. Spores ellipsoidal with pointed ends forming a rough s-shape. Length of spores 9.14 µm, width 6.75-7.2 µm. Polar capsules oval and equal, situated in spore extremities, 2.7-2.9 × 2.25 µm. Coelozoic in gall bladder of *Abudefduf marginatus*……....***M. abudefdufi*** **Kpatcha, Diebakate and Toguebaye, 1996** (Fig. 7.128).

2b. Spores ellipsoid and s-shaped, length 7-10 µm and width 4.5-8 µm. Polar capsules pyriform and equal, 1.5-2.7 × 1.5-2.7 µm. Parasites in intestine of *Elops senegalensis*……***M. elopsi*** **Kpatcha, Diebakate and Toguebaye, 1996** (Fig. 7.129).

3a. Spores fusiform with pointed ends. Length of spores 19-20 µm and width 8-10 µm. Polar capsules pyriform 4-5.4 × 2-3 µm. Coelozoic in gall bladder of *Raja miraletus*……..……***M. giganteum*** **Doflein, 1898** (Fig. 7.130).

3b. Extremely large spindle shaped to semicircular spores, slightly s-shaped. Length of spores 42.5-97.5 µm and width 5-8.5 µm. Polar capsules large, pyriform to ovoid, with 13-14 coils per filament. Coelozoic in gall bladder of *Alepocephalus australis*……..…….***M. gigantissimum*** **Dubina and Isakov, 1976** (Fig. 7.131).

Genus *Myxobolus* Bütschli, 1882

Spores ellipsoidal, ovoid or rounded in valvular view, biconvex in sutural view. Shell valves smooth. Two mostly pyriform polar capsules situated in anterior end of spore, parallel to the

sutural plane. Posteriorly sutural ridge may extend into a crescentic ledge. Binucleate sporoplasm, often with an iodinophilous vacuole. Plasmodia large, polysporic with pansporoblast formation. Histozoic in freshwater fishes, occasionally, some in marine (mostly estuarine) fishes. More than 450 species throughout the world, 12 species from marine fishes in Africa.

1a. Spores spherical or subspherical….2
1b. Spores ellipsoid, oval or ovoid…...9

2a. Spores with smooth sutural edge….3
2b. Spores with notches along sutural edge……6

3a. Intercapsular process present……4
3b. Intercapsular process absent…….5

4. Spores spherical in frontal view, 13-15 µm in diameter. Polar capsules pyriform, occupying more than half the spore cavity, 7-9 × 5-6 µm. Forms whitish, ovoid cysts in the gill arches measuring 1.3–2.2 mm in length by 0.7–1.5 mm in width. Histozoic in gill arches of *Mugil cephalus*……..…… ……..***M. hannensis*** **Fall, Kpatcha, Diebakate and Toguebaye, 1997** (Fig. 7.136).

5. Spores spherical, 10-13 µm in diameter. Polar capsules pyriform, 4-5 × 2-4 µm. Intercapsular process is absent. Polysporous plasmodia are found within the gill lamellae. Several sutural edge markings. Histozoic in the gills of *Mugil cephalus*……..….***M. goreensis*** **Fall, Kpatcha, Diebakate and Toguebaye, 1997** (Fig. 7.135).

6a. Intercapsular process present……7
6b. Intercapsular process absent…….8

7a. Spores mostly spherical with 8 to 11 markings along the sutural edge, 14-14.5 µm in diameter. Polar capsules pyriform and convergent, 6-7 × 5.5-6 µm with 6-7 coils per filament. Capsules exceed midlength of spore. Elongated plasmodia in the primary gill lamellae, measuring 0.22-2.3 × 0.4-0.8 mm of *Mugil cephalus*…….***M. bizerti*** **Bahri and Marques, 1996** (Fig. 7.132).

7b. Anterior of spores slightly pointed. Sutural edge with 6 markings. Length of spores 8-9 µm, width 6-7 µm. Histozoic in gills, scales and fins of *Mugils cephalus, M. chelo* and *Abramis abrama*……..….***M. exiguus*** **Thélohan, 1895** (Fig. 7.134).

8a. Spores subspherical in frontal view, length 7-9 µm and width 7-8 µm.

Sutural edge with numerous markings. Intercapsular process absent. Numerous spherical plasmodia on brachiospines of gill arches of *Mugil curema*…....***M. hani*** **Faye, Kpatcha, Diebakate, Fall and Toguebaye, 1999** (Fig. 7.137).

8b. Spores quite spherical, length 13-14 µm, width 12-13 µm. Sutural edge with 9 to 11 sutural markings. Polar capsules oval reaching to half the length of the spore, 5-6 × 4-4.3 µm. Polar filament with 7-8 coils. No intercapsular process. Discharging orifices of the polar capsules situated on both sides of sutural line are elongated and close together. No iodinophilous vacuole. Plasmodia found clustered at the base of the filaments, 2.2 to 4.0 × 1.0 to 3.0 mm, of *Mugil cephalus*……....***M. ichkeulensis*** **Bahri and Marques, 1996** (Fig. 7.138).

9a. Spores with smooth sutural edge...10
9b. Spores with notches along sutural edge……..……13

10a. Intercapsular process present…...11
10b. Intercapsular process absent……12

11. Spores ovoid, becoming broader towards the anterior region. Length of spores 14-16 µm, width 12-13 µm. Intercapsular process present. Polar capsules pyriform, 5-6.5 × 3-4 µm. Histozoic in liver of *Mugil cephalus*.. ……..……..***M. raibauti*** **Fall, Kpatcha, Diebakate and Toguebaye, 1997** (Fig. 7.141).

12. Spores ovoid, length 7.4 µm and width 7.3 µm. Polar capsules pyriform and unequal. Larger polar capsules, 3.64 × 2.11 µm with 6-8 coils per filament. Smaller polar capsules, 2.4 × 1.21 µm with 5-6 coils per filament. Plasmodia yellowish in colour, linear (2.1 × 0.2 mm). Histozoic in gills of *Mugil cephalus*……..……***M. mugilis*** **Negm-Eldin, Govedich and Davies, 1999** (Fig. 7.139).

13a. Intercapsular process present…...14
13b. Intercapsular process absent……15

14. Spores oval with large intercapsular process. Length of spores 12-14 µm and width 10-11 µm. Sutural edge markings distinct. Polar capsules pyriform, 4-6 × 3-4 µm. Plasmodia up to 4 mm. Histozoic in the gills of *Mugil cephalus*.. ……..…***M. muelleri*** **Bütschli, 1882** (Fig. 7.140).

15a. Spores oval in frontal view and tapered at the anterior end, length 8-9 µm, width 6-7 µm. Polar capsules pyriform, 3.5-4.5 × 1.5-2.5 µm with 5-6 coils per filament. No intercapsular

process. Five to 6 markings along the sutural edge. Spores sometimes covered with a porous envelope of coagulated mucus. Parasitising scales of *Mugil cephalus* ……..…….***M. episquamalis*** **Egusa, Maeno and Sorimachi, 1990** (Fig. 7.133).

15b. Spores regularly ellipsoidal in front view, length 11-13 µm, width 9-11 µm. Numerous small sutural markings (12 to 14) present along sutural edge. Polar capsules oval, their posterior ends do not reach the midpoint of the spore, 4-5.5 × 2-3.5 µm, with 4-5 coils per filament. No intercapsular appendage. Infecting the intestine and gall bladder of *Mugil cephalus*…….***M. spinacurvatura*** **Maeno, Sorimachi, Ogawa and Egusa, 1990** (Fig. 7.142).

Genus *Ortholinea* Shulman, 1962

Spherical to subspherical spores that may be slightly flattened parallel to the sutural plane or pointed posteriorly. Polar capsules subspherical to pyriform set wide apart in the sutural plane with capsula foramina directed away from each other at an angle. Sporoplasm binucleate. Trophozoites mono- to polysporic. Coelozoic in the urinary tract of marine fishes. Only seven species throughout the world. One described from Africa.

1. Pseudoplasmodia round to ellipsoid floating in urine. Many trophozoites attached to wall of urinary bladder. Polysporous (180 µm), some mono- and di-sporous. Spores subspherical in valvular view, slightly compressed in sutural view with valvular ridges conspicuous. Length of spores 12-15 µm, width 11.8-13 µm. Polar capsules pyriform, set wide apart with their foramina opening into almost opposite directions, 4-4.8 × 3-3.4 µm, with 4-5 coils per filament. Coelozoic in urinary bladder of *Clinus agilis*…….. ……..…….***Ortholinea basma*** **Ali, 2000** (Fig. 7.143).

Genus *Palliatus* Shulman, Kovaleva and Dubina, 1979

Subspherical spores with a prominent anterior sutural ridge. Spores enveloped in a membranous veil which in non mature spores is twisted into two cords around the spore. Polar capsules pyriform. Binucleate sporoplasm. Trophozoites with one to six disporic pansporoblasts. Coelozoic in the gall bladder of marine fishes. Only three species all described from Africa. These species were described by Shulman *et al.* (1979).

1. ***P. mirabilis*** **Shulman, Kovaleva and Dubina, 1979** (Figs. 7.144a, b).

2. ***P. grandis*** **Shulman, Kovaleva and Dubina, 1979** (Fig. 7.145).

3. ***P. indecorus*** **Shulman, Kovaleva and Dubina, 1979** (Fig. 7.146).

Genus *Sphaeromyxa* Thélohan, 1892

Two polar capsules lie in opposite, tapering and truncate ends of the elongated, sometimes slightly curved spore. They open in the level of the sutural plane connecting both ends and bisecting the spore. Very short polar filament, unlike any myxosporean, is not tube-like, but broad and flat at the base and gradually tapering tot the end. It is also not spirally wound, but folded several times. Coelozoic in marine fishes. Thirty species throughout the world with one known from Africa.

1. Plasmodia up to 4 mm. Spores straight with longitudinal ridges, length 23 µm, width 6 µm. Polar capsules ellipsoidal 8.5 × 4 µm, with 4 coils per filament. Coelozoic in urinary bladder of *Abudefduf marginatus, Sardinella maderensis*……..***S. balbiani*** **Thélohan, 1892** (Fig. 7.147).

Genus *Unicapsula* Davis, 1924

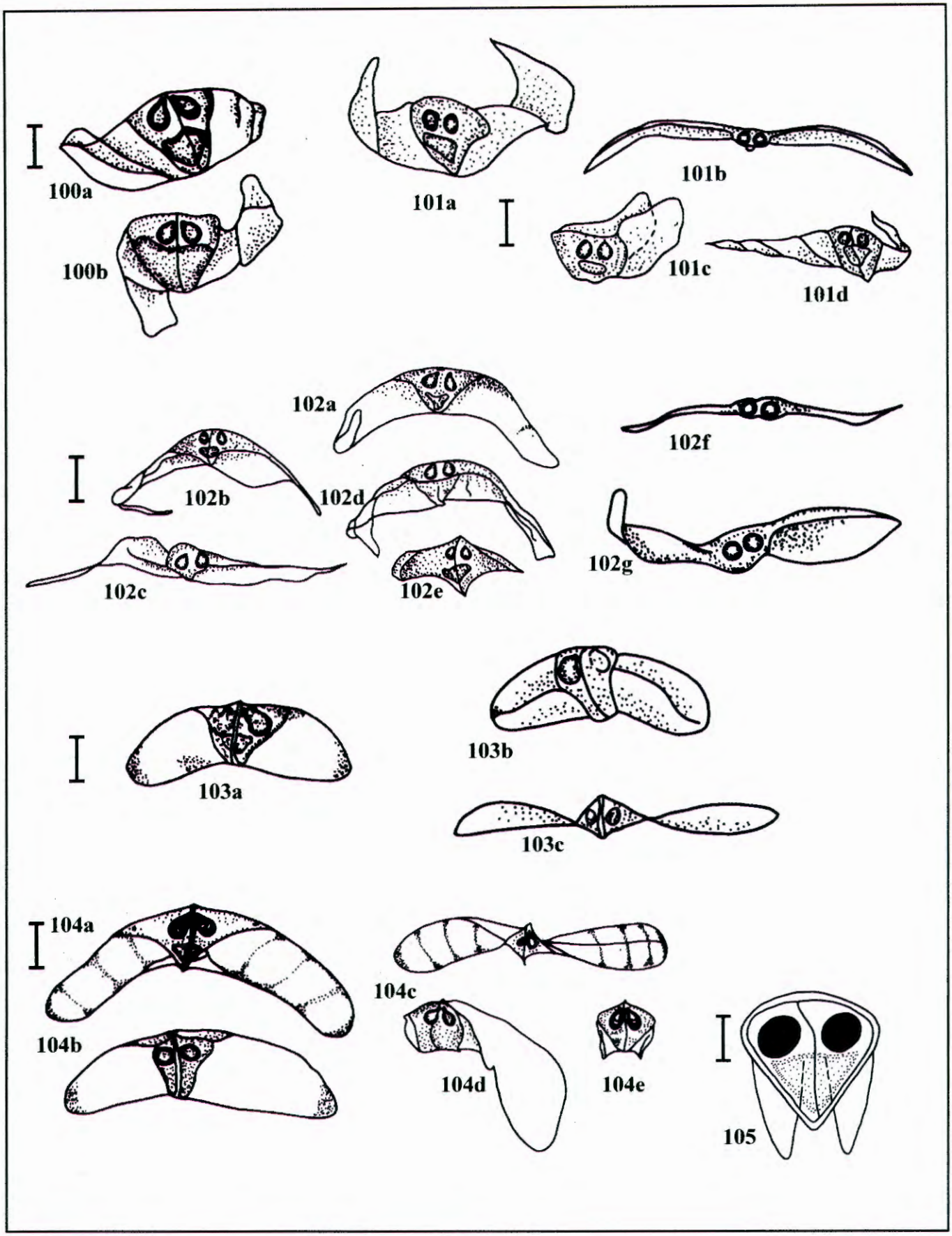
Subspherical spores with three unequal shell valves. One small valve covers a single spherical polar capsule. Two larger, bilaterally symmetrically arranged valves contain two capsular rudiments difficult to distinguish by light microscopy. Two uninucleate sporoplasms, one enveloping the other. Large polysporic trophozoites histozoic in the muscles of marine fishes. Only five species known throughout the world, one known from Africa.

1. Plasmodia elongated (1-3 mm). Spores pyramidal with three valves. Length of spores 6.13 µm, width 7.18 µm. Only one valve contains a developed spherical polar capsule which is 3.01 µm in diameter. Infecting the gills of *Polydactylus quadrifilis*……. ……..…….***U. marquesi*** **Diebakate, Fall, Faye and Toguebaye, 1999** (Fig. 7.148).

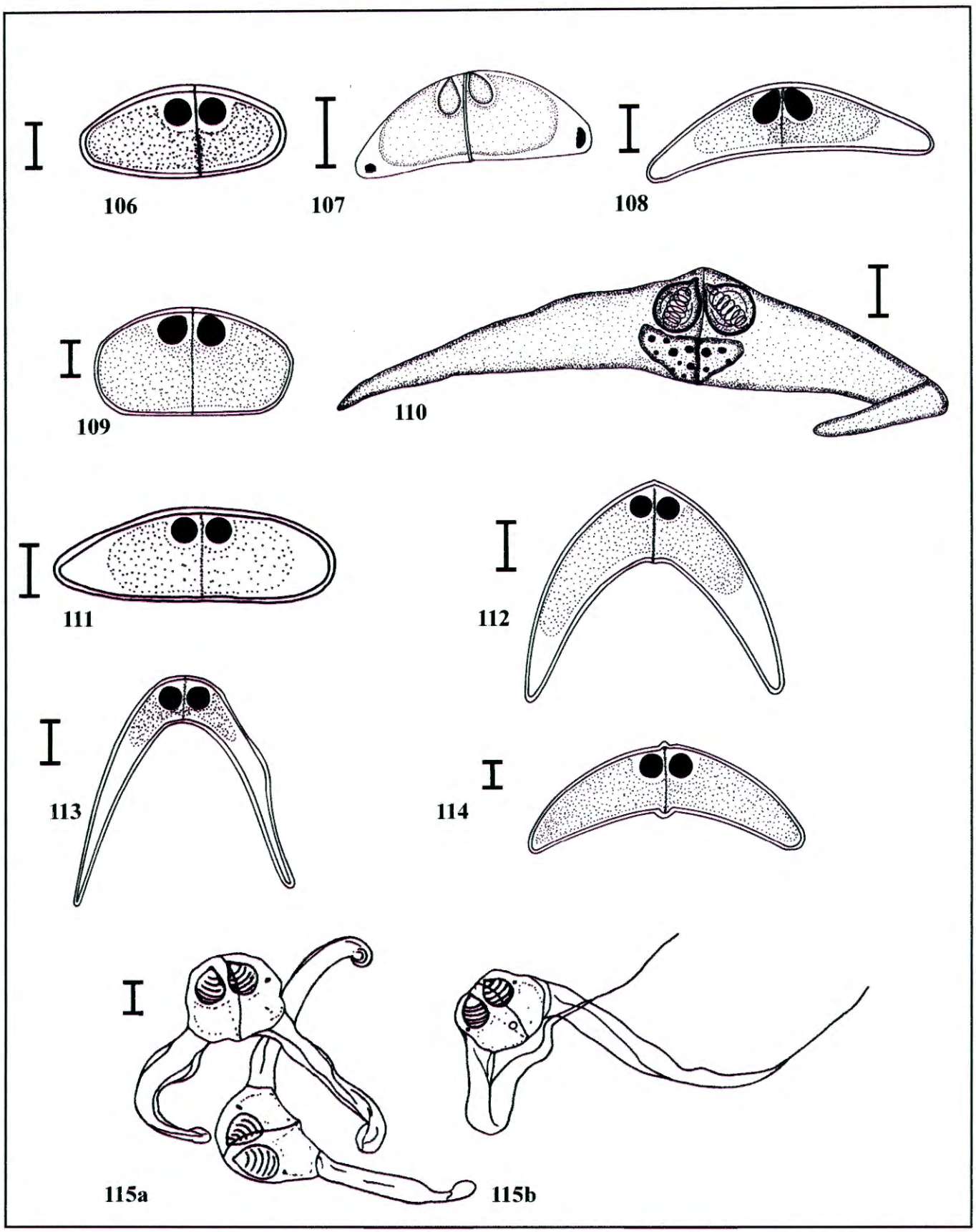
Genus *Zschokkella* Auerbach, 1910

Spores ellipsoidal in sutural view and slightly bent or semicircular in valvular view, with rounded or bluntly pointed ends. Sutural line straight, curved or sinuous. Almost spherical polar capsules open slightly subterminally and both to one side. One binucleate sporoplasm. Trophozoites di- to polysporic with pansporoblast formation. Coelozoic in marine and freshwater fishes. More than 50 species throughout the world with one described from a marine fish in Africa.

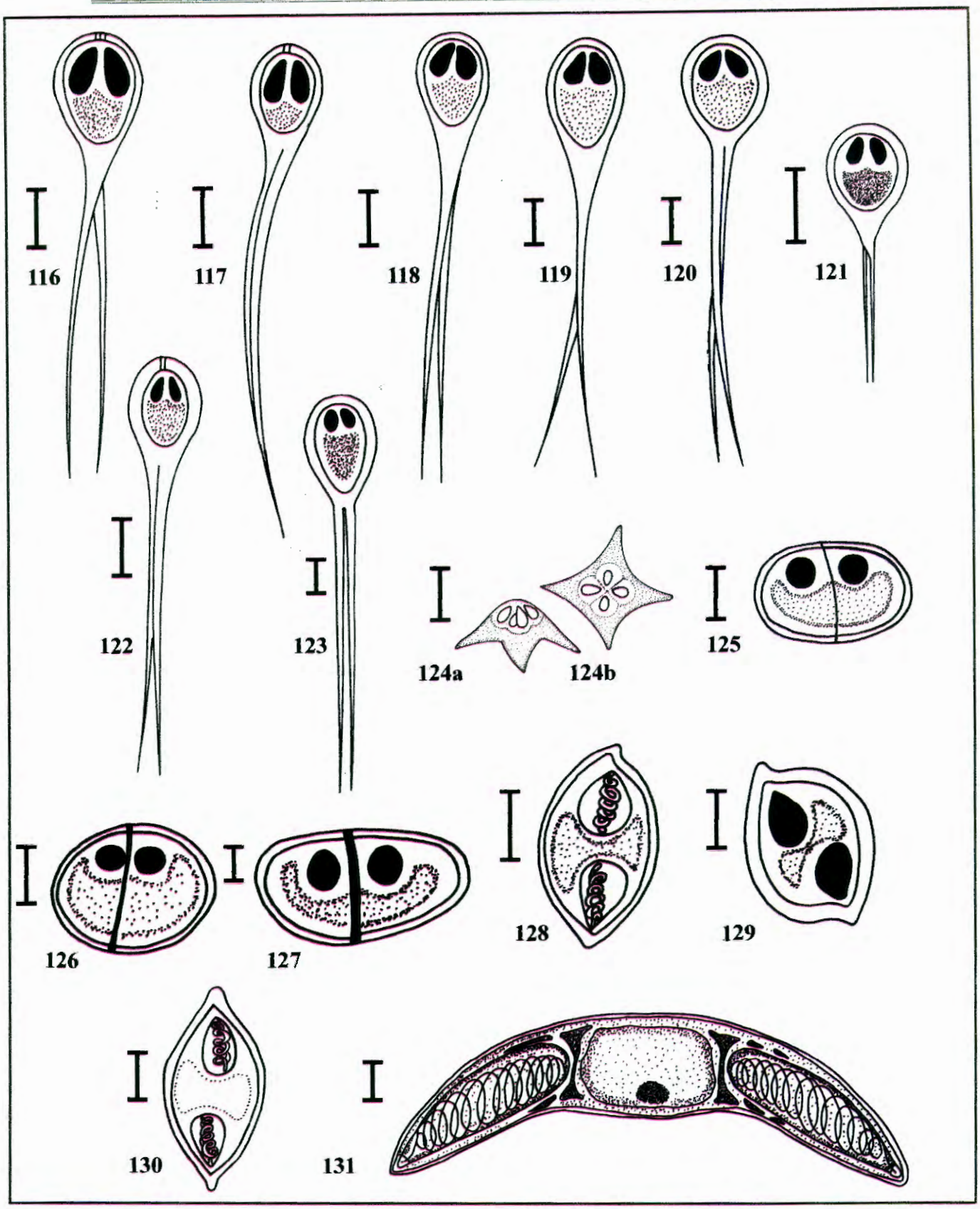
1. Spores large, ovoid and ends equally rounded. Length of spores 13.5-18 µm and width 9-13.5 µm. Polar capsules spherical and equal measuring 2.5-4 µm in diameter. Coelozoic in gall bladder of *Mugil capurii*……...***Z. mugilidae*** **Kpatcha, Diebakate and Toguebaye, 1996** (Fig. 7.149).



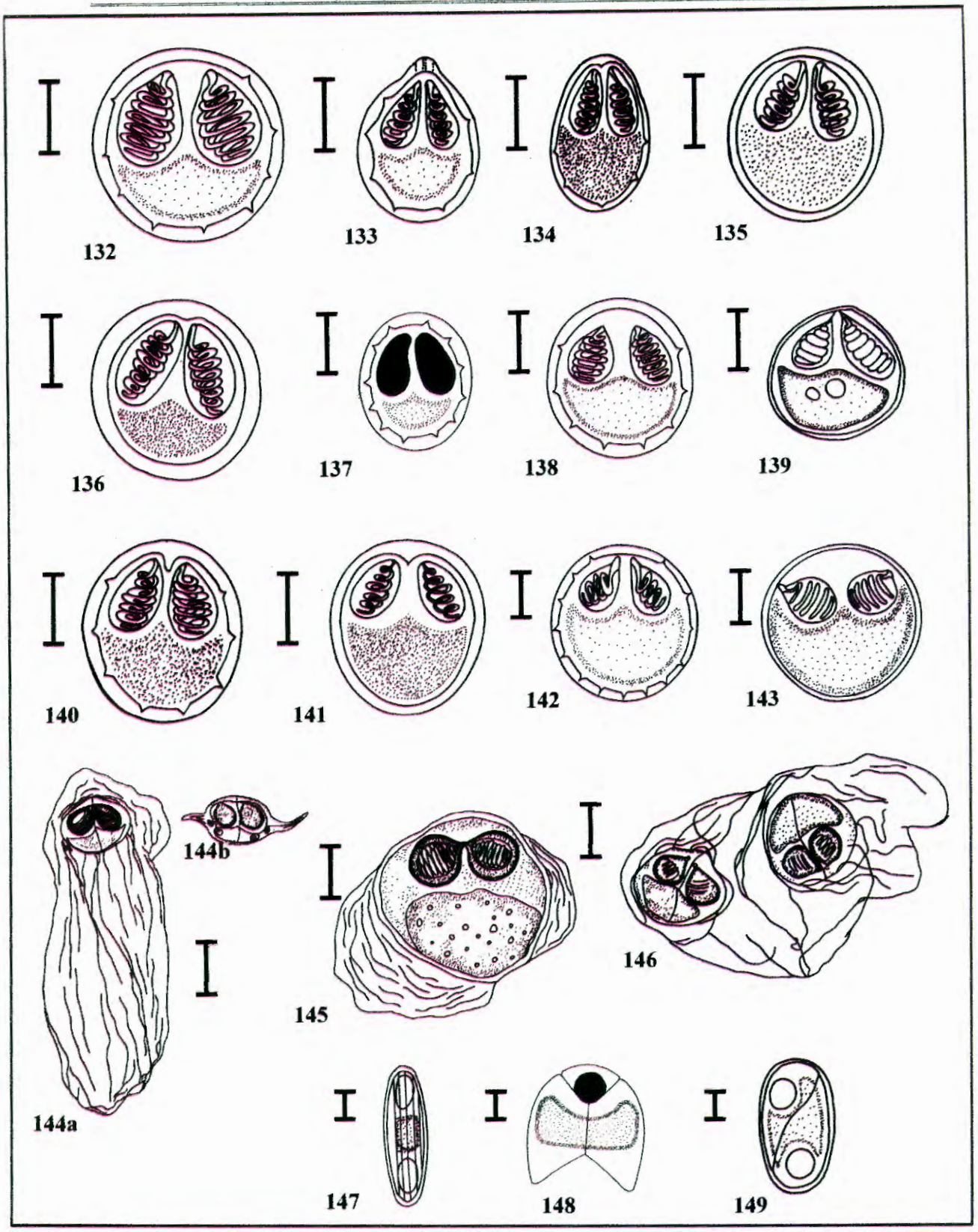
Figures 7.100-7.105: Spores. 100a, b. *Alatospora africana* Shulman, Kovaleva and Dubina, 1979. **101a-d.** *A. dracoidea* Shulman, Kovaleva and Dubina, 1979. **102a-g.** *A. contrariocapsularia* Shulman, Kovaleva and Dubina, 1979. **103a-c.** *A. parvicapsula* Shulman, Kovaleva and Dubina, 1979. **104a-e.** *A. samaroidea* Shulman, Kovaleva and Dubina, 1979. **105.** *Bibteria admiranda* Kovaljova, Zubchencho and Krasin, 1983. Scale bars: 5µm. Figure 105 redrawn from Kpatcha, Diebakate and Toguebaye (1996), all remaining figures redrawn from original descriptions.



Figures 7.106-7.115: Spores. 106. *Ceratomyxa acanthuri* Kpatcha, Diebakate, Faye and Toguebaye, 1996. **107.** *C.australis* Gaevskaya and Kovaleva, 1979. **108.** *C. fistulariae* Kpatcha, Diebakate, Faye and Toguebaye, 1996. **109.** *C. lagocephali* Kpatcha, Diebakate, Faye and Toguebaye, 1996. **110.** *C. shulmani* Dubina and Isakov, 1976. **111.** *C. syacii* Kpatcha, Diebakate, Faye and Toguebaye, 1996. **112.** *C. trachinocephali* Kpatcha, Diebakate, Faye and Toguebaye, 1996. **113.** *C. trichuiri* Kpatcha, Diebakate, Faye and Toguebaye, 1996. **114.** *C. truncata* Thélohan, 1895. **115a, b.** *Davisia donecae* Gaevskaya and Kovaleva, 1979. Scale bars: 5µm. Figure 114 redrawn from Kpatcha, Diebakate, Faye and Toguebaye (1996), all other figures redrawn from original descriptions.



Figures. 7.116-7.131. Spores. 116. *Henneguya brachideuteri* Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997. **117.** *H. joalensis* Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997. **118.** *H. kayarensis* Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997. **119.** *H. lutjani* Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997. **120.** *H. mbourensis* Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997. **121.** *H. ouakamensis* Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997. **122.** *H. priacanthi* Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997. **123.** *H. yoffensis* Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997. **124a, b.** *Kudoa thyristes* (Gilchrist, 1924). **125.** *Leptotheca elongata* Thélohan, 1895. **126.** *L. lutjani* Kpatcha, Diebakate and Toguebaye, 1996. **127.** *L. pegusae* Kpatcha, Diebakate and Toguebaye, 1996. **128.** *Myxidium abudefdufi* Kpatcha, Diebakate and Toguebaye, 1996. **129.** *M. elopsi* Kpatcha, Diebakate and Toguebaye, 1996. **130.** *M. giganteum* Doflein, 1898. **131.** *M. gigantissumum* Dubina and Isakov, 1976. Scale bars: 5µm. Figure 124 redrawn from Lom and Dykova (1992), figures 125 and 130 redrawn from Kpatcha, Diebakate and Toguebaye (1996). All other figures redrawn from original descriptions.



Figures 132-149. Spores. 132. *Myxobolus bizerti* Bahri and Marques, 1996. **133.** *M. episquamalis* Egusa, Maeno and Sorimachi, 1990. **134.** *M. exiguus* Thélohan, 1985. **135.** *M. goreensis* Fall, Kpatcha, Diebakate and Toguebaye, 1997. **136.** *M. hannensis* Fall, Kpatcha, Diebakate and Toguebaye, 1997. **137.** *M. hani* Faye, Kpatcha, Diebakate, Fall and Toguebaye, 1999. **138.** *M. ichkeulensis* Bahri and Marques, 1996. **139.** *M. mugilis* Negm-Eldin, Govedich and Davies, 1999. **140.** *M. muelleri* Bütschli, 1882. **141.** *M. raibauti* Fall, Kpatcha, Diebakate and Toguebaye, 1997. **142.** *M. spinacurvatura* Maeno, Sorimachi, Ogawa and Egusa, 1990. **143.** *Ortholinea basma* Ali, 2000. **144a, b.** *Palliatus mirabilis* Shulman, Kovaleva and Dubina, 1979. **145.** *P. grandis* Shulman, Kovaleva and Dubina, 1979. **146.** *P. indecorus* Shulman, Kovaleva and Dubina, 1979. **147.** *Sphaeromyxa balbiani* Thélohan, 1892. **148.** *Unicapsula marquesi* Diebakate, Fall, Faye and Toguebaye, 1999. **149.** *Zschokkella mugilidae* Kpatcha, Diebakate and Toguebaye, 1996. Scale bars: 5µm. Figure 134 redrawn from Fomena and Bouix (1997), figures 140 and 147 redrawn from Kpatcha, Diebakate

8. General discussion and concluding remarks

The combined results obtained from five years (1997-2002) of myxosporean research conducted by the author for both her MSc. (Reed 2000) as well as this current study, in two very unique localities in southern Africa, have revealed the discovery of many new species and new geographical records of existing species. Approximately 44 new myxosporean records, of which only six species were described from elsewhere in Africa, have been recorded for the first time in southern Africa as a result of these two studies.

African myxosporeans

Since the onset of research on fish-infecting myxosporeans in Africa during the late 1800s, remarkable progress has been made in establishing a network of myxosporean researchers across the continent. The majority of these researchers are, however, based in countries north of the equator. This is most likely due to the large aquaculture and fisheries industries driving the economies of many of those Northern, Central, Eastern and West African countries. Research on pathogens that may have devastating effects on such primary industries is very important and subsequently, in terms of research, has resulted in the publication of a valuable amount of information on African myxosporeans.

All of the myxosporean species known to infect freshwater fishes in Africa were originally described from Africa or nearby Israel. This reflects the existence of a very unique diversity of myxosporean fauna infecting freshwater fishes throughout Africa. The spread of freshwater myxosporean research into southern Africa during the 20th century and the diversity of results obtained have provided even greater evidence of this unique fauna composition presented by the African myxosporeans.

The same is true for myxosporeans infecting marine and estuarine fishes along the coast of Africa. Of the approximate 52 myxosporean species known to infect marine and estuarine fishes along the African coast, only six species were not originally described from Africa. These species (*Ceratomyxa truncata*, *Myxidium giganteum*, *Myxobolus episquamalis*, *M. exiguus*, *M. muelleri*, *Sphaeromyxa balbiani*) were all described from universally distributed hosts, which are not necessarily endemic or isolated to the African coast. As with research on myxosporeans infecting freshwater fishes in Africa, the marine myxosporean research has been concentrated in countries where marine fisheries form important components of those countries economies.

Sadly, research on myxosporeans infecting important freshwater and marine fisheries and aquaculture species in southern Africa has been largely neglected, even though, marine fisheries in particular, have been in existence for many years. Complaints about typical *Kudoa* infections resulting in postmortem myoliquefaction of the hosts flesh have been reported from several of these coastal fisheries in southern Africa. In fact, fishing industries along the coast of Namibia have raised tremendous concerns regarding the high prevalence of *Kudoa thyristes* in both their hake and snoek catches (pers. comm.)[1].

Okavango myxosporeans

The results of this study (1997-2001) have provided an overview of myxosporean species infecting the skin and gills of fishes in the Okavango River and Delta region. Twenty-nine different myxosporean species were found infecting 26 Okavango fish species. Of these species only six (*Henneguya suprabranchiae*, *Myxobolus africanus*, *M. camerounensis*, *M. hydrocyni*, *M. nyongana* and *M.* cf. *tilapiae*) were previously described from other countries in Africa. These are the first records of these species in southern Africa. This subsequently reflects on the association of these species with the specific hosts they infect, indicating that they were probably distributed across the African continent together with their hosts and have maintained quite a long evolutionary relationship with them. The remaining 23 species have never been recorded before. Many of these species are associated with specific fish hosts that are endemic to southern Africa (see Chapter 5). It can be assumed that these myxosporeans are most likely also endemic to southern Africa.

Host preferences reflected by the Okavango myxosporeans seem to be consistent with most myxosporeans described throughout Africa, revealing definite generic or family host specificity.

The results of this study have revealed the presence of ***two*** major ***genera*** infecting fishes in the Okavango. These are ***Henneguya*** and ***Myxobolus***, with the latter genus representing the most species. Only nine species from the genus *Henneguya* were identified. This coincides with general myxosporean trends, since the genus *Myxobolus* is the most abundant of all the African freshwater myxosporean genera and also represents the largest myxosporean genus in the world (Lom and Dyková 1992).

[1] Charles Cleghorn, NovaNam Limited, Luderitz, Namibia.

The myxosporean species identified during this study have mostly been described from the gills and skins of these fishes (see Chapter 5). All the recorded infections have been ***histozoic*** with the development of macroscopic, polysporic plasmodia. No ***coelozoic*** species were recorded or collected during this specific study. It should be emphasized, however, that sampling for this study concentrated on searching mostly for macroscopic histozoic infections. During a recent summer survey (2002/2003) not included in this study, several coelozoic myxosporeans were noted in the gall bladders of many of the Okavango *Barbus* species (pers. comm.)[2].

Reflecting on the ***distribution*** records obtained to date, it seems that the myxosporean infections are generally distributed evenly throughout the Okavango River and Delta.

The Okavango River and Delta comprise distinct mainstream, lagoon, permanent and temporary floodplain regions. Assessing comparisons of ***infection prevalences*** and ***species diversity*** between ***lagoon*** and ***mainstream*** environments becomes very problematic in a region such as this. The great diversity of habitats provides very specific niches for certain fish species and subsequently the myxosporean species found within the different habitats will be determined by the different habitat preferences of the hosts they infect.

The overall ***infection prevalence*** of myxosporeans infecting Okavango fishes was generally low. The Okavango River and Delta is considered to be a largely pristine system and subsequently the well-being of the fishes inhabiting this region reflect this. This generally low infection prevalence is thus indicative of the present ecological state of the Okavango River and Delta. Interestingly, protozoal infections of fishes collected within the flood plains of the Okavango Delta were much higher than those from the Panhandle (pers. comm.)[2]. Reasons deduced for this trend were that the floodplain habitats are more unstable and stressful for the fishes living there, with dramatically fluctuating water temperatures and water levels. The same infection prevalences as those noted for the protozoans were, however, not noted for the myxosporean infections in the Delta proper.

[2] Prof. Linda Basson, Aquatic Parasitology Research Group, Department of Zoology and Entomology, University of the Free State, Bloemfontein, South Africa.

Most surveys conducted in the Okavango River and Delta for the purpose of this study took place between June/July and October/November each year. The results therefore reflect only a ***winter/spring season***. The possibility therefore exists that infection prevalences and species diversities could very well be different during the other seasons.

Infection prevalences of myxosporean species infecting the Okavango fishes were generally low. However, as with most parasitic infections, some ***pathological effects*** on the hosts were inevitable. Many of the Okavango myxosporeans were found infecting vital organs such as the gills or, in the case of *Henneguya suprabranchiae*, the secondary accessory breathing organs. Naturally, the extent of the pathological effects are all determined by the intensity of these infections.

The ***pathogenic potential*** of gill-infecting myxosporeans was observed with *Henneguya xarensis* infecting the gills of *Schilbe intermedius*. Reed (2000) found several individuals with more than a 1000 *H. xarensis* plasmodia per gill arch. Histological sections of these infected gills revealed severe compression of the uninfected gill filaments. The respiratory function of gills infected with such high numbers of plasmodia will most certainly be negatively affected. The infections of *Henneguya suprabranchiae* within the secondary accessory-breathing organs of *Clarias* species could have similarly devastating effects. The plasmodia of *H. suprabranchiae* tend to severely distort and eventually replace the cartilaginous tissue within the secondary-accessory breathing organ. Catfishes are dependent on these organs in times when oxygen concentrations in the water are low and they the need arises for them to migrate over land to different pools. Parasitic infections such as this could render this organ dysfunctional. Fortunately water quality within the Okavango is still very high, with only naturally seasonal flooding taking place each year, resulting in certain times with lower oxygen concentrations.

Parasitic infections in the reproductive organs of fishes, such as *Myxobolus gariepinus* in the ovaries of *C. gariepinus*, are also of serious concern. High infections of this particular myxosporean within the ovaries could ultimately result in the ***parasitic castration*** of the host fish. In the event of dramatic water quality deterioration taking place in the Okavango, these infections would naturally proliferate, seriously affecting the reproductive potential of the *Clarias* population. These infections would be of particular

concern in *Clarias* hosts due to the potential they hold for aquaculture development in the Okavango.

The fishes of the Okavango River and Delta form a very valuable natural resource for the people living on its periphery. It is important to take into consideration the potentially pathogenic effects parasites such as myxosporeans may have on these natural fish populations. Unfortunately, the exact extent of these pathological effects is very difficult to determine since the percentage of diseased fish eliminated by predators and by natural selection remains unknown. A basic knowledge of myxosporean species in the Okavango has been established and it is now possible to predict the outcomes of overexploitation of certain fish species and the pathological effects associated with subsequent elevated myxosporean infections. Currently the myxosporean infections exhibit a natural over-dispersed pattern, as would be expected. The constantly growing human population within the Okavango River and Delta, however, places increasing pressure on the natural fish populations. Increasing human population numbers result in a series of negative impacts on the natural environment such as:

- Increased use of motor boats for fishing, which results in increased fuel pollution.
- Increased water use and abstraction.
- Increased diamond mining activities.
- Increased pressure on the entire system.
- Increased need to feed the growing population.
- Increased demand for fish.
- Increased pressure on natural fish populations.

Due to the ever-increasing needs of these local communities living in and around the Okavango River and Delta, as well as the growing tourism industry, a great demand has been placed on the natural fish populations. Inevitably the development of a lucrative aquaculture industry is looming. Many fish species occurring in the Okavango have successfully been farmed in several African countries. Potential aquaculture fish species from the Okavango include catfish species from the genus *Clarias*, cichlids, such as *Oreochromis*, *Tilapia* and *Serranochromis* species, *Schilbe intermedius* and the mormyrids. Myxosporean species have been recorded from members of all the above-mentioned fishes within the Okavango River and Delta. In the event of establishing an

aquaculture industry using these fishes, the pathogenic potential held by the myxosporean species found naturally infecting these fishes should be fully understood. Attempts have already been made by local communities to establish aquaculture industries and associated parasitic problems have already been experienced (pers. comm.)[2].

Many local communities living in and around the Okavango River and Delta still make use of basic subsistence basket fishing on the floodplains, as well as simple rod and line methods in the mainstream environment. Several reports of myxosporean spores in humans have been recorded. In all these cases the infections were thought to be merely coincidental and it was assumed that the spores simply passed through the digestive tracts of the infected individuals. Very little is, however, known about the association of myxosporeans and mammalian hosts. The potential risk of myxosporeans infecting humans should not be ignored and forms an unknown component of the well being of local Okavango communities.

Future research

The future of myxosporean research in the Okavango River and Delta holds many opportunities and will certainly provide many rewards. The next step in continuing this research will be to attempt answering some of the questions that arose during this study.

In terms of continuing research on the ***diversity*** of myxosporeans infecting Okavango fishes, future sampling should include the examination of all the fish host organs. Particular attention should be paid to searching for the presence of coelozoic myxosporeans inhabiting the gall- and urinary bladders of fishes. Secondly an investigation into the presence of truly histozoic species such as members of the genera *Kudoa* and *Sphaerospora* should also be undertaken.

The results presented in this thesis only generally represent the months June to October. Myxosporean species throughout the world are known to sometimes exhibit strong ***seasonal occurrences***. The diversity of myxosporeans could very well be much greater than has been reflected from this study. A summer survey of Okavango fish parasite fauna in general, not included in the results of this thesis, during December and January

[2] Prof. Linda Basson, Aquatic Parasitology Research Group, Department of Zoology and Entomology, University of the Free State, Bloemfontein, South Africa.

2002/2003 revealed the presence of a greater myxosporean diversity and higher infection prevalences (pers. comm.)[2]. The ***seasonal occurrence*** of these myxosporeans should, therefore, be investigated, particularly in light of the potential aquaculture development in the Okavango.

As research on the Okavango myxosporeans progresses, the possibility of broadening the investigations to include ***life cycle*** studies on these parasites becomes a priority. The Okavango River and Delta forms an incredibly vast expanse of water and papyrus making the investigations into linking the life cycles of these myxosporeans almost mind-boggling. Elucidating these life cycles will be challenging. As is widely accepted throughout the world that, many myxosporean species have actinosporeans, inhabiting oligochaete worms, as alternating life forms in a single life cycle. The Okavango generally has very little benthic fauna, making the life cycle strategies of these myxosporeans very interesting. Furthermore, many predator fishes such as *Hepsetus odoe* and *Hydrocynus vittatus* were found infected with myxosporeans. The possibility exists that the life cycles of these myxosporeans may either depend on a direct fish to fish transmission, or may even include a second fish host as well as an oligochaete. This will, however, have to be examined.

Molecular analyses not only plays a vital role in distinguishing closely related species, but also in the linking of myxozoan life cycles. In a vast system such as the Okavango River and Delta the use of molecular systematics in determining the intermediate life cycle stages of the myxosporeans will be very useful and probably a necessity.

Cape South Coast myxosporeans

The study on the diversity of myxosporeans infecting intertidal and surf zone fishes from three localities along the Cape south coast of South Africa has revealed 15 different myxosporean species infecting 10 different fish host species. None of the myxosporeans had ever been described before.

Many of the intertidal fish species along the southern Cape coast such as the Clinid species as well as *Chorisochismus dentex*, *Pavoclinus graminis* and *Fucominus mus*, are

[2] Prof. Linda Basson, Aquatic Parasitology Research Group, Department of Zoology and Entomology, University of the Free State, Bloemfontein, South Africa.

endemic to southern Africa. Obviously the myxosporeans found infecting them would also likely be ***endemic*** to the southern African coastline. Furthermore, most myxosporean species found along the Cape South coast appear to be associated with specific hosts. This ***host specificity*** correlates with many of the other African marine myxosporean species described.

Almost all the myxosporean species found during this study were coelozoic species, inhabiting the gall bladders of the fishes. Only two of the 15 species were recorded from the gills of the hosts. These specific ***site preferences*** are consistent with general trends in many of the marine myxosporean genera. The Cape south coast myxosporean species were represented by eight different ***genera*** of which five (*Ceratomyxa*, *Chloromyxum*, *Myxidium*, *Sphaeromyxa* and *Zschokkella*) were typically coelozoic genera. The remaining genera, (*Henneguya*, *Myxobolus* and *Sphaerospora*), were all typically histozoic species, with the exception of the *Myxobolus* sp. observed within the urinary bladders of some *Clinus superciliosus* individuals.

Most fishes were sampled within the De Hoop Nature Reserve resulting in greater record of ***host diversity*** for this locality (see chapter 6). The diversity of fish hosts found infected with myxosporeans in the De Hoop Nature Reserve ranged from residential and transient intertidal fishes, surf zone fishes and even an elasmobranch. The infection prevalences of these fishes were generally low, as would be expected in such an extensive marine protected area. Some individuals in the host population showed over dispersal of parasites, which is characteristic of natural conditions (see chapter 6).

Although a much smaller host diversity and sample size was sampled at Jeffrey's Bay it was interesting to note that the infection prevalences of those fish hosts were considerably higher than the fishes sampled in De Hoop Nature Reserve (see Table 6.6, chapter 6). Jeffrey's Bay is developing at a great pace as one of South Africa's busiest tourist and fishing destinations. Consequently intertidal fish populations are one of the first to suffer the effects such serious anthropogenic activities. Furthermore, the city of Port Elizabeth is situated in close proximity to Jeffrey's Bay and boasts a huge international harbour. The nearby fish populations must surely feel the effects of the effluent, fuel and general harbour activities. It can be assumed that the higher infection prevalence's found in the Jeffrey's Bay fishes are directly related to the surrounding anthropogenic activities.

Histological examination of some myxosporean infections from the De Hoop Nature Reserve revealed the ***potential pathogenicity*** associated with myxosporeans, even under natural conditions. Some of the *Ceratomyxa* species revealed a close association with the hosts' gall bladder epithelium (see Chapter 6), possibly resulting in some pathological effects such as vacuolation, deformation and even necrosis of the epithelial cells. The functioning of the bile ducts of infected individuals were possibly also severely affected since they were packed full with developing plasmodia and spores. The histozoic *Henneguy*a species found within the cartilage of *Clinus superciliosus* resulted in the severe distortion of the entire gill arch and subsequent compression of nearby gill filaments. Compression of these gill filaments would result in a decrease in surface area for oxygen uptake by the gills. Since these fish live in an already highly variable and stressful intertidal environment, parasitic infections such as this that impact severely on the functioning of vital organs such as the gills, could have devastating effects on entire fish populations. Fishes living in a region such as Jeffrey's Bay are at even greater risk, since they have to deal with many other influences, in conjunction with living in the already stressed intertidal zone.

Future research

The study on the ***diversity*** of myxosporeans infecting marine fishes along the Cape south coast has laid the foundation for expanding this very important field of study in South Africa. This study is still very much in the exploratory phase and the results obtained thus far are based on surveys conducted at only three localities. Future research on the diversity of these myxosporeans should include the expansion of sampling localities to include sites that are representative of the entire South African coastline.

One of the most important research needs that should be addressed in future is an in-depth investigation into the presence of disease causing myxosporeans in ***economically important*** aquaculture and fisheries species. As mentioned before, the marine fisheries industry along the coast of South Africa is enormous and in dire need for research on important pathogenic parasites such as myxosporeans.

An investigation into the host specificity of these myxosporeans would be of great interest. Most species were also found associated with only one host species or host genus, it is however possible that some species may have a wider host range. Greater

host diversity would have to be examined in order to truly establish their specific ***host preferences***.

Molecular analysis plays an important role in distinguishing between closely related species and more importantly linking the intermediate life cycle stages of these myxosporeans. Unfortunately the advances in understanding the ***life cycles*** of marine myxosporeans have not reached the same level as in the case of freshwater species (Kent *et al.* 2001). Once the diversity of myxosporean fauna has been established in a region such as the De Hoop Nature Reserve, the next obvious step would be to attempt elucidating the life cycles of these myxosporeans.

Furthermore, interest in gall bladder parasites of marine fish has, in the past, been related to their use as biological tags for fish stocks (Mackenzie and Kalavati 1995). The more information gathered regarding gall bladder parasites of fishes along the coast of South Africa, the greater the possibility becomes for implementing such a tool.

Outcomes

The results obtained from this study on the fish infecting myxosporeans from the Okavango River and Delta in Botswana, and the Cape south coast of South Africa will be published in a series of taxonomic papers. The following species will be described as new:

From the Okavango River and Delta, Botswana

Henneguya sp. A infecting the gills of *Mormyrus lacerda*

Myxobolus sp. A infecting the skin of *Tilapia sparrmanii*

From the Cape south coast, South Africa

Ceratomyxa sp. A infecting the gall bladder of *Clinus cottoides*

Ceratomyxa sp. B infecting the gall bladder of *C. superciliosus*

Ceratomyxa sp. C infecting the gall bladder of *Amblyrhynchotes honckenii*

Henneguya sp. B infecting the gills and gill arches of *C. superciliosus*

Myxidium sp. A infecting the gall bladder of *Chorisochismus dentex*

Myxidium sp. B infecting the gall bladder of *Diplodus sargus capensis*

Sphaeromyxa sp. A infecting the gall bladder of *Pavoclinus graminis*

The miscellaneous myxosporean species recorded that require more material for the completion of entire species descriptions will be described as soon as sufficient material is collected. These include:

From the Okavango River and Delta, Botswana

Henneguya sp. infecting the buccal cavity of *T. rendalli*

Henneguya sp. infecting the gills of *Ctenopomae multispine*

Henneguya sp. infecting the gills of *Microctenopomae intermedium*

Myxobolus sp. 1 infecting the gills and skin of *Barbus haasianus*

Myxobolus sp. 2 infecting the gills of *B. miolepis*

Myxobolus sp. 3 infecting the gills of *B. paludinosus*

Myxobolus sp. 4 infecting the skin of *B. uniteaniatus*

Myxobolus sp. 5 infecting the gills of *Coptostomabarbus wittei*

Myxobolus sp. 6 infecting the gills and skin of *Rhabdalestes maunensis*

Myxobolus sp. 7 infecting the skin of *Clarias stappersii*

Myxobolus sp. 8 infecting the skin of *Pseudocrenilabrus philander*

Myxobolus sp. 9 infecting the gills of *T. ruweti*

Myxobolus sp. 10 infecting the gills of *Ctenopomae multispine*

Myxobolus sp. 11 infecting the gills of *C. multispine*

From the Cape south coast, South Africa

Ceratomyxa sp. infecting the gall bladder of *Fucominus mus*

Ceratomyxa sp. infecting the gall bladder of *Liza richardsonii*

Chloromyxum sp. infecting the gall bladder of *Torpedo fuscomaculata*

Myxobolus sp. infecting the gills of *Liza richardsonii*

Myxobolus sp. infecting the urinary bladder of *Clinus superciliousus*

Sphaerospora sp. infecting the liver of *Clinus superciliosus*

Sphaerospora sp. infecting the liver of *Lithognathus lithognathus*

Zschokkella sp. infecting the gall bladder of *Liza richardsonii*

The ***key*** compiled for the identification of myxosporeans infecting freshwater fishes in Africa (Chapter 7) will be published as an update of the key compiled by Fomena and Bouix (1997). The key to myxosporeans infecting marine and estuarine fishes along the coast of Africa will be the first of its kind to be published for African marine myxosporean species.

Concluding remarks

The study on myxosporeans infecting fishes in southern Africa will remain an ongoing process for many years to come and the results obtained from this project have only just scratched the surface. In retrospect, however, the results obtained from this study have fulfilled the aims and objectives set out at the onset of this project. The long-term goal would be to determine an overview of myxosporean species in southern Africa and to establish a database of these species. This would be useful in terms of recording the occurrence of pathogenic myxosporeans and enabling the prediction of the effects they might have on potential aquaculture fish species.

In general, research on marine and freshwater fishes in southern Africa is still in an exploratory phase (Skelton 2001). Therefore, research on potential disease causing pathogens, such as myxosporeans, form an invaluable source of information that may ensure the successful development of future fishing industries.

So many options still exist for myxosporean research in southern Africa. Naturally we first need to establish the diversity of species occurring here. The results from this study have laid the cornerstone for myxosporean research in southern Africa. What remains is a dedicated continuation of this research, in order to fully expand the already growing network of myxosporean researchers in Africa.

9. References

ABOLARIN, M. O. 1971. A new species of *Henneguya* (Myxosporida, Protozoa) from West African Catfish, *Clarias lazera* Val. with a review of the genus *Henneguya* Thélohan, 1892. *African Journal of Tropical Hydrobiological Fisheries* **1**: 93-105.

ABOLARIN, M. O. 1974. *Myxobolus tilapiae* sp. nov. (Protozoa: Myxosporida) from three species of freshwater tilapia in Nigeria. *Journal of the West African Science Association* **19**: 109-114.

ALI, M. A. 1998. Light and scanning electron microscopy of *Chloromyxum vanasi* sp. n. (Myxozoa: Myxosporea) infecting the gall bladder of the Nile Catfish *Bagras bayad* (Forskal, 1775) (Teleosti: Bagridae). *Acta Protozoologica* **37**: 57-61.

ALI, M. A. 1999. *Henneguya ghaffari* sp. n. (Myxozoa: Myxosporea), infecting the Nile perch, *Lates niloticus* (Teleostei: Centropomidae). *Diseases of Aquatic Organisms* **38**: 225-230.

ALI, M. A. 2000. *Ortholinea basma* n. sp. (Myxozoa: Myxosporea) from the Agile Klipfish *Clinus agilis* (Teleostei: Clinidae). Light and scanning electron microscopy. *European Journal of Protistology* **36**: 100-102.

ALI, M. A., SAKRAN, T. H. and ABDEL-BAKI, A. S. 1999. Studies on species of the genus *Myxidium* Bütschli, 1882 (Myxozoa: Myxosporea) parasitising some Nile fishes. *Journal of the Union of Arab Biologists* **12**: 157-171.

ALVAREZ-PELLITERO, P. E. and SITJÁ-BOBADILLA, A. 1993a. Pathology of Myxosporea in marine fish culture. *Diseases of Aquatic Organisms* **17**: 229-238.

ALVAREZ-PELLITERA, P. E. and SITJÁ-BOBADILLA, A. 1993b. *Ceratomyxa* spp. (Protozoa: Myxosporea) infections in wild and cultured sea bass, *Dicentrarchus labrax*, from the Spanish Mediterranean area. *Journal of Fish Biology* **42**: 889-901.

ANDERSON, C. L., CANNING, E. U. and OKAMURA, B. 1998. A triploblast origin for Myxozoa? *Nature* **392**: 346.

ANDERSON, C. L., CANNING, E. U., SCHÄFER, S. M., YOKOYAMA, H. and OKAMURA, B. 2000. Molecular confirmation of the life cycle of *Thellohanellus hovorkai* Achmerov, 1960 (Myxozoa: Myxosporea). *Bulletin of the European Association of Fish Pathologists* **20**: 111-114.

ASHMAWY, K. I., ABU-ELWAFA, S. A., IMAM, E. A. and EL-OTIFI, Y. Z. 1989. Description of newly recorded myxosporidian protozoa of freshwater fishes in Behera Province, Egypt. *Journal of the Egyptian Veterinary Medical Association* **49**: 43-53.

AZEVEDO, C. and MATOS, E. 1995. *Henneguya adherens* n. sp. (Myxozoa: Myxosporea) parasite of the Amazonian fish, *Acestrohyncus falcalus*. *Journal of Eukaryotic Microbiology* **42**: 515-518.

BAHRI, S., HASSINE, O. K. B. and MARQUÉS, A. 1996. *Henneguya* sp. (Myxosporea, Bivalvulida) infecting the gills of wild gilthead sea bream *Sparus aurata* L., from the coast of Tunisia. *Bulletin for the European Association of Fish Pathologists* **16**: 51-53.

BAHRI, S. and MARQUÉS, A. 1996. Myxosporean parasites of the genus *Myxobolus* from *Mugil cephalis* in Ichkeul Lagoon, Tunisia: description of two new species. *Diseases of Aquatic Organisms* **27**: 115-122.

BAHRI, S., MARQUÉS, A., COSTE, F., BOUIX, G. and HASSINE, O. K. B. 1995. Presence of cutaneous myxosporidian in Tunisian *Mugil cephalus* (Linnaeus, 1758). *Bulletin for the European Association of Fish Pathologists* **15**: 54- 57.

BAKER, J. R. 1963. Three new species of *Myxosoma* (Protozoa: Myxosporidia) from East African freshwater fish. *Parasitology* **53**: 285-292.

BAILEY, A. 1998. *Okavango: Africa's wetland wilderness*. Struik Publishers, Cape Town.

BALFOUR, D. 1996. *Okavango: An African Paradise*. Struik Publishers, Cape Town.

BARTHOLOMEW, J. 1998. Parasitology: The Myxosporean-Actinosporean connection. *Proceedings for the Third International Symposium on Aquatic Animal Health* 76-79.

BARTHOLOMEW, J. L., WHIPPLE, M. J., STEVENS, D. G. and FRYER, J. L. 1997. The life cycle of *Ceratomyxa shasta*, a myxosporean parasite of salmonids, requires a freshwater polychaete as an alternative host. *Journal of Parasitology* **83**: 859-868.

BASSON, L. and VAN AS, J. G. 2002. Trichodinid ectoparasites (Ciliophora: Peritrichia) of freshwater fishes of the family Anabantidae from the Okavango River and Delta (Botswana). *Folia Parasitologica* **49**: 169-181.

BENAJIBA, M. H. and MARQUES, A. 1993. The alternation of Actinomyxidian and myxosporidian sporal forms in the development of *Myxidium giardi* (parasite of *Anguilla anguilla*) through oligochaetes. *Bulletin for the European Association of Fish Pathologists* **13**: 100-103.

*BOULENGER, G. A. 1911. Parental care in an African fish. *The Field* **118**: 968.

BOREHAM, R. E., HENDRICK, S., O'DONOGHUE, P. J. and STENZEL, D. J. 1998. Incidental finding of *Myxobolus* spores (Protozoa: Myxozoa) in stool samples from patients with gastrointestinal symptoms. *Journal of Clinical Microbiology* **36**: 3728-3730.

BRANCH, G. M. and BRANCH, M. 1995. *The living shores of southern Africa*. Struik Publishers, Cape Town.

BRANCH, G. M, GRIFFITHS, C. L., BRANCH, M. L. and BECKLEY, L. E. 1994. *Two Oceans: A guide to the marine life of southern Africa*. Fist edition. David Philip Publishers, Claremont, South Africa.

BRANCH, G. M, GRIFFITHS, C. L., BRANCH, M. L. and BECKLEY, L. E. 2002. *Two Oceans: A guide to the marine life of southern Africa*. Fifth edition. David Philip Publishers, Claremont, South Africa.

BRICKLE, P., KALAVATI, C. and MACKENZIE, K. 2001. Two new species of myxozoan parasites (Myxosporea, Bivalvulida) from toothfish *Dissostichus eleginoides* Smitt, 1898 (Pisces, Nototheniidae). *Acta Parasitologica* **46**: 250-253.

BROWNE, R. K., SCHELTINGA, D. M., POMERING, M and MAHONY, M. 2002. Testicular myxosporidiasis in anurans, with a description of *Myxobolus fallax* n. sp. *Systematic Parasitology* **52**: 97-110.

BRUTON, M. N. 1984. A preliminary investigation into the feeding habits of *Hydrocynus vittatus* (Castelnau, 1861) (Pisces: Characidae) in the Okavango Delta, Botswana. Zoology third year project, Rhodes University, Grahamstown.

BÜTSCHLI, O. 1882. Myxosporidien. *Zoologisch Jahrbuecher* **1**: 162-164.

BURTLE, G. J., HARRISON, L. R. and STYER, E. L. 1991. Detection of a Triactinomyxid myxozoan in an oligochaete from ponds with proliferative gill disease in channel catfish. *Journal of Aquatic Animal Health* **3**: 281-287.

CANNING, E. U., CURRY, A., ANDERSON, C. L. and OKAMURA, B. 1999. Ultrastructure of *Myxidium trachinorum* sp. nov. from the gall bladder of the lesser weever fish *Echiichthys vipera*. *Parasitology Research* **85**: 910-919.

CANNING, E. U., CURRY, A. FEIST, S. W., LONGSHAW, M. and OKAMURA, B. 1999. *Tetracapsula bryosalmonae* n. sp. for PKX organism the cause of PKD in salmonid fish. *Bulletin of the European Association of Fish Pathologists* **19**: 203-206.

CANNING, E. U., CURRY, A. FEIST, S. W., LONGSHAW, M. and OKAMURA, B. 2000. A new class and order of Myxozoans to accommodate parasites of Bryozoans with ultrastructural observations on *Tetracapsula bryosalmonae* (PKX Organism). *Journal of Eukaryotic Microbiology* **45**: 456-468.

CAVALIER-SMITH, T. 1998. A revised six-kingdom system of life. *Biological Reviews* **73**: 203-266.

*CAVALIER-SMITH, T., ALLSOPP, M. T. E. P., CHAO, E. E., BOURY-ESNAULT, N. and VACELET, J. 1996. Sponge phylogeny, animal monophyly and the origin of the nervous system: 18S rRNA evidence. *Canadian Journal of Zoology* **74**: 2031-2045.

CHRISTISON K.W., REED C.C., SMIT N.J., BASSON L. and VAN RENSBURG C. 2000. Some parasites of the African pike, *Hepsetus odoe*, from the Okavango Delta, Botswana. *Journal of the South African Veterinary Association* **71**: 138.

COWLING, R. and RICHARDSON, D. 1995. *Fynbos: South Africa's unique floral kingdom*. Fernwood Press, Cape Town.

*DANIELS, S. B., HERMAN, R. L. and BURKE, C. N. 1976. Fine structure of an unidentified protozoan in the epithelium of rainbow trout exposed to water with *Myxosoma cerebralis*. *Journal of Protozoology* **23**: 402-410.

DAVIES, R. and BEYERS, E. 1947. A protozoal disease of South African trawled fish and its routine detection by fluorescence. *Nature* **159**: 714.

DIAMANT, A. 1992. A new pathogenic histozoic *Myxidium* (Myxosporea) in cultured gilt-head sea bream *Sparus aurata* L. *Bulletin for the European Association of Fish Pathologists* **12**: 64-66.

DIAMANT, A. 1997. Fish-fish transmission of a marine myxosporean. *Diseases of Aquatic Organisms* **30**: 99-105.

DIAMANT, A. and PAPERNA, I. 1985. The development and ultrastructure of *Nosema ceratomyxae* sp. nov., a microsporidian hyperparasite of the myxosporean *Ceratomyxa* sp. from Red sea Rabbitfish (Siganidae). *Protistologica* **21**: 249-258.

DIAMANT, A. and PAPERNA, I. 1989. Cytopathology of *Ceratomyxa* sp. (Myxosporea) hyperparasitized with the microsporidian *Nosema Ceratomyxae*. *Diseases of Aquatic Organisms* **6**: 75-79.

DIAMANT, A., LOM, J. and DYKOVÁ, I. 1994. *Myxidium leei* n. sp. a pathogenic myxosporean of cultured sea bream *Sparus aurata*. *Diseases of Aquatic Organisms* **20**: 137-141.

DIEBAKATE, C., FALL, M., FAYE, N. and TOGUEBAYE, B. S. 1999. *Unicapsula marquesi* n. sp. (Myxosporea, multivalvulida) parasite des branchies de *Polydactylus quadrifilis* (Cuvier, 1829) (Poisson, Polynemidae) des côtes Sénégalaises (Afrique de l' Quest). *Parasite* **6**: 231-235.

DUBINA, V. R. and ISAKOV, L. S. 1976. New species of myxosporidians from the gall bladder of Bathial fishes. *Parazitologiya* **10**: 556-560.

DYKOVÁ, I. and LOM, J. 1999. *Nosema notabilis* (Microsporidia), its ultrastructure and effect on the myxosporean host *Ortholinea polymorpha*. *Diseases of Aquatic Organisms* **35**: 69-76.

EGUSA, S., MAENO, Y. and SORIMACHI, M. 1990. A new species of Myxozoa, *Myxobolus episquamalis* sp. nov. infecting the scales of the mullet *Mugil cephalus* L. *Fish Pathology* **25**: 87-91.

EIRAS, J. C. 2002. Synopsis of the species of the genus *Henneguya* Thélohan, 1892 (Myxozoa: Myxosporea: Myxobolidae). *Systematic Parasitology* **52**: 43-54.

EL-MANSY, A. and BASHTAR, A. R. 2002. Histopathological and ultrastructural studies of *Henneguya suprabranchiae* Landsberg, 1987 (Myxosporea: Myxobolidae) parasitizing the suprabranchial organ of freshwater catfish *Clarias gariepinus* (Burchell, 1822) in Egypt. *Parasitology Research* **88**: 617-626.

EL-MANSY, A. and MOLNÁR, K. 1997a. Extrapiscine development of *Myxobolus drjagini* Akhmerov, 1954 (Myxosporea: Myxobolidae) in oligochaete alternative hosts. *Acta Veterinaria Hungarica* **45**: 427-438.

EL-MANSY, A. and MOLNÁR, K. 1997b. Development of *Myxobolus hungaricus* (Myxosporea: Myxobolidae) in oligochaete alternate hosts. *Diseases of Aquatic Organisms* **31**: 227-232.

EL-MANSY, A., MOLNÁR, K. and SZÉKELY, C. 1998. Development of *Myxobolus portucalensis* Saraiva and Molnar, 1990 (Myxosporea: Myxobolidae) in the oligochaete *Tubifex tubifex* (Müller). *Systematic Parasitology* **41**: 95-103.

EL-MATBOULI, M., FISCHER-SCHERL, T. and HOFFMANN, R. W. 1992. Transmission of *Hoferellus carassii* Achmerov, 1960 to goldfish *Carassius auratus* via an aquatic oligochaete. *Bulletin for the European Association of Fish Pathologists* **12**: 54-56.

EL-MATBOULI, M. and HOFFMANN, R. W. 1989. Experimental transmission of two *Myxobolus* spp. developing bisporogeny via tubificid worms. *Parasitology Research* **75**: 461-464.

EL-MATBOULI, M. and HOFFMANN, R. W. 1993. *Myxobolus carassii* Klokaceva, 1914 also requires an aquatic oligochaete, *Tubifex tubifex* as an intermediate host in its life cycle. *Bulletin of the European Association of Fish Pathologists* **13**: 189-192.

EL-MATBOULI, M. and HOFFMANN, R. W. 1998. Light and electron microscopic study on the chronological development of *Myxobolus cerebralis* in *Tubifex tubifex* to the actinosporean stage triactinomyxon. *International Journal of Parasitology* **28**: 195-217.

EL-MATBOULI, M., HOFFMANN, R. W. and MANDOK, C. 1995. Light and electron microscopic observations on the route of the triactinomyxon-sporoplasm of *Myxobolus cerebralis* from epidermis into rainbow trout cartilage. *Journal of Fish Biology* **46**: 919-935.

ELLERY, K and ELLERY, W. 1997. *Plants of the Okavango Delta; a field guide*. Tsaro Publishers, Durban.

ESZTERBAUER, E., SZÉKELY, C. S., MOLNÁR, K and BASKA, F. 2000. Development of *Myxobolus bramae* (Myxosporea: Myxobolidae) in an oligochaete alternate host, *Tubifex tubifex*. *Journal of Fish Diseases* **23**: 19-25.

FAHMY, M. A., MANDOUR, A. M. and EL-NAFFAR, M. K. 1971. *Myxobolus niloticus* n. sp. in the fish *Labeo niloticus* from the river Nile of Assuit. *Journal of Egyptian Society of Parasitology* **1**:39-46.

FAISAL, M. and SHALABY, S. I. 1987. *Myxosoma tilapiae* as a new species (Myxosoma: Myxosporea) in wild *Oreochromis niloticus* in Lower Egypt. *Egyptian Journal of Veterinary Science* **24** 73-86.

FALL, M., KPATCHA, T. K., DIEBAKATE, C., FAYE, N. and TOGUEBAYE, B. S. 1997. Observations sur des myxosporidies (Myxozoa) du genre *Myxobolus* parasites de *Mugil cephalus* (Poisson, Téléostéen) du Sénégal. *Parasite* **2**: 173-180.

FALL, M., FOMENA, B., KOSTOÏNGUE, B., DIEBAKATE, C., FAYE, N. and TOGUEBAYE, B. S. 2000. Myxosporidies (Myxoza, Myxosporea) parasites des poissons Cichlidae du Cameroun, du

Sénégal et du Tchad avec la description de deux nouvelles espéces. *Annales des Sciences Naturelles* **21**: 81-92.

FANTHAM, H. B. 1919. Some parasitic protozoans found in South Africa, II. *South African Journal of Science* **16**: 185-191.

FANTHAM, H. B. 1930. Some parasitic protozoans found in South Africa, XIII. *South African Journal of Science*, **27**: 376-390.

FANTHAM, H. B. and PORTER, A. 1914. *Myxosporidiasis: Some obvious and some concealed diseases of fishes*. In: *Some minute animal Parasites* pp 236- 259.

FAYE, N., KPATCHA, T. K., FALL, M. and TOGUEBAYE, B. S. 1997. Heart infections due to myxosporean (Myxozoa) parasites in marine and estuarine fishes from Senegal. *Bulletin or the European Association of Fish Pathologists* **17**: 115-117.

FAYE, N. KPATCHA, T. K., DIEBAKATE, C., FALL, M. and TOGUEBAYE, B. S. 1999. Gill infections due to myxosporean (Myxozoa) parasites in fishes from Senegal with descriptions of *Myxobolus hani* sp. n. *Bulletin of the European Association of Fish Pathologists* **19**: 14-16.

FEIST, S. W. and RINTIMÄKI, P. 1994. *Chloromyxum truttae* Léger, 1906 infection in cultured salmonids from Finland. *Bulletin of the European Association of Fish Pathologists* **14**: 51.

*FLETCHER, A. W. 1888. On a myxosporidium infesting Australian frogs. *Report of the Australasian Association for the Advancement of Science* No. 1.

FOMENA, A. and BOUIX, G. 1986. Contribution à l'étude des Myxosporidies des poissons d'eau douce de Cameroun. *Acta Tropica* **43**: 319-333.

FOMENA, A. and BOUIX, G. 1987. Contribution á l'étude des Myxosporidies des poissons d'eau douce du Cameroun 111-Espèces nouvelles des genres *Henneguya* Thélohan, 1892 et *Thelohanellus* Kudo, 1933. *Revue de Zoologie Africaine* **101**: 43-53.

FOMENA, A. and BOUIX, G. 1994. New Myxosporidea species (Myxozoa) from freshwater teleosts in southern Cameroon (Central Africa). *Journal of African Zoology* **108**: 481-491.

FOMENA, A. and BOUIX, G. 1996. New species of *Henneguya* Thélohan, 1892 (Myxozoa: Myxosporea) parasites of freshwater fishes in Cameroon. *Journal of African Zoology* **110**: 413-423.

FOMENA, A. and BOUIX, G. 1997. Myxosporea (Protozoa: Myxozoa) of the freshwater fishes in Africa. Keys to the genera and species. *Systematic Parasitology* **37**: 161-178.

FOMENA, A. and BOUIX, G. 2000. *Henneguya mbakaouensis* sp. nov., *Myxobolus noumensis* sp. nov. and *M. hydrocyni* Kostoïngue and Toguebaye, 1944, Myxosporea (Myxozoa) parasites of of Centropomidae, Cichlidae and Characidae (Teleosts) of the Sanaga Basin in Cameroon (Central Africa). *Parasite* **7**: 209-214.

FOMENA, A. BOUIX, G. and BIRGI, É. 1985. Contribution à l'étude des Myxosporidies des poissons d'eau du Cameroun II. Espéces nouvelles du genre *Myxobolus* Bütschli, 1882. *Bulletin de l' Institut Fondamental d' Afrique Noire* **46**: 1-2.

FOMENA, A., MARQUÉS, A. and BOUIX, G. 1993. Myxosporidea (Myxozoa) of *Oreochromis niloticus* (Linnaeus 1757) (Teleoste Cichlidae) in fish farming pools at Melen (Yaounde, Cameroon, Central Africa). *Journal of African Zoology* **107**: 45-56.

FOMENA, A., MARQUÉS, A., BOUIX, G. and NJINÉ, T. 1994. *Myxobolus bilongi* n. sp., *Thellohanellus assambai* n. sp., *T. sanagaensis* n. sp., Myxosporidies parasites de *Labeo* sp. (Téléostéen, Cyprinidae) du basin de la Sanaga au Cameroon (Afrique Centrale). *Annales de la Faculté des Sciences de Yaoundé*, 131-142.

FRIEDRICH, C., INGOLIC, E., FREITAG, B., KASTBERGER, G., HOHMANN, V. SKOFITSCH, G., NEUMEISTER, U. and KEPKA, O. 2000. A myxozoan-like parasite causing xenomas in the brain of the mole, *Talpa europaea* L., 1758 (Vertebrata, Mammalia). *Parasitology* **121**: 483-492.

GAEVYSKAYA, A. V. and KOVALEVA, A. A. 1979. Two new species of Myxosporidia *Davisia donecae* n. sp. and *Ceratomyxa australis* n. sp. from the horse mackeral in the southeastern Atlantic. *Biologica Morya (Vladivostok)* **3**: 80-83.

GBANKOTO, A., PAMPOULIE, C., MARQUES, A. and SAKITI, G. N. 2001a. *Myxobolus dahomeyensis* infection in the ovaries of Tilapia species from Benin (West Africa). *Journal of Fish Biology* **58**: 883-886.

GBANKOTO, A., PAMPOULIE, C., MARQUES, A. and SAKITI, G. N. 2001b. Occurrence of myxosporean parasites in the gills of two tilapia species from Lake Nokoué (Bénin, West Africa): effect of host size and sex, and seasonal patterns of infection. *Diseases of Aquatic Organisms* **44**: 217-222.

GHAFFAR, F. A., EL-SHAHAWI, G. and NAAS, S. 1995. Myxosporidia infecting some Nile fishes in Egypt. *Parasitological Research* **81** 163-166.

≈ GILCHRIST, J. D. F. 1918.

GILCHRIST, J. D. F. 1924. A protozoal parasite *Chloromyxum thyrsites* sp. n. of the Cape sea fish, the "snoek" (*Thyrsites atun*, Euplin). *Transactions of the Royal Society of South Africa* **11**: 263-273.

GIOIA, I. and CORDIERO, N da S. 1996. Brazilian myxosporidians checklist (Myxozoa). *Acta Protozoologica* **35**: 137-149.

GRACIA, M. P., MAÍLLO, P. A., AMIGÓ, J. M. and SALVADÓ, H. 1997. Ultrastructural study of *Sphaeromyxa balbianii* Thélohan, 1892 (Myxozoa: Myxosporea: Bivalvulida) a parasite of *Cepola macrophthalma* Linaeus, 1758. *Acta Protozoologica* **36**: 171-179.

*GRASSE, P. P. and LAVETTE, A. 1978. La myxosporidie Sphaeromyxa sabrazei et le novel embranchment de Myxospoaire (Myxozoa). Recherches sur l'état pluricellulaire primitif et considerations phylogenetiques. *Annales des Sciences Naturelles Zoologie* **2**: 193-285.

GROBLER, N., CHRISTISON, K. W., J. VAN RENSBURG, REED, C. C., SMIT, N. J. and BASSON, L. 2001. Parasites found on the blacktail, *Diplodus sargus capensis*, from the south and east coasts of South Africa. *Journal of the South African Veterinary Association* **72**: 173-180.

*GROSSHEIDER, G. and KÖRTING, W. 1992. First evidence that *Hoferellus cyprini* (Doflein, 1898) is transmitted by *Nais* sp. *Bulletin of the European Association of Fish Pathologists* **12**: 17-20.

*GROSSHEIDER, G. and KÖRTING, W. 1993. Experimental transmission of *Sphaerospora renicola* to common carp *Cyprinus carpio* fry. *Diseases of Aquatic Organisms* **16**: 91-95.

GURLEY, R. R. 1893. On the classification of the Myxosporidia, a group of protozoan parasites infesting fishes. *Bulletin of the United States Fish Commission* **11**: 407-431.

*GURLEY, R. R. 1894. The myxosporidia, or Psorosperms of fishes and the epidermis produced by them. *Report of the United States Commission on Fish* **18**: 65-34.

HALLETT, S. L. and DIAMANT, A. 2001. Ultrastructure and small-subunit ribosomal DNA sequence of *Henneguya lesteri* sp. n. (Myxosporea), a parasite of sand whiting *Sillago analis* (Sillaginidae) from the coast of Queensland, Australia. *Diseases of Aquatic Organisms* **46**: 197-212.

HEUPEL, M. R. and BENNETT, M. B. 1996. A myxosporean parasite (Myxosporea: Multivalvulida) in the skeletal muscle of epaulette sharks, *Hemiscyllium ocellatum* (Bonnaterre), from the Great Barrier Reef. *Journal of Fish Diseases* **19**: 189-191.

HÖFER, B. 1903. Über die Drehkrankheid der Regenbogenforelle. *Allgemeinen Fischerei-Zeitung* **28**: 7-8.

HOFFMAN, G. L. 1970. Intercontinental and transcontinental dissemination and transfaunation of fish parasites with emphasis on whirling disease (*Myxosoma cerebralis*). In: Snieszko, S. F. (ed.), *Symposium on the Diseases of Fish and Shellfishes*, Washington D.C. *American Fisheries Society Monograph* 69-81.

IVERSEN, E. S., CHITTY, N. and VAN METER, N. 1971. Some myxosporidia from fishes in south Florida. *Journal of Protozoology* **18**: 82-86.

JAYASRI, M. and HOFFMANN, G. L. 1982. Review of *Myxidium* (Protozoa: Myxozoa: Myxosporea). *Protozoological abstracts* **6**: 61-91.

KABRÉ, B. G., SAKITI, N. G., MARQUÉS, A. and SAWADAGO, L. 1995. Presence of myxosporeans (Myxozoa, Myxosporea) of the genus *Henneguya* (Thélohan, 1892), parasites of fishes caught in fisheries of Burkina Faso. *Bulletin of the European Association of Fish Pathologists* **17**: 43-46.

KENT, M. L., ANDREE, K. B., BARTHOLOMEW, J. L., EL-MATBOULI, M., DESSER, S. S., DEVLIN, R. H., FEIST, S. W., HEDRICK, P. P., HOFFMANN, R. W., KHATTA, J., HALLETT, S. L., LESTER, R. J. G., LONGSHAW, M., PALENZUELA, O., SIDDALL, M. E. and XIAO, C. 2001. Recent advances in our knowledge of the Myxozoa. *The Journal of Eukaryotic Microbiology* **48**: 395-413.

KENT, M. L., WHITAKER, D. J. and MARGOLIS, L. 1993. Transmission of *Myxobolus articus* Pugachev and Khokhlov, 1979 a myxosporean parasite of Pacific salmon, via triactinomyxon from the aquatic oligochaete *Stylodrilus heringianus* (Lumbriculidae). *Canadian Journal of Zoology* **71**: 1207-1211.

KIM, J., KIM, W. and CUNNINGHAM, C. W. 1999. A new perspective on lower metazoan relationships from 18S rDNA sequences. *Molecular Biological Evolution* **16**: 423-427.

*KOROTNEFF, A. 1892. *Myxosporidium bryzoides*. *Zeitschrift fuer Wissenschaftliche Zoologie* **53**: 591-596.

KOSTOÏNGUE, B., DIEBAKATE, C., M., FAYE, N and TOGUEBAYE, B. S. 2001. Presence of Myxosporidea (Myxozoa: Myxosporea) of the genus *Henneguya* Thélohan, 1892 in freshwater fishes from Chad (Central Africa). *Acta Protozoologica* **40**: 117-123.

KOSTOÏNGUE, B. and TOGUEBAYE, B. S. 1994. Le genre *Myxobolus* (Myxozoa, Myxosporea) chez poissons d' eau douce du Tchad avec la description de trois nouvelles espéces. *Bulletin de l' Institut Fondamental d' Afrique Noire* **47**: 63-71.

KOSTOÏNGUE, B. FALL, M., FAYE, N and TOGUEBAYE, B. S. 1999. Three new myxosporidian (Myxozoa: Myxosporea) parasites of freshwater fishes from Chad (Central Africa). *Acta Protozoologica* **38**: 323-326.

KOSTOÏNGUE, B., FAYE, N. and TOGUEBAYE, B. S. 1998. Nouvelles espéces de Myxosporidies des genres *Myxidium* Bütschli, 1882 et *Myxobolus* Bütschli, 1882 (Myxozoa, Myxosporea) chez des poissons d'eau douce du Tchad (Afrique centrale). *Journal of African Zoology* **112**: 250-259.

KPATCHA, T. K., DIEBAKATE, C. and TOGUEBAYE, B. S. 1996a. Myxosporidies (Myxozoa, Myxosporea) des genres *Sphaeromyxa* Thélohan, 1892, *Myxidium* Bütschli, 1882, *Zschokkella* Auerbach, 1910, *Bipteria* Kovaljova Zubtchenko and Krasin, 1983 et *Leptotheca* Thélohan, 1895

parasites des poissons des côtes Sénégalaises (Afrique de l' Quest). *Journal of African Zoology* **110**: 309-319.

KPATCHA, T. K., DIEBAKATE, C., FAYE, N. and TOGUEBAYE, B. S. 1996b. Quelques nouvelles espéces de Myxosporidies du genre *Ceratomyxa* Thélohan, 1895 parasites des poissons marins du Senegal Afrique de l' Quest. *Parasite* **3**: 223-228.

KPATCHA, T. K., DIEBAKATE, C., FAYE, N. and TOGUEBAYE, B. S. 1999. Light and electron microscopic observations on *Kudoa boopsi* sp. n. (Myxosporea: Kudoidae), a gill parasite of *Boops boops* (Pisces: Telostei: Sparidae) from Coasts of Senegal (West Africa). *Acta Protozoologica* **38**: 317-321.

KPATCHA, T. K., FAYE, N., DIEBAKATE, C., FALL, M. and TOGUEBAYE, B. S. 1997. Nouvelles espèces d'*Henneguya* Thélohan, 1895 (Myxozoa, Myxosporea) parasites des poisons marins du Sénégal: Étude en microscopie photonique et électronique. *Annales des Sciences naturelles Zoologie* **18**: 81-91.

*KUDO, R. R. 1920. Studies on Myxosporidia. A synopsis of genera and species of Myxosporidia. *Biological Monograph* 1-265.

KUDO, R. R. 1944. Morphology and development of *Nosema notabilis* Kudo. *Illinois Boilogical Monographs* **20**: 1-83.

LABBÉ, A. 1899. Sporozoa. *Das Tierreich*, **5**: 1-80.

LANDSBERG, J. H. 1985. Myxosporean infections in cultured tilapias in Israel. *Journal of Protozoology* **32**: 194-201.

LANDSBERG, J. H. 1987. Myxosporean parasites of the catfish, *Clarias lazera* (Valenciennes). *Systematic Parasitology* **9**: 73-81.

LANDSBERG, J. H. and LOM, J. 1991. Taxonomy of the genus *Myxobolus* (Myxobolidae: Myxosporea): current listing of species and revision of synonyms. *Systematic Parasitology* **18**: 165-186.

*LANKESTER, E. R. 1877. Notes on the embryology and classification of the animal kingdom. *Quarterly Journal of Microscopical Science* **17**: 395-454.

LIN, D., HANSON, L. A. and POTE, L. M. 1999. Small subunit ribosomal RNA sequences of *Henneguya exilis* (Class Myxosporea) identifies the actinosporean stage from an oligochaete host. *Journal of Eukaryotic Microbiology* **46**: 66-68.

LOM, J. 1990. Phylum Myxozoa. In: L. Margulis, J. O. Corliss, M. Melkonian and D. J. Chapman (eds.), *Handbook of Protoctista*, Boston.

LOM, J. and ARTHUR, J. R. 1989. A guideline for the preparation of species descriptions in Myxosporea. *Journal of Fish Diseases* **12**: 151-156.

LOM, J. and DE PUYTORAC, P. 1965. Studies on the myxosporidian ultrastructure and polar capsule development. *Protistologica* **1**: 53-65.

LOM, J. and DYKOVÁ, I. 1992. *Developments in Aquaculture and fisheries sciences, volume 26: Protozoan parasites of fishes.* Elsevier Publishers, Amsterdam.

LOM, J. and DYKOVÁ, I. 1994. Studies on protozoan parasites of Australian fishes, 3 species of the genus *Myxobolus* Bütschli, 1882. *European Journal of Protistology* **30**: 431-439.

LOM, J. and DYKOVÁ, I. 1995. Myxosporea (Phylum: Myxozoa) In: *Fish diseases and disorders. Volume one: Protozoan and metazoan infections* (ed.) P. T. K. Woo. University Press, Cambridge.

LOM, J. and NOBLE, E. R. 1984. Revised classification of the class Myxosporea Bütschli, 1881. *Folia Parsitologica* **31**: 193-205.

LOM, J., McGEORGE, J., FEIST, S. W., MORRIS, D. and ADAMS, A. 1997. Guidelines for the uniform characterisation of the actinosporean stages of parasites of the Phylum Myxozoa. *Diseases of Aquatic Organisms* **30**: 1-9.

LONGSHAW, M., FEIST, S. W., CANNING, E. U. and OKAMURA, B. 1999. First identification of PKX in bryozoans from the United Kingdom – molecular evidence. *Bulletin of the European Association of Fish Pathologists* **19**: 146-148.

MACKENZIE, K. and KALAVATI, C. 1995. Species in the genus *Myxidium* Bütschli, 1882 (Myxosporea: Bivalvulida) parasitizing the gall bladders of gadid fish in the northeast Atlantic. *Journal of Natural History* **29**: 851-863.

*MAENO, Y., SORIMACHI, M., OGAWA, K. and EGUSA, S. 1991. *Myxobolus spinacurvatura* sp. n. (Myxosporea: Bivalvulida) parasitic in deformed mullet, *Mugil cephalus*. *Fish Pathology* **25**: 37-41.

MANDOUR, A. M., GALAL, and ABED, G. H. 1993. *Myxobolus clarii* n. sp. in the testis of the fish, *Clarias lazera* from the River Nile of Assuit. *Assuit Veterinary and Medical Journal* **29**: 109-115.

McARTHUR, C. P. and SENGUPTA, S. 1982. Antigenic mimicry of eel tissues by myxosporidian parasite. *Zeitschrift für Parasitenkunde* **66**: 249-255.

McCLELLAND, R. S., MURPHY, D. M. and CONE, D. K. 1997. Report of spores of *Henneguya salmonicola* (Myxozoa) in human stool specimens: possible source of confusion with human spermatozoa. *Journal of Clinical Microbiology* **35**: 2815-2818.

MERRON, G. S. 1991. The ecology and management of the fishes of the Okavango Delta, Botswana, with particular reference to the role of the seasonal floods. Phd. thesis. Rhodes University, Grahamstown.

MERRON, G. S. and BRUTON, M. N. 1986. Where are all the Okavango Fishes. *Kalahari Conservation Society Newsletter* **13**: 4-5.

MOLNÁR, K., EL-MANSY, A., SZÉKELY, C. and BASKA, F. 1999a. Development of *Myxobolus dispar* (Myxosporea: Myxobolidae) in an oligochaete alternate host, *Tubifex tubifex*. *Folia Parasitologica* **46**: 15-21.

MOLNÁR, K., EL-MANSY, A., SZÉKELY, C. and BASKA, F. 1999b. Experimental identification of the actinosporean stage of *Sphaerospora renicola* Dyková and Lom, 1982 (Myxosporea: Sphaerosporidae) in oligochaete alternate hosts. *Journal of Fish Diseases* **22**: 143-153.

MONCAĎA, L. I., LÓPEZ, M. C., MURCIA, M. I., NICHOLLS, S., LEÓN, F., GUÍO, O. L. and CORREDOR, A. 2001. *Myxobolus* sp., another opportunistic parasite in immunosuppressed patients? *Journal of Clinical Microbiology* **39**: 1983-1940.

MORAN, J. D. W. and KENT, M. L. 1999. *Kudoa thyristes* (Myxozoa: Myxosporea) infections in pen-reared Atlantic salmon in the Northeast Pacific Ocean with a survey of potential non-salmonid reservoir hosts. *Journal of Aquatic Animal Health* **11**: 101-109.

MORRIS, D. J., ADAMS, A. and RICHARDS, R. H. 2000. In situ hybridization identifies the gill as a portal entry for PKX (Phylum Myxozoa), the causative agent of proliferative kidney disease in salmonids. *Parasitology Research* **89**: 950-956.

*MÜLLER, J. 1838. Über Psorospermien. *Archiv Anatomic physiologie und wissenschaften Medicine* **5**: 477-496.

NARASIMHAMURTI, C. C., KALAVATI, C., ANURADHA, I. and PADMA DOROTHY, K. 1990. Studies on protozoan parasites of deep-water fishes from the Bay of Bengal. *Proceedings of the First Workshop on Scientific Resolutions* 325-336.

NEGM-ELDIN, M. M., GOVEDICH, F. R. and DAVIES, R. W. 1999. Gills myxosporeans on some Egyptian freshwater fish. *Deutsche Tierärztliche Wochenschrift* **106**: 459-465.

OBIEKEZIE, A. I. and ENYENIHI, U. K. 1988. *Henneguya chrysichthyi* sp. nov. (Protozoa: Myxozoa) from the gills of estuarine catfish *Chrysichthys nigrodigitatus* (Lacépède)(Pisces: Bagridae) in Nigeria. *Journal of African Zoology* **102**: 33-42.

OBIEKEZIE, A. I. and OKAEME, A. N. 1987. Myxosporea (Protozoa) infections of cultured tilapias in Nigeria. *Journal of African Zoology* **104**: 77-91.

OHLMACHER, A. P. 1893. Myxosporidia in the common toad, with preliminary observations on two chromophilic substances in their spores. *Journal of the American Medical Association* **20**: 561-567.

OKAMURA, B., CURRY, A., WOOD, T. S. and CANNING, E. U. 2002. Ultrastructure of *Buddenobrockia* identifies it as a myxozoan and verifies the bilaterian origin of the Myxozoa. *Parasitology* **124**: 215-223.

ÖZER, A. and WOOTTEN, R. 2000. The life cycle of *Sphaerospora truttae* (Myxozoa: Myxosporea) and some features of the biology of both the actinosporean and myxosporean stages. *Diseases of Aquatic Organisms* **40**: 33-39.

OVERSTREET, R. M. 1976. *Fabespora vermicola* sp. n., the first myxosporidian from a platyhelminth. *Journal of Parasitology* **62(5)**: 680-684.

PADMA-DOROTHY. K. and KALAVATI, C. 1992. Two new myxosporean parasites of the mullet, *Liza macrolepis* (Smith). *Uttar Pradesch Journal of Zoology* **12**: 15-19.

PAPERNA, I. 1973. Occurrence of Cnidospora infections in freshwater fishes in Africa. *Bulletin de l' Institut Fondamental d' Afrique Noire* **3**: 509-521.

PAPERNA, I. HARTLEY, A. H. and CROSS, R. 1985. Ultrastructural studies on the plasmodium of *Myxidium giardi* (Myxosporea) and its attachment to the epithelium of the urinary bladder. *International Journal for Parasitology* **17**: 813-819.

PETERS, H. M. 1971. Sporozoan cysts, the basis of purported "mouth-brooding" in the African Labyrinthine fish, *Ctenopoma multispinis* (Pisces: Anabantidae). *American Society of Ichthyology* **1**: 185.

POTE, L. M., HANSON, L. A. and SHIVAJI, R. 2000. Small subunit ribosomal RNA sequences link the cause of proliferative gill disease in channel catfish to *Henneguya* n. sp. (Myxozoa: Myxosporea). *Journal of Aquatic Animal Health* **12**: 230-240.

REED, C. C. 2000. Myxosporean parasites (Myxozoa: Myxosporea) infecting fishes in the Okavango River System, Botswana. MSc. dissertation, University of the Free State, Bloemfontein.

REED, C. C., BASSON, L. and VAN AS, L. L. 2001. Preliminary report on myxosporean parasites infecting fishes in the Okavango River and Delta, Botswana. *Journal of the South African Veterinary Association* **72**: 115.

REED, C. C., SMIT, N. J., CHRISTISON, K. W. and BASSON, L. 2001. Some parasites of the butter barbel, *Schilbe intermedius* Rüppell, 1832 from the Okavango Delta, Botswana. *Journal of the South African Veterinary Association* **72**: 175.

REED, C. C., BASSON, L. and VAN AS, L. L. 2002a. Myxozoans infecting the sharptooth catfish, *Clarias gariepinus* (Burchell, 1822) in the Okavango River and Delta, Botswana. *Journal of the South African Veterinary Association* **74**: 94.

REED, C. C., BASSON, L. and VAN AS, L. L. 2002b. *Myxobolus* species (Myxozoa), parasites of fishes in the Okavango River and Delta, Botswana, including descriptions of two new species. *Folia Parasitologica* **49**: 81-88.

REED, C. C., BASSON, L. and VAN AS, L. L. 2003a. Myxozoans infecting the sharptooth catfish, *Clarias gariepinus* in the Okavango River and Delta, Botswana, including descriptions of two new species, *Henneguya samochimensis* sp. n. and *Myxobolus gariepinus* sp. n. *Folia Parasitologica* **50**: 183-189.

REED, C. C., BASSON, L. and VAN AS, L. L. (in prep). *Henneguya macrolepidotus* sp.n. and *H. xarensis* sp. n., two new myxosporeans form the Okavango River and Delta, Botswana.

REED, C. C., BASSON, L. and VAN AS, L. L. 2003b. Myxozoans infecting intertidal fishes along the Cape south coast of South Africa. 6th International Symposium on Fish Parasites, Bloemfontein, South Africa, page 33.

REED, C. C., KRUGER, J., VAN AS, J. G., and BASSON, L. 1999. Histopathological study of a myxosporean from the gills of *Schilbe intermedius* Rüppell (1832). *Microscopy Society of Southern Africa-Proceedings* 29: 74.

REED, C. C., and VAN AS, L. L. 1999. Myxosporeans occurring on the gills of fish in the Okavango Delta, Botswana. 5th International Symposium on Fish parasites, Céske Budejovice, Czech Republic, page 118.

REED, C.C. VAN AS, J. G. and BASSON, L. 1998. Myxosporea of some southern African Fish. *Microscopy Society of Southern Africa-Proceedings* **28**: 82.

REED, C. C. BASSON, L., VAN AS, L. L. and DYKOVÁ, I. 2002. Observations of a *Ceratomyxa* sp. (Myxozoa) in the bile of the Super Klipfish. *Proceedings of the 15th International Conference on Electron Microscopy* **15**: 585-586.

ROBERTS, L. S. and JANOVY, J. Jr. 2000. Gerald D. Schmidt and Larry S. Roberts' *Foundations of Parasitology*. 6th edition. McGraw-Hill. Singapore.

ROSS, K. 2003. *Okavango, jewel of the Kalahari*. Struik Publishers, Cape Town, 215 pp.

RUIDISCH, S., EL-MATBOULI, M. and HOFFMANN, R. W. 1991. The role of tubificid worms as an intermediate host in the life cycle of *Myxobolus pavlovskii* (Achmerov, 1954). *Parasitological Research* **77**: 663-667.

SAKITI, N., BLANC, E., MARQUÉS, A. and BOUIX, G. 1991. Myxosporidies (Myxozoa: Myxosporea) du genre *Myxobolus* Bütschli, 1882 parasites de poissons Cichlidae du lac Nokoué au Bénin (Afrique de l' Quest). *Journal of African Zoology* **105**: 173-186.

SAKITI, P. N., TARER, V., JACQUEMINI, D. and MARQUÉS, A. 1996. Présence en Méditerranée occidentale d'une Myxosporidie histozoïque pathogène dans les élevages de Daurade, *Sparus aurata* L. *Annales des Sciences naturelles, Zoologie, Paris* **17**: 123-127.

SARKAR, N. K. and PRAMANIK, A. K. 1993. *Ceratomyxa daysciaenae* sp. n. (Myxozoa: Ceratomyidae) a myxosporean parasite in the gall bladder of a teleost from the Hooghly Estuary, West Bengal, India. *Acta Protozoologica* **33**: 121-124.

SCHLEGEL, M. LOM, J., STECHMANN, A., BERNHARD, D., LEIPE, D., DYKOVÁ, I. and SOGIN, M. L. 1996. Phylogenetic analysis of complete small subunit ribosomal RNA coding region of *Myxidium lieberkuehni*: evidence that Myxozoa are Metazoa and related to Bilateria. *Archiv fuer Protistenkunde* **147**: 1-9.

SCHULMAN, S. S., KOVALEVA, A. A. and DUBINA, V. R. 1979. New Myxosporidians from fishes of the Atlantic coast of Africa. *Parazitologiya* **13**: 71-79.

*SHULMAN, S. S. 1966. Myxosporidia of the fauna of the USSR. Nauka, Moscow.

SHULMAN, S. S., KOVALEVA, A. A. and DUBINA, V. R. 1979. New myxosporidians from fishes of the Atlantic coast of Africa. *Parazitogiya* **13**: 71-79.

SIAU, Y. 1971. Myxosporidies de *Synodontis ansorgii* Boulen. Ann. Et.Mag N. H. 1911 et de *Eleotris* (Kribia) *kriebensis* Boulenger 1964, poissons des eaux saumâtres de la lagune de Porto-novo (Dahomey). *Bulletin de la Société Zoologique de France* **96**: 563-570.

SIAU, Y. 1978. Contribution à la connaissance des Myxosporidies. Etude de *Myxobolus exiguus* Thélohan, 1895. Thése Doctorat d'Etat, U.S.T.L. Montpellier.

SIDDALL, M. E., MARTIN, D. S., BRIDGE, D., DESSER, D. K. and CONE, D. K. 1995. The demise of a phylum of protists: Phylogeny of myxozoa and other parasitic cnidaria. *Journal of Parasitology* **81 (6)**: 961-967.

SITJÁ-BOBADILLA, A. and ÁLVAREZ-PELLITERO, P. 1990. *Sphaerospora testicularis* sp. nov. (Myxosporea: Sphaerosporidae) in wild and cultured sea bass, *Dicentrarchus labrax* (L.), from Spanish Mediterranean. *Journal of Fish Diseases* **13**: 93-203.

SITJÁ-BOBADILLA, A. and ÁLVAREZ-PELLITERO, P. 1993. *Zschokkella mugilis* n. sp. (Myxosporea: Bivalvulida) from mullets (Teleostei: Mugilidae) of Mediterranean waters: light and electron microscopic description. *Journal of Eukaryotic Microbiology* **40**:755-764.

SITJÁ-BOBADILLA, A. PALENZUELA, O. and ÁLVAREZ-PELLITERO, P. 1995. *Ceratomyxa sparusaurati* n. sp. (Myxosporea: Bivalvulida) a new parasite from cultured gilthead seabream (*Sparus aurata*) (Teleostei: Sparidae) light and electron microscopic description. *Journal of Eukaryotic Microbiology* **42**: 529-539.

SKELTON, P. 1993. *A complete guide to the Freshwater fishes of southern Africa.* Southern Book Publishers, Halfway house.

SKELTON, P. 2001. *A complete guide to the Freshwater fishes of southern Africa*. Southern Book Publishers, Halfway house.

SMITH, M and HEEMSTRA, P. C. 1986. *Smith's sea fishes*. MacMillan South Africa, Johannesburg.

SMOTHERS, J. F., VON DOHLEN, C. D., SMITH, C. D. and SPALL, R. D. 1994. Molecular evidence that the myxozoan protists are metazoan. *Science* **265**: 1719-1721.

STEMPELL, W. 1919. Utersuchungen über *Leptotheca coris* sp. nov. und das in dieser schmarotzende *Nosema marionis* Thélohan. *Archiv fuer Protistekunde* **40**: 113-157.

STOFFREGEN, D. A. and ANDERSON, W. I. 1990. A myxosporean parasite in the skeleton muscle of a black tip reef shark, *Caracharinus melanopterus* (Quoy and Caimard, 1824). *Journal of Fish Disease*, **13**: 549-552.

*STOLC, A. 1899. Actinomyxidies, noveau groupe de Mesozaires parent des Myxosporidies. *Bulletin de l' International Academia de Sciences, Bohemia* **22**: 1-12.

STYER, E. L., HARRISON, L. R. and BURTLE, G. J. 1991. Experimental production of proliferative gill disease in channel catfish exposed to a myxozoan-infected oligochaete, *Dero digitata*. *Journal of Aquatic Animal Health* **3**: 288-291.

SU, X-G. and WHITE, R. W. G. 1994. New myxosporean (Myxozoa: Myxosporea) from Marine fishes of Tasmania, Australia. *Acta Protozoologica* **33**: 251-259.

SZÊKELY, C., EL-MANSY, A., MOLNAR, K. and BASKA, F. 1998. Development of *Thelohanellus hovorkai* and *Thelohanellus nikolskii* (Myxosporea, Myxozoa) in oligochaete alternate hosts. *Fish Pathology* **33**: 107-114.

SZÉKELY, C., MOLNÁR, K., ESZTERBAUER, E. and BASKA, F. 1999. Experimental detection of the actinospores of *Myxobolus pseudodispar* (Myxosporea: Myxobolidae) in oligochaete alternate hosts. *Diseases of Aquatic Organisms* **38**: 219-224.

*THÊLOHAN, P. 1892. Observations sur les Myxosporidies et essai de classification des ces organismes. *Bulletin Societe Philomatique,* Paris **4**: 165-178.

*THÉLOHAN, P. 1895. Recherches sur les Myxosporidies. *Bulletin Scientifique de la France et Belgique,* Paris **26**: 100-394.

*TRIPATHI, Y. R. 1953. Studies on parasites of Indian fishes. I. Protozoa Myxosporidia together with a checklist of parasitic protozoa described from Indian fishes. *Records of the Indian Museum* **50**: 63-88.

TUN, T., OGAWA, K. and WAKABAYASHI, H. 2002. Pathological changes induced by three myxosporeans in the intestine of cultured tiger puffer, *Takifugu rubribes* (Temminck and Schlegel). *Journal of Fish Diseases* **25**: 63-72.

URAWA, S. 1994. Life cycle of *Myxobolus articus*, a myxosporean parasite of salmonid fishes. In: Program and Abstracts International Symposium on Aquatic Animal Health, Seattle, pages W-10.3.

USPENSKAYA, A. V. 1995. Alternation of actinosporean and myxosporean phases in the life cycle of *Zchokkella nova* (Myxozoa). *Journal of Eukaryotic Microbiology* **42**: 665-668.

*VAN WYK, G. F. 1968. Annual report No. 24, 1967. Jonkershoek Hatchery, Division of inland Fisheries, Department of Nature Conservation, Province of Good Hope, Republic of South Africa.

VAN DER ELST, R. 1995. *A guide to the common sea fishes of southern Africa*. Struik Publishers, Cape Town.

*WEILL, R. 1938. L'interpretation des Cnidosporidies et la valeur taxonomique de leur cnidome. Leur cycle compare á la phase larvaire des Narcomeduses Cunindes. *Travaux de la Station Zoologique de Wimereaux* **13**: 727-744.

WHITNERY, J. B. 1893. Some additional notes on a myxosporidian infection in the common toad. *New York Medical Journal* **18**: 660-662.

WOLF, K. and MARKIW, M. E. 1984. Biology contravenes taxonomy in the Myxozoa: New discoveries show alternation of invertebrate and vertebrate hosts. *American Association for the advancement of Science, Science year* **225**: 1449-1452.

YASUDA, H., OOYAMA, T., IWATA, K., TUN, T., YOKOYAMA, H. and OGAWA, K. 2002. Fish-to-fish transmission of *Myxidium* spp. (Myxozoa) in cultured tiger puffer suffering from emaciation disease. *Fish Pathology* **37**: 29-33.

YOKOYAMA, H. 1997. Transmission of *Thelohanellus hovorkai* Achmerov, 1960 (Myxosporea: Myxozoa) to common carp *Cyprinus carpio* through the alternate oligochaete host. *Systematic Parasitology* **36**: 79-84.

YOKOYAMA, H. and FUKUDA, Y. 2001. *Ceratomyxa seriolae* n. sp. and *C. buri* n. sp. (Myxozoa: Myxosporea) from the gall-bladder of cultured yellowtail *Seriola quinqueradiata*. *Systematic Parasitology* **48**: 125-130.

YOKOYAMA, H. and MASUDA, K. 2001. *Kudoa* sp. (Myxozoa) causing post-mortem myoliquifaction of the North-Pacific giant octopus *Paroctopus dofleini* (Cephalopoda: Octopodidae). *Bulletin of the European Association of Fish Pathologists* **21**: 266-268.

YOKOYAMA, H., OGAWA, K. and WAKABAYASHI, H. 1993. Involvement of *Branchiura sowerbyi* (Oligochaeta: Annelida) in the transmission of *Hoferellus carassii* (Myxosporea:

Myxozoa) the causative agent of kidney enlargement disease (KED) of goldfish *Carassius auratus*. *Gyobyo Kenkyo* **28**: 135-139.

YOKOYAMA, H., OGAWA, K. and WAKABAYASHI, H. 1995. *Myxobous cultus* n. sp. (Myxosporea: Myxobolidae) in the goldfish *Carrasius auratus* transformed from the actinosporean stage in the oligochaete *Branchiura sowerbyi*. *Journal of Parasitology* **81**: 446-451.

XIAO, C and DESSER, S. S. 2000. The longevity of Actinosporean spores from Oligochaetes of Lake Sasajewan, Algonquin Park, Ontario and their reaction to fish mucus. *Journal of Parasitology* **86**: 193-195.

*** Reference not seen in original form**
≈Article referred to by Fantham (1919), but omitted in his reference list.

Acknowledgments

I would like to express my sincere appreciation to the following persons and institutions that enabled the successful completion of my PhD thesis:

My promotors ***Prof. Linda Basson*** and ***Dr. Liesl van As***, from the University of the Free State, Bloemfontein, for the continued support, guidance, friendship, understanding and patience they offered throughout my entire postgraduate career.

My co-promotor, ***Prof Iva Dyková*** from the Institute of Parasitology, Ceske Budejovice, Czech Republic, for her sincere assistance, guidance and help with the southern African myxosporeans. Also for the processing of some of my samples.

Prof. Jo van As, for his support and for the many opportunities he has created for us to conduct research in some of the most beautiful places in the world.

To my ***Mom and Dad***, for always supporting me with everything I ever wanted to do, no matter what the circumstances.

Dr. Nico Smit for his true friendship, love, guidance, support and understanding throughout my entire post graduate career.

Prof. Angela Davies, for her guidance, friendship and support and for the opportunity to spend time at Kingston University, London.

To all my friends, you know who you are! Thank you for being so supportive and understanding, in particular during the last few years.

Trevor Farr, ***Ian Allen***, ***Nadia Günter*** and all the staff at Potberg Environmental Education Centre for their friendship, interest and for the use of all the facilities during fieldtrips. In particular ***Matthew Prophet*** and ***Keith Spencer*** for their assistance with the collection of fishes.

The ***Government of Botswana***, for their permission and support to undertake the Okavango Fish Parasite Project.

The ***Debswana Diamond Company*** for their financial support of the Okavango Fish Parasite Project.

The ***National Research Foundation*** for the many bursaries received in support of my entire postgraduate career.

Cannon Collins Trust for southern African Education, for financially supporting me for two visits to Kingston University, London.

The ***Department of Zoology and Entomology***, University of the Free State, Bloemfontein, for the many happy years spent there and for the opportunity to make use of all the departmental facilities.

Western Cape Nature Conservation Board, for their patience and understanding. Also to my friends and colleagues in George, for having to put up with me whilst I was writing up!

Abstract

Myxozoans form a diverse and economically important group of endoparasites that have been intriguing researchers ever since the early1800's. These parasites are notorious, having been associated with the devastating effects many species have shown in aquaculture and fisheries industries throughout the world. Research on both freshwater and marine myxosporeans in Africa is limited to a few countries and has, until recently, been largely neglected in southern Africa. In recognition of the need to investigate the presence of fish-infecting myxosporeans in both the freshwater and marine environments of southern Africa, a study was initiated in 1997 investigating the biodiversity of myxosporeans infecting fishes in two very unique southern African localities. Firstly, the Okavango River and Delta in Botswana contains one of the worlds largest inland deltas composed of about 18 000 km^2 waterways. Situated in the middle of the Kalahari Desert, this pristine wetland is the only one of its kind that forms an inland delta and one of the few river systems in the world that is visible from space. The research on myxosporeans infecting marine fishes was conducted along the Cape south coast of South Africa, which has one of the most diverse marine fauna and flora compositions in the world of which 13 % is endemic. This study aimed to review all existing literature concerning freshwater and marine fish-infecting myxosporeans in Africa, report on the biodiversity and prevalence of fish-infecting myxosporeans in the Okavango River and Delta, Botswana, investigate the pathogenic potential of myxosporeans infecting the Okavango fishes, determine the taxonomic status, species biodiversity and prevalence of myxosporeans infecting fishes along the Cape south coast, South Africa and investigate the pathogenic potential of myxosporeans infecting intertidal and surf zone fishes along the Cape south coast of South Africa. The examination of 2858 fishes representing 14 families and 65 species on several field trips to the Okavango River and Delta from 1997 to 2001 revealed the presence of 29 different fish infecting myxosporeans representing the genera *Henneguya* Thélohan, 1892 and *Myxobolus* Bütschli, 1882. Six of these species have been described as new in three articles prior to this study. Another two new species have been recorded in this thesis, together with the records of 14 miscellaneous species that have never been described before, but require more material for the completion of species descriptions. During the course of nine surveys conducted along the Cape south coast of South Africa since March 1998, a total of 410 fishes

representing 33 species were examined for parasitic infections. Results from these surveys revealed the presence of 15 different myxosporean species. Three species from the genus *Ceratomyxa* Thélohan, 1892, one species from the genus *Henneguya*, two from the genus *Myxidium* Bütschli, 1882, one species from the genus *Myxobolus* and one species from the genus *Sphaeromyxa* Thélohan, 1892 are described in this thesis. Two keys for the identification of both the freshwater, as well as marine and estuarine fish-infecting myxosporeans in Africa are presented as a conclusion to this study. The results obtained from this study have laid the foundation for the continuation of research on these parasites in southern Africa and has provided an insight into the great diversity of myxosporeans infecting southern African fishes.

Keywords: Botswana, Cape south coast, *Ceratomyxa*, freshwater, fishes, *Henneguya*, marine, *Myxidium*, *Myxobolus*, *Sphaeromyxa*

Opsomming

Verteenwoordiges van die Myxozoa vorm 'n diverse en ekonomies belangrike groep endoparasiete wat al sedert die vroeë 1800s navorsers betower. Hierdie parasiete word met die vernietigende effekte geassosieer wat hulle in die akwakultuur en vissery-industrieë wêreldwyd veroorsaak. Navorsing op albei die varswater en mariene miksosporidia in Afrika is tot 'n paar lande beperk en het, tot onlangs, omtrent geensins 'n bestaan in suidelike Afrika gehad nie. Na aanleiding van die tekort aan inligting in verband met varswater en mariene miksosporidia in suidelike Afrika, is 'n projek in 1997 begin om die biodiversiteit van varswater en mariene miksosporidia in twee baie unieke lokaliteite in suidelike Afrika te ondersoek. Eerstens, die Okavangorivier en -delta in Botswana huives een van die wêreld se grootse binnelandse deltas wat uit omtrent 18 000 km² se vloedvlaktes bestaan. Hierdie ongerepte vleiland is in die middel van die Kalahariwoestyn geleë en is een van die enigste riviere ter wêreld wat van die buite ruim besigtig kan word. Navorsing op die mariene miksosporidia is teen die Kaapse suidkus van Suid-Afrika gedoen, wat een van die mees diverse en spesieryke fauna en flora ter wêreld het en waarvan 13% endemies is. Hierdie studie beoog om alle bestaande literatuur in verband met beide varswater en mariene miksosporidia in Afrika te hersien, te rapporteer op die biodiversiteit en infeksievlakke van visinfekterende miksosporidia in the Okavangrivier en -delta, om die taksonomiese status, spesiediversitiet en voorkoms van miksosporidia in visse van die Kaapse suidkus te ondersoek en om die patogeniese potentiaal van hierdie miksosporidia te bepaal. 'n Totaal van 2858 visse van 14 families en 65 spesies is op verskeie navorsingsopnames vir parasiete ondersoek. Die resultate het die teenwoordigheid van 29 verskillende miksosporia van die genera *Henneguya* Thélohan, 1892 en *Myxobolus* Bütschli, 1882 gelewer. Ses van hierdie spesies is vooraf in artikels beskryf. 'n Verdere twee word in hierdie proefskrif beskryf, saam met 'n lys van onbekende spesies wat addisionele inligting benodig vir hul spesiebeskrywings. Gedurende nege opnames aan die Kaapse suidkus van Suid-Afrika sedert Maart, 1998, is 'n totaal van 410 visse van 33 spesies vir miksosporidia infeksies ondersoek. Resultate lewer die teenwoordigheid van 15 verskillende miksosporidia spesies op. Drie spesies van die genus *Ceratomyxa* Thelohan, 1892, een spesie van die genus *Henneguya*, twee spesies van die genus *Myxidium* Bütschli, 1882 en een spesie van die genus *Myxobolus* word in hierdie

proefskrif beskryf. Twee sleutels vir die identifikasie van beide die varswater en mariene miksosporidia in Afrika word as 'n afsluiting tot die proefskrif voorgestel. Die resultate van hierdie studie het die fondasies vir die voortgesette navorsing op hierdie parasiete in suidelike Afrika neergelê en het insig tot die ongelooflike diversiteit van miksosporidia in suidelike Afrika gelewer.

Appendix I

FOLIA PARASITOLOGICA 49: 81-88, 2002

Myxobolus species (Myxozoa), parasites of fishes in the Okavango River and Delta, Botswana, including descriptions of two new species

Cecilé C. Reed, Linda Basson and **Liesl L. Van As**

Department of Zoology and Entomology, University of the Free State, P.O. Box 339, Bloemfontein, 9300, South Africa

Key words: Myxozoa, *Myxobolus*, new species, taxonomy, fish parasites, Botswana

Abstract. Fieldwork was conducted in 1998 and 1999 in the Okavango River and Delta and a total of 275 fishes representing 31 species were examined for the presence of myxosporean parasites. A total of seven myxosporeans of the genus *Myxobolus* Bütschli, 1882 were found infecting the fishes. Two new species namely *Myxobolus etsatsaensis* sp. n. from *Barbus thamalakanensis* Fowler, 1935 and *M. paludinosus* sp. n. from *Barbus paludinosus* Peters, 1852 are described. *Myxobolus africanus* Fomena, Bouix et Birgi, 1985, *M. camerounensis* Fomena, Marqués et Bouix, 1993, *M. hydrocyni* Kostoïngue et Toguebaye, 1994, *M. nyongana* (Fomena, Bouix et Birgi, 1985) and *M. tilapiae* Abolarin, 1974 are recorded for the first time in Botswana and descriptions of these species are provided.

Myxosporean research in Africa dates back to the late 19th century with Gurley (1893) being one of the earliest authors referring to the continent. The African continent boasts over a 100 myxosporean species from freshwater, brackish and marine fishes of which 84 infect primarily freshwater fishes (Fomena and Bouix 1997) and this number is continuously growing. When comparing the known African myxosporeans to the more than 1,300 species described worldwide, it is evident that for a huge continent with such high fish diversity, a large gap exists in the knowledge on the occurrence and distribution of these parasites.

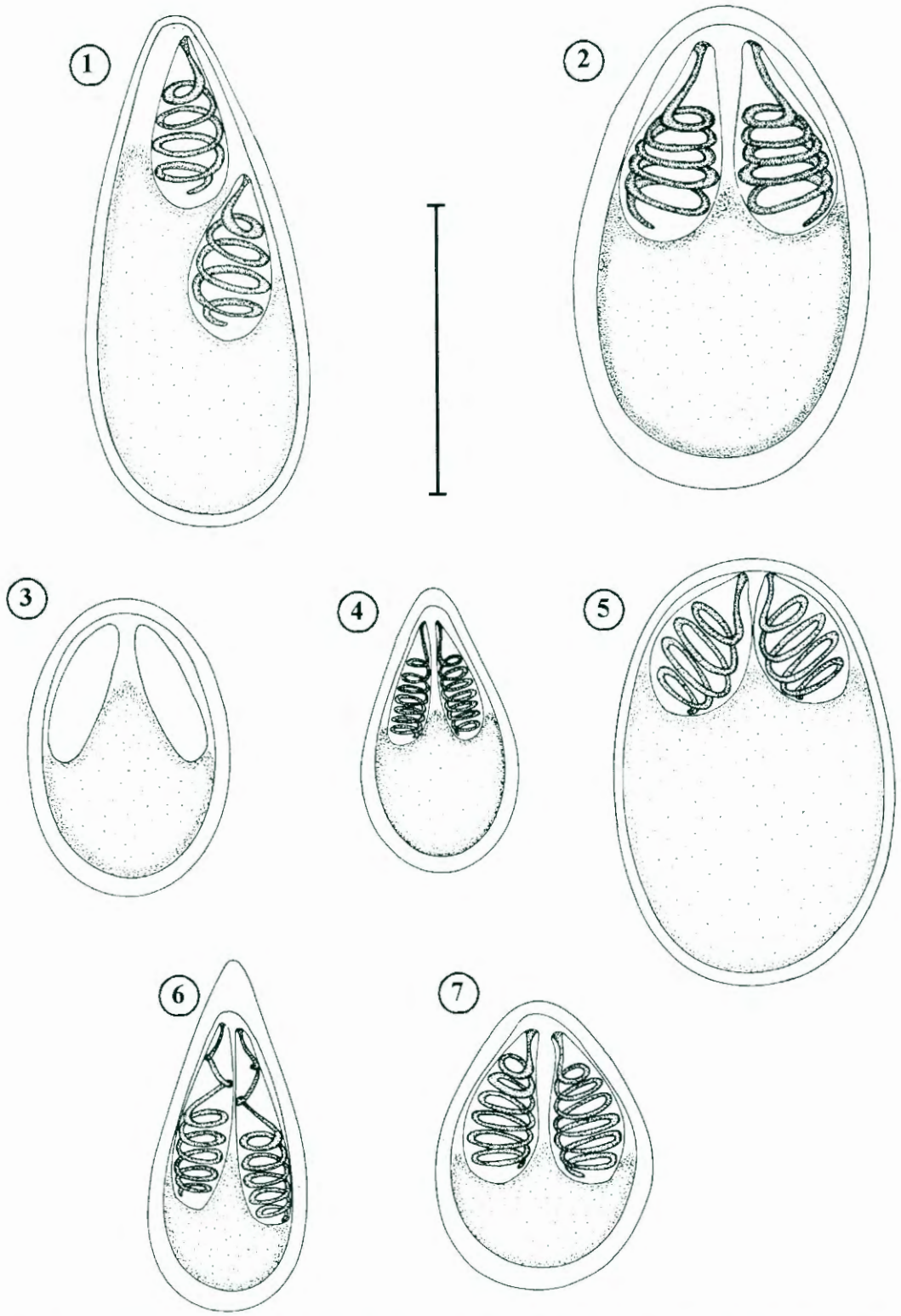
In southern Africa little research has been conducted on myxosporean parasites of fish, with only a few publications appearing largely on marine myxosporeans from South Africa such as Fantham (1919, 1930), Gilchrist (1924), Paperna et al. (1987) and Ali (2000). The only record ever of a freshwater myxosporean from Botswana is that of Peters (1971), commenting on Boulenger (1911) who published a brief note on an anabantid showing a mouth-brooding habit from the Okavango River. According to Peters (1971), Boulenger commented the following: "On examining a female, about 5 ins. long, I found seven or eight eggs about one line in diameter, closely packed on each side in a cavity behind the gills, entirely covered by operculum". While conducting comparative studies on the ethology of African Anabantidae, Peters (1971) examined the rounded bodies, which did look like eggs, and discovered that they were in fact mature plasmodia from a myxosporean infection.

Now, 30 years later, the results of the first investigation into myxosporean parasites infecting fishes in the Okavango River and Delta are presented. Over a period of two years (1998 and 1999) a total of 275 fishes from the Okavango Delta, representing 31 species and 9 families were examined for the presence of myxosporean parasites. This paper reports on the occurrence of seven myxosporeans of the genus *Myxobolus* Bütschli, 1882 found infecting eight different host fish species in the Okavango River and Delta, Botswana.

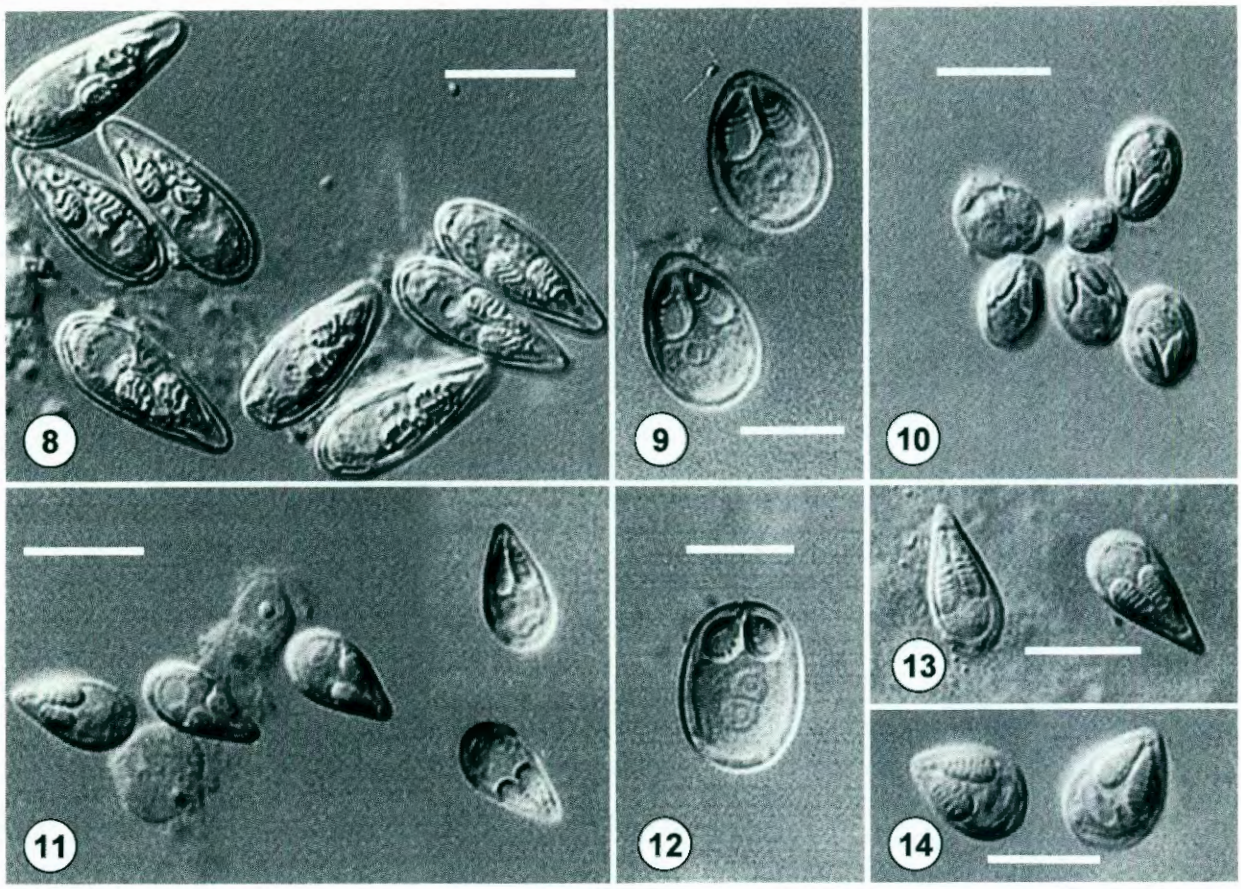
MATERIALS AND METHODS

Fieldwork was conducted in the Okavango River and Delta in Botswana during June and July in both 1998 and 1999. Fishes were collected using hand nets, cast nets, sein nets and a series of gill nets from mainstream and lagoon environments. Live fishes were taken back to a mobile field laboratory where they were kept in aerated aquaria. The fishes were identified and anaesthetised with a dosage of benzocaine sufficient to kill them. Standard techniques when working with myxosporeans requires the observation and photography of live spores, but due to the isolated collection localities mature myxosporean spores found in plasmodia were fixed in 10% buffered neutral formalin. Due to the formalin fixation of the spores, some structures could not be observed in the material, such as intercapsular appendices and iodinophilous vacuoles. Since most of the plasmodia in the present study were very small, spores from a number of plasmodia were measured. However, in all cases the plasmodia were obtained from the same host specimen. The fixed spores were photographed using a Zeiss Axiophot microscope with differential interference contrast on a layer of 0.5% non-nutrient agar and were measured according to the guidelines provided by Lom and Arthur (1989). Minimum and maximum values of spore measurements are provided in micrometres (μm), followed in parentheses by the arithmetic mean and standard deviation. Permanent preparations were made by impregnating myxosporean spores with silver nitrate. Myxoboli described in the

Address for correspondence: L. Basson, Department of Zoology and Entomology, University of the Free State, P.O. Box 339, Bloemfontein, 9300, South Africa. Phone: ++27 51 401 3244; Fax: ++ 27 51 448 8711; E-mail: bassonl.sci@mail.uovs.ac.za



Figs. 1-7. *Myxobolus* Bütschli, 1882 species collected from the Okavango River and Delta, Botswana; microscope projection drawings of formalin-fixed spores. **Fig. 1.** *Myxobolus africanus* Fomena, Bouix et Birgi, 1985 from the gills and fins of *Hepsetus odoe* (Bloch, 1794). **Fig. 2.** *Myxobolus camerounensis* Fomena, Marqués et Bouix, 1993 from the gill arch of *Oreochromis andersonii* (Castelnau, 1861). **Fig. 3.** *Myxobolus hydrocyni* Kostoïngue et Toguebaye, 1994 from the gills of *Hydrocynus vittatus* Castelnau, 1861. **Fig. 4.** *Myxobolus nyongana* (Fomena, Bouix et Birgi, 1985) from the gills of *Barbus poechii* Steindachner, 1911. **Fig. 5.** *Myxobolus* cf. *tilapiae* Abolarin, 1974 from the buccal cavity of *Tilapia rendalli rendalli* (Boulenger, 1896). **Fig. 6.** *Myxobolus etsatsaensis* sp. n. from the gills of *Barbus thamalakanensis* Fowler, 1935. **Fig. 7.** *Myxobolus paludinosus* sp. n. from the gills of *Barbus paludinosus* Peters, 1852. Scale bar = 10 μm.



Figs. 8-14. *Myxobolus* Bütschli, 1882 species collected from the Okavango River and Delta, Botswana; differential interference contrast micrographs of formalin-fixed spores. **Fig. 8.** *Myxobolus africanus* Fomena, Bouix et Birgi, 1985 from the gills and fins of *Hepsetus odoe* (Bloch, 1794). **Fig. 9.** *Myxobolus camerounensis* Fomena, Marqués et Bouix, 1993 from the gill arch of *Oreochromis andersonii* (Castelnau, 1861). **Fig. 10.** *Myxobolus hydrocyni* Kostoïngue et Toguebaye, 1994 from the gills of *Hydrocynus vittatus* Castelnau, 1861. **Fig. 11.** *Myxobolus nyongana* (Fomena, Bouix et Birgi, 1985) from the gills of *Barbus poechii* Steindachner, 1911. **Fig. 12.** *Myxobolus* cf. *tilapiae* Abolarin, 1974 from the buccal cavity of *Tilapia rendalli rendalli* (Boulenger, 1896). **Fig. 13.** *Myxobolus etsatsaensis* sp. n. from the gills of *Barbus thamalakanensis* Fowler, 1935. **Fig. 14.** *Myxobolus paludinosus* sp. n. from the gills of *Barbus paludinosus* Peters, 1852. Scale bars = 10 μm.

one resembles the species collected from the Okavango in Botswana. More material from the type host and type locality of *M. tilapiae* would have to be examined to determine whether this species does show such great variation. *Myxobolus tilapiae* is similar to *M. heterosporus* (Baker, 1963) type (I) in overall spore shape. The polar capsules of *M. heterosporus* are, however, more pyriform, compared with the more spherical polar capsules of *M. tilapiae*. *Myxobolus tilapiae* is similar to *M. polycentropsi* Fomena, Bouix et Birgi, 1985 and *M. synodonti* Fomena, Bouix et Birgi, 1985, parasites of *Polycentropsis abbreviata* and *Synodontis batesii* respectively. The former myxosporean species, *M. polycentropsi*, is similar to *M. tilapiae* in having anterior and posterior ends that are both bluntly rounded. The polar capsules of *M. polycentropsi* are, however, more pyriform (Fomena et al. 1985), compared to the almost spherical ones in *M. tilapiae*. Finally, *Myxobolus synodonti* is distinct from *M. tilapiae* in having the anterior end slightly more tapered than the more rounded posterior end. The polar capsules of *M. synodonti* are much larger and elongated, compared to the more spherical polar capsules of *M. tilapiae*.

This represents both a new geographical and host record for *M. tilapiae*.

Myxobolus etsatsaensis sp. n. Figs. 6, 13, 19

Description of vegetative stages: Polysporous plasmodia found within secondary gill lamellae, whitish, very small and rounded.

Description of spores (based on 9 spores from fully mature plasmodia): In valvular view, spores extremely elongated, pyriform to teardrop-shaped, with anterior end tapering sharply to blunt point and posterior end rounded, 12.8-15.0 (13.0 ± 0.94) in length. Two smooth

Description of spores (based on 10 spores from fully mature plasmodia): In valvular view, spore body pyriform to ovoid with anterior end tapering to blunt point and posterior end rounded, 11.2-13.7 (12.0 ± 0.87) in length. Widest region of spore observed towards posterior ends of polar capsules, 7.5-10.0 (8.6 ± 0.75) in width. Two smooth shell valves visible with sutural ridge along edge of spore, becoming broader posteriorly. Two polar capsules of equal size situated in anterior end of spore, 5.0-6.8 (5.7 ± 0.88) long × 2.0-2.5 (2.4 ± 0.21) wide. Polar filaments have six to seven coils within polar capsules. Sporoplasm situated in posterior half of spore.

Type host: *Barbus paludinosus* Peters, 1852.

Site of infection: Secondary gill lamellae.

Type locality: Etsatsa Mainstream (18°51'470"S; 22°25.5'06"E), Okavango River and Delta, (Botswana).

Etymology: Named after the type host.

Type material: Holotype, slide 1999/07/05-11 (NMBP 24) and paratypes, spores in 10% neutral buffered formalin, 1999/07/03-06A (NMBP 25), 1999/07/03-06B (NMBP 220) in the collection of the National Museum, Bloemfontein, South Africa.

Remarks: *Myxobolus paludinosus* does not conform to the description of any other *Myxobolus* species described in Africa. When compared to those found parasitising *Barbus* hosts in Africa the following differences can be found. *Myxobolus paludinosus* is distinct from *M. njinei* described by Fomena et al. (1985), in having an anterior end that tapers to a blunt point and polar capsules that are completely spherical. *Myxobolus paludinosus* differs from *M. nkolyaensis* in that the latter species also has an almost spherical shape, with sub-spherical polar capsules. The spore dimensions of *M. nkolyaensis* are smaller than that of *M. paludinosus*. *Myxobolus nyongana* is similar to *M. paludinosus* in having a spore body that tapers anteriorly to a blunt point with a rounded posterior end, but the spores of *M. paludinosus* are not as slender as those of *M. nyongana*. The polar capsules of *M. paludinosus* do not lie parallel to one another, as in the case of *M. nyongana*. *Myxobolus paludinosus* is distinct from *M. oloi* as the latter species has an almost entirely spherical body with two unequal polar capsules.

Myxobolus paludinosus is overall similar to *M. amieti* described by Fomena et al. (1985), but differs, since the latter has a more slender, pyriform spore, with slender polar capsules that take up two thirds of the spore body. Although having a similar spore shape, *M. paludinosus* is distinct from *M. beninensis* in that the latter species has two polar capsules that take up two thirds of the spore body. The spores of *M. paludinosus* are also slightly wider than those of *M. beninensis*. *Myxobolus paludinosus* is very similar to *M. israelensis* Landsberg, 1985, in having similar spore dimensions, but the anterior end of the latter species is more rounded than the anterior end of the former species. The polar capsules of *M. israelensis* also take up more space in the spore body, leaving little place for the sporoplasm (Landsberg 1985). *Myxobolus paludinosus* appears to conform to the description of *Myxobolus* sp. 2 (Fomena et al. 1985), but there are differences in spore sizes.

Acknowledgements. This study was funded by the Debswana Diamond Company, Botswana as well as the National Research Foundation (NRF) of South Africa. Sincere gratitude to Prof. Iva Dyková from the Institute of Parasitology, Academy of Sciences of the Czech Republic, České Budějovice, Czech Republic, for her assistance during the preparation of the draft copy.

REFERENCES

ABOLARIN M.O. 1974: *Myxobolus tilapiae* sp. nov. (Protozoa: Myxosporida) from three species of freshwater tilapia in Nigeria. J. West Afr. Sci. Assoc. 19: 109-114.

ALI M.A. 2000: *Ortholinea basma* n. sp. (Myxozoa: Myxosporea) from Agile Klipfish *Clinus agilis* (Teleostei: Clinidae), light and scanning electron microscopy. Eur. J. Protistol. 36: 100-102.

BAKER J.R. 1963: Three new species of *Myxosoma* (Protozoa: Myxosporidia) from East African freshwater fish. Parasitology 53: 285-292.

BOULENGER G.A. 1911: Parental care in an African fish. The Field 118: 968.

FAISAL M., SHALABY S.I. 1987: *Myxosoma tilapiae* as a new species (Myxosoma: Myxosporea) in wild *Oreochromis niloticus* in Lower Egypt. Egypt. J. Vet. Sci. 24: 73-86.

FANTHAM H.B. 1919: Some parasitic Protozoa found in South Africa - XVI. S. Afr. J. Sci. 16: 185-191.

FANTHAM H.B. 1930: Some parasitic Protozoa found in South Africa - XIII. S. Afr. J. Sci. 27: 376-390.

FOMENA A., BOUIX G. 1994: New Myxosporidea species (Myxozoa) from freshwater teleosts in southern Cameroon (Central Africa). J. Afr. Zool. 108: 481-491.

FOMENA A., BOUIX G. 1997: Myxosporea (Protozoa: Myxozoa) of the freshwater fishes in Africa: keys to the genera and species. Syst. Parasitol. 37: 161-178.

FOMENA A., BOUIX G., BIRGI É. 1985: Contribution à l'étude des Myxosporidies des poissons d'eau du Cameroun II. Espèces nouvelles du genre *Myxobolus* Bütschli, 1882. Bull. Inst. Fond. Afr. Noire 46: 167-192.

FOMENA A., MARQUÉS A., BOUIX G. 1993: Myxosporidea (Myxozoa) of *Oreochromis niloticus* (Linnaeus 1757) (Teleost: Cichlidae) in fish farming pools at Melen (Yaounde, Cameroon, Central Africa). J. Afr. Zool. 107: 45-56.

GILCHRIST J.D.F. 1924: A protozoal parasite *Chloromyxum thyrsites* sp. n. of the Cape sea fish, the "snoek" (*Thyrsites atun*, Euplin). Trans. R. Soc. S. Afr. 11: 263-273.

FOLIA PARASITOLOGICA 50: 183–189, 2003

Myxozoans infecting the sharptooth catfish, *Clarias gariepinus* in the Okavango River and Delta, Botswana, including descriptions of two new species, *Henneguya samochimensis* sp. n. and *Myxobolus gariepinus* sp. n.

Cecilé C. Reed, Linda Basson and **Liesl L. Van As**

Department of Zoology and Entomology, University of the Free State, P.O. Box 339, Bloemfontein, 9300, South Africa

Key words: Myxozoa, *Myxobolus*, *Henneguya*, new species, taxonomy, *Clarias*, Botswana

Abstract. During a recent investigation of parasites infecting fishes from the Okavango River and Delta, Botswana (southern Africa) fourteen sharptooth catfish, *Clarias gariepinus* (Burchell, 1822) (Siluriformes: Clariidae) were examined for the presence of myxozoan infections. Results revealed the presence of two species of the genus *Henneguya* Thélohan, 1895 and one species of the genus *Myxobolus* Bütschli, 1882 infecting this fish host. Two of the sampled fish exhibited large plasmodia of *Henneguya suprabranchiae* Landsberg, 1987 in the cartilage of the accessory breathing organ, another two individuals were infected with *H. samochimensis* sp. n. plasmodia in the gills and another three individuals revealed an infection with *Myxobolus gariepinus* sp. n. plasmodia in the ovaries.

The sharptooth catfish, *Clarias gariepinus* (Burchell, 1822) (Siluriformes: Clariidae) is probably the most widely distributed fish species in Africa, with many names such as *C. mossambicus* Peters, 1852 and *C. lazera* Valenciennes, 1840 being recognised as its junior synonyms (Skelton 1993). The economic importance of this fish species has increased greatly in recent years as a result of its extensive use in aquaculture (Skelton and Teugels 1992). Furthermore, natural populations of *C. gariepinus* form a staple diet for many subsistence farmers throughout the African continent. Coinciding with the growing economic value of this fish is the increased interest in its parasite loads and what effect they might hold for the aquaculture industry. One particular group of parasites, the myxozoans, is well known for the diseases they cause in commercially important fish hosts. Fortunately, the pathological species represent merely a fraction of the more than 1350 described species throughout the world (Kent et al. 2001).

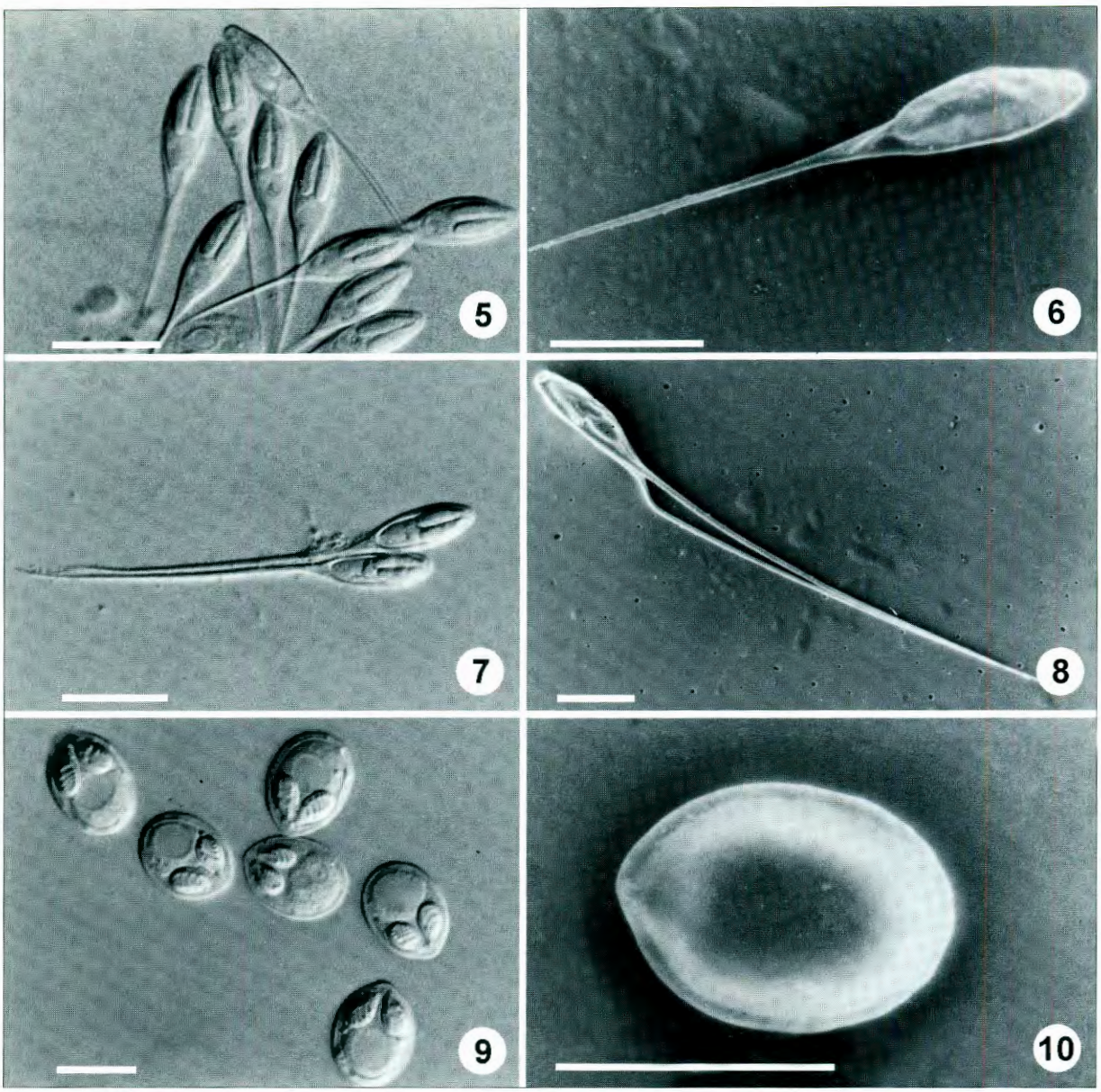
In Africa more than 135 species of myxozoans are known to infect freshwater, brackish and marine fishes (Kostoïngue et al. 2001). Seven of these, representing two genera, have been described from *Clarias* Scopoli, 1777 species in Africa (Table 1). *Henneguya clariae* Abolarin, 1971 was the first species to be described from the gills of *C. lazera* in Nigeria by Abolarin (1971). This description also appears to be the first record of the genus *Henneguya* Thélohan, 1892 in Africa. Several years later Landsberg (1987) described *H. laterocapsulata* Landsberg, 1987 and *H. suprabranchiae* Landsberg, 1987 from the skin and suprabranchial organs, respectively, of the same host in Israel. Ashmawy et al. (1989) described *H. branchialis* Ashmawy, Abu-Elwafa, Imam et El-Otifi, 1989 from the gills of *C. lazera* in Egypt. Some dispute has existed regarding the identification of this species and recently Ali (1999) suggested that *H. branchialis* is in fact a synonym of *H. suprabranchiae*. *Myxobolus clarii* Mandour, Galal et Abed, 1993 was described from the testis of *C. lazera* in Egypt by Mandour et al. (1993), afterwhich *M. comoei* Kabré, Sakiti, Marqués et Sawadago, 1995 was described from the gills of *C. anguillaris* Linnaeus, 1758 in Burkina Faso by Kabré et al. (1995). Most recently, Kostoïngue et al. (1999) described *H. fusiformis* Kostoïngue, Fall, Faye et Toguebaye, 1999 from the gills of *C. anguillaris* in Chad.

This paper presents preliminary results of the first investigation into myxozoan parasites infecting the sharptooth catfish, *Clarias gariepinus* in the Okavango River and Delta in Botswana. Two new species, *Henneguya samochimensis* sp. n. and *Myxobolus gariepinus* sp. n. are described, whilst *H. suprabranchiae* is recorded for the first time in southern Africa.

MATERIALS AND METHODS

Fourteen *Clarias gariepinus* specimens were captured and examined for the presence of myxozoan infections. During June and July (1998–2000) as well as in August 2001 fish were sampled using a series of gill nets from the lagoon environments within the Okavango River Panhandle and Delta regions in Botswana. Captured fish were killed using high concentrations of anaesthetic benzocaine (2.5×10^{-5} g/l) (ethyl-4-aminobenzoate), and then identified using Skelton (1993), measured and examined for the presence of myxozoan

Address for correspondence: L. Basson, Department of Zoology and Entomology, University of the Free State, P.O. Box 339, Bloemfontein, 9300, South Africa. Phone: ++27 51 401 3244; Fax: ++27 51 448 8711; E-mail: bassonl.sci@mail.uovs.ac.za



Figs. 5–10. Photomicrographs (Figs. 5, 7, 9) and scanning electron micrographs (Figs. 6, 8, 10) of formalin-fixed spores of myxozoans from the gills and ovaries of *Clarias gariepinus* from the Okavango River and Delta, Botswana. **Figs. 5, 6.** *Henneguya suprabranchiae* Landsberg, 1987. **Figs. 7, 8.** *Henneguya samochimensis* sp. n. **Figs. 9, 10.** *Myxobolus gariepinus* sp. n. Scale bars = 10 μm.

RESULTS AND DISCUSSION

An average of six *Henneguya suprabranchiae* plasmodia was found situated within the tips of cartilage in the accessory breathing organ of two of the 14 individual *C. gariepinus* collected. The second *Henneguya* species was found infecting the primary gill filaments of two *C. gariepinus* specimens, with one to four plasmodia situated in the primary gill lamellae of the infected individuals. Ovaries of three of the captured *C. gariepinus* were infected with plasmodia of the *Myxobolus* species. In each case an average of 16 plasmodia were seen distributed throughout the ovaries.

Henneguya suprabranchiae Landsberg, 1987

Figs. 1, 2, 5, 6, 11

Description of vegetative stages. Sporogonic plasmodia found in cartilage at tips of suprabranchial respiratory organ. Polysporous plasmodia round, yellowish, 2–4 mm in diameter.

Prevalence: 14.3% (2/14).

Etymology: Named after the type locality.

Material: Syntypes; spores in 10% neutral buffered formalin, 2000/08/12-03 (NMBP 276); spores in 10% neutral buffered formalin, 1999/07/02-33 (NMBP 277) and 1999/07/02-01 (NMBP 278); in the collection of the National Museum, Bloemfontein, South Africa.

Remarks. Significant differences can be seen when comparing the morphology and spore measurements of *H. samochimensis* to that of the other African *Henneguya* species parasitizing *Clarias* hosts (Table 2). *Henneguya samochimensis* differs from *H. clariae*, which has fused caudal appendages (Abolarin 1971) and a much longer total spore length (Table 2). The shape of the spore body of *H. clariae* has an almost sharply pointed anterior end with two unequally-sized polar capsules. *Henneguya samochimensis* differs significantly from *H. fusiformis* since the latter species has a fusiform spore body that contains two polar capsules with one situated behind the other (Kostoïngue et al. 1999). *Henneguya samochimensis* is also distinct from *H. laterocapsulata* in having two polar capsules both positioned next to each other in the anterior of the spore and not having one polar capsule that discharges laterally as in the case of the latter. The caudal appendages of *H. laterocapsulata* extend from a thick caudal base (Landsberg 1987), which is absent in *H. samochimensis*. Furthermore, the caudal appendages of *H. laterocapsulata* are also thick and divergent, curving outwards half way along their length. This is distinctly different from the thin filiform caudal appendages of *H. samochimensis*. Compared to *H. suprabranchiae*, *H. samochimensis* has a much longer average total spore length, whilst the polar capsules of *H. samochimensis* are proportionally smaller than those of *H. suprabranchiae* (Table 2). Morphologically *H. samochimensis* resembles *H. bopeleti* Fomena et Bouix, 1987 described from *Chrysichthys nigrodigitatus* in Cameroon by Fomena and Bouix (1987). The spore body length of *H. samochimensis* is, however, shorter, and the total spore length is longer than that of *H. bopeleti*. Another morphologically similar species is *Henneguya nyongensis* Fomena et Bouix, 1996, found in the gills of *Marcusenius moori* in Chad by the same authors (Fomena and Bouix 1996), but is distinguished from *H. samochimensis* in having very characteristic 'neck-like' appearances at the anterior ends of the polar capsules.

Myxobolus gariepinus sp. n. Figs. 4, 9, 10, 13

Description of vegetative stages. Sporogonic plasmodia found in ovaries. Polysporous plasmodia spherical, whitish, 2–3 mm in diameter.

Description of spores (based on 10 formalin-fixed spores from fully mature plasmodia). In valvular view, spore body ovoid to spherical with anterior end bluntly rounded, 13.7–15.0 (13.9 ± 0.4) long. Widest region of the spore observed towards posterior ends of polar capsules, measuring 10.0–11.2 (10.8 ± 0.5). Two smooth shell valves visible with two pyriform polar capsules of equal size converging in anterior part of spore, 6.0–6.2 (6.2 ± 0.1) long × 3.0–3.7 (3.5 ± 0.13) wide. Five to six coils of polar filament in polar capsules. Intercapsular process absent. Large iodinophilous vacuole present in sporoplasm.

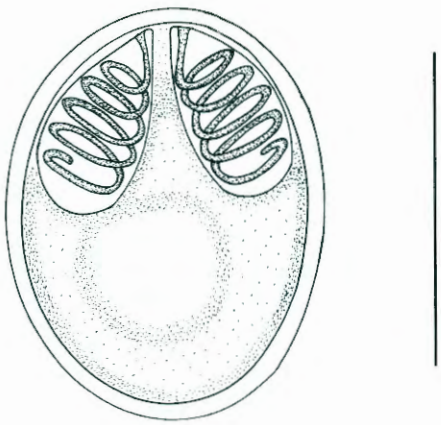


Fig. 13. *Myxobolus gariepinus* sp. n. infecting *Clarias gariepinus* from the Okavango River and Delta, Botswana; microscope projection drawing of formalin-fixed spore. Scale bar = 10 μm.

Type host: *Clarias gariepinus* (Burchell, 1822) (Siluriformes: Clariidae).

Type locality: Samochima Lagoon (18°25'26.08"S; 21°54'09.26"E), Okavango River, Botswana.

Site of infection: Ovaries.

Prevalence: 21% (3/14).

Etymology: Species name derived from the type host.

Material: Syntypes; spores in 10% neutral buffered formalin, 1999/07/02-39 (NMBP 279); spores in 10% neutral buffered formalin, 1999/07/02-31 (NMBP 280) and 1999/02/02-02 (NMBP 281); in the collection of the National Museum, Bloemfontein, South Africa.

Remarks. *Myxobolus gariepinus* shows similarities to *M. clarii* Mandour, Galal et Abed, 1993 (Table 1), but differs in having a small blunt point, which appears to be absent in *M. clarii*. The overall shape of *M. gariepinus* also resembles *M. comoei* Kabré, Sakiti, Marqués et Sawadago, 1995 (Table 1) in having a similar almost spherical spore body, the latter species, however, has two polar capsules that take up about half the space in the spore cavity while the polar capsules of *M. gariepinus* only take up about one third of the spore cavity. The small blunt point at the anterior end of *M. gariepinus* is also absent in *M. comoei*. Other morphologically similar species include *M. bilongi* Fomena, Marqués, Bouix et Njiné, 1994, *M. fotoi* Fomena, Marqués et Bouix, 1993 and *M. njinei* Fomena, Bouix et Birgi, 1985. Firstly, *M. gariepinus* is distinct from *M. bilongi*, found in the gills of a *Labeo* sp. by

REFERENCES

ABOLARIN M.O. 1971: A new species of *Henneguya* (Myxosporida, Protozoa) from West African Catfish, *Clarias lazera* Val. with a review of the genus *Henneguya* Thélohan, 1892. Afr. J. Trop. Hydrobiol. Fish. 1: 93–105.

ALI A.A. 1999: *Henneguya ghaffari* sp. n. (Myxozoa: Myxosporea), infecting the Nile perch *Lates niloticus* (Teleostei: Centropomidae). Dis. Aquat. Org. 38: 225–230.

ASHMAWY K.I., ABU-ELWAFA S.A., IMAM E.A., EL-OTIFI Y.Z. 1989: Description of newly recorded myxosporidian protozoa of freshwater fishes in Behera Province, Egypt. J. Egypt. Vet. Med. Assoc. 49: 43–53.

EL-MANSY A., BASHTAR A.-R. 2002: Histopathological and ultrastructural studies of *Henneguya suprabranchiae* Landsberg, 1987 (Myxosporea: Myxobolidae) parasitizing the suprabranchial organ of the freshwater catfish *Clarias gariepinus* Burchell, 1822 in Egypt. Parasitol. Res. 88: 617–626.

FOMENA A., BOUIX G. 1987: Contribution á l'étude des Myxosporidies des poissons d'eau douce du Cameroun. III. Espèces nouvelles des genres *Henneguya* Thélohan, 1892 et *Thelohanellus* Kudo, 1933. Rev. Zool. Afr. 101: 43–53.

FOMENA A., BOUIX G. 1996: New species of *Henneguya* Thélohan, 1892 (Myxozoa: Myxosporea) parasites of freshwater fishes in Cameroon. J. Afr. Zool. 110: 413–423.

FOMENA A., BOUIX G., BIRGI É. 1985: Contribution à l'étude des Myxosporidies des poissons d'eau du Cameroun. II. Espéces nouvelles du genre *Myxobolus* Bütschli, 1882. Bull. Inst. Fond. Afr. Noire, Sér A. 46:1–2.

FOMENA A., MARQUÉS A., BOUIX G. 1993: Myxosporidea (Myxozoa) of *Oreochromis niloticus* (Linnaeus 1757) (Teleoste Cichlidae) in fish farming pools at Melen (Yaounde, Cameroon, Central Africa). J. Afr. Zool. 107: 45–56.

FOMENA A., MARQUÉS A., BOUIX G., NJINÉ T. 1994: *Myxobolus bilongi* n. sp., *Thelohanellus assambai* n. sp., *T. sanagaensis* n. sp., Myxosporidies parasites de *Labeo* sp. (Téléostéen, Cyprinidae) du bassin de la Sanaga au Cameroon (Afrique Centrale). Ann. Fac. Sci. Cameroun 1: 31–42.

KABRÉ G.B., SAKITI N.G., MARQUÉS A., SAWADAGO L. 1995: *Myxobolus comoei* n. sp. et *Myxobolus burkinei* n. sp., nouvelles Myxosporidies histozoîques chez *Clarias anguillaris* et *Labeo coubie* capturés dans les pêcheries au Burkina Faso (Afrique de l'Ouest). Bull. Inst. Fond. Afr. Noire, Sér A. 48: 49–55.

KENT M.L., ANDREE K.B., BARTHOLOMEW J.L., EL-MATBOULI M., DESSER S.S., DEVLIN R.H., FEIST S.W., HEDRICK R.P., HOFFMANN R.W., KHATTRA J., HALLETT S.L., LESTER R.J.G., LONGSHAW M., PALENZUELA O., SIDDALL M.E., XIAO C.X. 2001: Recent advances in our knowledge of the Myxozoa. J. Eukaryot. Microbiol. 48: 395–413.

KOSTOÏNGUE B., FALL M., FAYE N., TOGUEBAYE S. 1999: Three new myxosporidian (Myxozoa: Myxosporea) parasites of freshwater fishes from Chad (Central Africa). Acta Protozool. 38: 323–326.

KOSTOÏNGUE B., DIEBAKATE C., FAYE N., TOGUEBAYE S. 2001: Presence of Myxosporidea (Myxozoa: Myxosporea) of the genus *Henneguya* Thélohan, 1892 in freshwater fishes from Chad (Central Africa). Acta Protozool. 40: 117–123.

LANDSBERG J.H. 1987: Myxosporean parasites of the catfish *Clarias lazera* (Valenciennes). Syst. Parasitol. 9: 73–81.

LOM J., ARTHUR J.R. 1989: A guideline for the preparation of species descriptions in Myxosporea. J. Fish Dis. 12: 151–156.

MANDOUR A.M., GALAL A.A., ABED G.H. 1993: *Myxobolus clarii* n. sp. in the testis of the fish *Clarias lazera* from the river Nile of Assiut. Assiut Vet. Med. J. 29: 109–115.

SKELTON P. 1993: A Complete Guide to the Freshwater Fishes of Southern Africa. Southern Book Publishers, Halfway House, 388 pp.

SKELTON P., TEUGELS G.G. 1992: Neotype description for the African catfish *Clarias gariepinus* (Burchell, 1882) (Pisces: Siluroidei: Clariidae). Ichthyol. Bull. 56: 1–7.

Received 5 August 2002

Accepted 17 March 2003

Appendix II

TELEGRAMS: PULA
TELEPHONE: 350800
TELEX: 2655 BD

REPUBLIC OF BOTSWANA

OFFICE OF THE PRESIDENT
PRIVATE BAG 001
GABORONE

OP 46/1 C (73)

30th October, 2002

KALAHARI CONSERVATION SOCIETY
P O. BOX 859 GABORONE

Mr. Felix Monggae
Kalahari Conservation Society
P. O. Box 859
Gaborone

Dear Sir,

RE: APPLICATION FOR A RESEARCH PERMIT EXTENSION: PROF. J. G. VAN AS

Your application for a research permit extension refers.

We are pleased to inform you that your permit OP 46/1 LVVII (90) has been revalidated by three (3) years effective October 30, 2002. You are requested to ensure that the project is completed within the stipulated period.

The extension is based on the following terms:

1. Conditions stipulated in the original permit remain valid and binding.
2. You maintain close collaboration with the Ministry of Agriculture through the Fisheries Section of the Department of Animal Health and Production through out the duration of the project.
3. You should consider involving locals to the extent of benefiting from their postgraduate scholarships instead of limiting such benefits only to foreigners.

Thank you

Yours faithfully

J. Moswela
for/PERMANENT SECRETARY TO THE PRESIDENT

cc: Permanent Secretary, Ministry of Agriculture
Director, Department of Animal Health and Production

DEPARTMENT: ENVIRONMENTAL AFFAIRS AND TOURISM
REPUBLIC OF SOUTH AFRICA
Private Bag X2, Roggebaai, 8012, Tel: (+27 21) 402 3911, Fax: (+27 21) 425 2920
Website: www.environment.gov.za

Ref No. V1/1/5/1
Enquiries: R Bodenham
Telephone: 4023064

Exe zool2002 per

EXEMPTION FOR PURPOSES OF SCIENTIFIC RESEARCH

In terms of Section 81(1) of the Marine Living Resources Act, 1998 (Act no. 18 of 1998), exemption is hereby given to DR L L VAN AS OF THE DEPARTMENT OF ZOOLOGY AND ENTOMOLOGY, UNIVERSITY OF THE FREE STATE, from those relevant provisions and restrictions of the Act to collect, possess, transport and dispose of any marine fish regardless of the size or condition for research purposes.

This exemption is subject to the following conditions:

1. Collections in terms of this exemption shall only be made for the purposes of *bona fide* research projects of the Department of Zoology and Entomology at the University of the Free State, as authorized by the Head of the Department.

2. A certified copy of this exemption shall be carried by staff during collections and must be shown to a Fishery Control Officer or any other authorized person on demand. Staff and students undertaking collections, shall identify themselves, if requested to do so, as staff members and students of the Department of Zoology and Entomology at the University of the Free State by means of an identification document issued by the Head of the Department.

3. Collections may only be made at the DE HOOP AND DE MOND NATURE RESERVES.

4. A maximum of 20 specimens per species may be collected, and returned to its original location wherever possible.

5. The holder of this exemption shall inform the relevant regional authority responsible for law enforcement under the Marine Living Resources Act of the sampling and survey date(s) and place(s) prior to each collection (Mr A. Reinecke at telephone 021-4307000).

6. Research report(s) that include descriptions of all collections that took place must be submitted to the Director of Research, Private Bag X2, Roggebaai 8012 and to Cape Nature Conservation, Private Bag X9086, Cape Town 8000 for attention Mr D Hignett, within 6 months after the expiry date of this exemption.

7. Fish caught in terms of this exemption shall not be sold or offered for sale.

8. This exemption is valid from date of issue to 31 DECEMBER 2002.

MINISTER
DATE: 27/02/02

Appendix III

Table 7.1. References to articles used for redrawing Africa freshwater myxosporean species. Species listed alphabetically.

Myxosporean species	Figure	Reference
Chloromyxum birgii Fomena and Bouix, 1994	7.1a, b	Fomena and Bouix (1994)
Chloromyxum vanasi Ali, 1998	7.2	Ali (1998)
Henneguya alestis Negm-Eldin, Govedich and Davies, 1999	7.3	Negm-Eldin, Govedich and Davies (1999)
Henneguya auchenoglanii Kostoïngue, Diebakate, Faye and Toguebaye, 2001	7.4	Kostoïngue, Diebakate, Faye and Toguebaye (2001)
Henneguya bopeleti Fomena and Bouix, 1987	7.5	Fomena and Bouix (1987)
Henneguya camerounensis Fomena and Bouix, 1987	7.6	Fomena and Bouix (1987)
Henneguya chrysichthyi Obiekezie and Enyenihi, 1988	7.7	Obiekezie and Enyenihi (1988)
Henneguya clariae Abolarin, 1971	7.8	Abolarin (1971)
Henneguya ctenopomae Fomena and Bouix, 1996	7.9	Fomena and Bouix (1996)
Henneguya cyprini Negm-Eldin, Govedich and Davies, 1999	7.10	Negm-Eldin, Govedich and Davies (1999)
Henneguya fusiformis Kostoïngue, Fall, Faye and Toguebaye, 1999	7.11	Kostoïngue, Fall, Faye and Toguebaye (1999)
Henneguya ghaffari Ali, 1999	7.12	Ali (1999)
Henneguya laterocapsulata Landsberg, 1987	7.13	Landsberg (1987)
Henneguya logonensis Kostoïngue, Diebakate, Faye and Toguebaye, 2001	7.14	Kostoïngue, Diebakate, Faye and Toguebaye (2001)
Henneguya mailaoensis Kostoïngue, Diebakate, Faye and Toguebaye, 2001	7.15	Kostoïngue, Diebakate, Faye and Toguebaye (2001)
Henneguya malapteruri Fomena and Bouix, 1996	7.16	Fomena and Bouix (1996)
Henneguya massi Kostoïngue, Diebakate, Faye and Toguebaye, 2001	7.17	Kostoïngue, Diebakate, Faye and Toguebaye (2001)
Henneguya mbakaouensis Fomena and Bouix, 2000	7.18	Fomena and Bouix (2000)
Henneguya mormyri Kostoïngue, Diebakate, Faye and Toguebaye, 2001	7.19	Kostoïngue, Diebakate, Faye and Toguebaye (2001)
Henneguya ntementis Fomena and Bouix, 1996	7.20	Fomena and Bouix (1996)
Henneguya nyongensis Fomena and Bouix, 1996	7.21	Fomena and Bouix (1996)
Henneguya odzai Fomena and Bouix, 1996	7.22	Fomena and Bouix (1996)
Henneguya samochimensis Reed, Basson and Van As, 2003	7.23	Reed, Basson and Van As (2003a)
Henneguya sarotherodoni Fall, Fomena, Kostoïngue, Diebakate, Faye and Toguebaye, 2000	7.24	Fall, Fomena, Kostoïngue, Diebakate, Faye and Toguebaye (2000)
Henneguya suprabranchiae Landsberg, 1987	7.25	Landsberg (1987)
Kudoa eleotrisi Siau, 1971	7.26a, b	Siau (1971)
Myxidium birgi Fomena and Bouix, 1986	7.27a, b	Fomena and Bouix (1986)
Myxidium bouixi Siau, 1971	7.28a, b	Siau (1971)
Myxidium brienomyri Fomena and Bouix, 1986	7.29a, b	Fomena and Bouix (1986)
Myxidium camerounensis Fomena and Bouix, 1986	7.30a, b, c	Fomena and Bouix (1986)
Myxidium distichodi Kostoïngue, Faye and Toguebaye, 1998	7.31	Kostoïngue, Faye and Toguebaye (1998)
Myxidium latesi Kostoïngue, Faye and Toguebaye, 1998	7.32	Kostoïngue, Faye and Toguebaye (1998)
Myxidium mendehei Fomena and Bouix, 1994	7.33a, b	Fomena and Bouix (1994)
Myxidium nyongensis Fomena and Bouix, 1986	7.34a, b	Fomena and Bouix (1986)
Myxidium petrocephali Fomena and Bouix, 1986	7.35 a, b	Fomena and Bouix (1986)
Myxidium schalli Ghaffer, Shahawi and Naas, 1995	7.36	Ghaffer, El-Shahawi and Naas (1995)
Myxidium schilba Ali, Sakran and Abdel-Baki, 1999	7.37	Ali, Sakran and Abdel-Baki (1999)
Myxidium shamama Ali, Sakran and Abdel-Baki, 1999	7.38	Ali, Sakran and Abdel-Baki (1999)
Myxobilatus accessobranchialis Obiekezie and Okaeme, 1987	7.39	Obiekezie and Okaeme (1987)
Myxobilatus synodontis Siau, 1971	7.40a, b, c	Siau (1971)
Myxobolus africanus Fomena, Bouix and Birgi, 1985	7.41	Fomena, Bouix and Birgi (1985)
Myxobolus agolus Landsberg, 1985	7.42	Landsberg (1985)
Myxobolus amieti Fomena, Bouix and Birgi, 1985	7.43	Fomena, Bouix and Birgi (1985)
Myxobolus bagri Negm-Eldin, Govedich and Davies, 1999	7.44	Negm-Eldin, Govedich and Davies (1999)

Table 7.1 continued. References to articles used for redrawing Africa freshwater myxosporean species. Species listed alphabetically.

Myxosporean species	Figure	Reference
Myxobolus beninensis Sakiti, Blanc, Marqués and Bouix, 1991	7.45	Sakiti, Blanc, Marqués and Bouix (1991)
Myxobolus bilongi Fomena, Marqués, Bouix and Njiné, 1994	7.46	Fomena, Marqués, Bouix and Njiné (1994)
Myxobolus brachysporus (Baker, 1963)	7.47	Baker (1963)
Myxobolus burkinei Kabré, Sakiti, Marqués and Sawadogo, 1995	7.48	Kabré, Sakiti, Marqués and Sawadogo (1995)
Myxobolus camerounensis Fomena, Marqués and Bouix, 1993	7.49	Fomena, Marqués and Bouix (1993)
Myxobolus chariensis Kostoïngue, Faye and Toguebaye, 1998	7.50	Kostoïngue, Faye and Toguebaye (1998)
Myxobolus chrysichtyi Negm-Eldin, Govedich and Davies, 1999	7.51	Negm-Eldin, Govedich and Davies (1999)
Myxobolus citharinopsi Kostoïngue, Faye and Toguebaye, 1998	7.52	Kostoïngue, Faye and Toguebaye (1998)
Myxobolus clarii Mandour, Galal and Abed, 1993	7.53	Mandour, Galal and Abed (1993)
Myxobolus comoei Kabré, Sakiti, Marqués and Sawadago, 1995	7.54	Kabré, Sakiti, Marqués and Sawadago (1995)
Myxobolus dahomeyensis Siau, 1971	7.55	Siau (1971)
Myxobolus distichodi Kostoïngue and Toguebaye, 1994	7.56	Kostoïngue and Toguebaye (1994)
Myxobolus dossoui Sakiti, Blanc, Marqués and Bouix, 1991	7.57	Sakiti, Blanc, Marqués and Bouix (1991)
Myxobolus equatorialis Landsberg, 1985	7.58	Landsberg (1985)
Myxobolus etsatsaensis Reed, Basson and Van As, 2002	7.59	Reed, Basson and Van As (2002a)
Myxobolus exiguus Thélohan, 1895	7.60	Fomena and Bouix (1997)
Myxobolus fotoi Fomena, Marqués and Bouix, 1993	7.61	Fomena, Marqués and Bouix (1993)
Myxobolus galileaus Landsberg, 1985	7.62	Landsberg (1985)
Myxobolus gariepinus Reed, Basson and Van As, 2003	7.63	Reed, Basson and Van As (2003a)
Myxobolus gandiolensis Fall, Fomena, Kostoïngue, Diebakate, Faye and Toguebaye, 2000	7.64	Fall, Fomena, Kostoïngue, Diebakate, Faye and Toguebaye (2000)
Myxobolus heterosporus (Baker, 1963)	7.65a, b, c	Baker (1963)
Myxobolus homeosporus Baker, 1963	7.66	Baker (1963)
Myxobolus hydrocyni Kostoïngue and Toguebaye, 1994	7.67	Kostoïngue and Toguebaye (1994)
Myxobolus israelensis Landsberg, 1985	7.68	Landsberg (1985)
Myxobolus kainjiae Paperna, 1973	7.69	Paperna (1973)
Myxobolus kriebiensis Fomena and Bouix, 1994	7.70	Fomena and Bouix (1994)
Myxobolus lates Negm-Eldin, Govedich and Davies, 1999	7.71	Negm-Eldin, Govedich and Davies (1999)
Myxobolus mailaoensis Kostoïngue, Faye and Toguebaye, 1998	7.72	Kostoïngue, Faye and Toguebaye (1998)
Myxobolus maraensis Kostoïngue, Faye and Toguebaye, 1998	7.73	Kostoïngue, Faye and Toguebaye (1998)
Myxobolus ndjamenaensis Kostoïngue, Faye and Toguebaye, 1998	7.74	Kostoïngue, Faye and Toguebaye (1998)
Myxobolus nilei Faisal and Shalaby, 1987	7.75	Faisal and Shalaby (1987)
Myxobolus niloticus Fahmy, Mandour and El-Naffar, 1971	No figure	Fahmy, Mandour and El-Naffar (1971)
Myxobolus njinei Fomena, Bouix and Birgi, 1985	7.76	Fomena, Bouix and Birgi (1985)
Myxobolus nkolyaensis Fomena and Bouix, 1994	7.77	Fomena and Bouix (1994)
Myxobolus nokoueensis Sakiti, Blanc, Marqués and Bouix, 1991	7.78	Sakiti, Blanc, Marqués and Bouix (1991)
Myxobolus nouensis Fomena and Bouix, 2000	7.79	Fomena and Bouix (2000)
Myxobolus nyongana Fomena, Bouix and Birgi, 1985	7.80	Fomena, Bouix and Birgi (1985)
Myxobolus oloi Fomena and Bouix, 1994	7.81	Fomena and Bouix (1994)
Myxobolus paludinosus Reed, Basson and Van As, 2002	7.82	Reed, Basson and Van As (2002a)
Myxobolus polycentropsi Fomena, Bouix and Birgi, 1985	7.83	Fomena, Bouix and Birgi (1985)
Myxobolus sarigi Landsberg, 1985	7.84	Landsberg (1985)
Myxobolus sarotherodoni Sakiti, Blanc, Marqués and Bouix, 1991	7.85	Sakiti, Blanc, Marqués and Bouix (1991)
Myxobolus stenosus Paperna, 1973	7.86	Paperna (1973)

Table 7.1 continued. References to articles used for redrawing Africa freshwater myxosporean species. Species listed alphabetically.

Myxosporean species	Figure	Reference
Myxobolus synodonti Fomena, Bouix and Birgi, 1985	7.87	Fomena, Bouix and Birgi (1985)
Myxobolus synodontis Negm-Eldin, Govedich and Davies, 1999	7.88	Negm-Eldin, Govedich and Davies (1999)
Myxobolus tilapiae Abolarin, 1974	7.89a, b	Abolarin (1974)
Myxobolus zillii Sakiti, Blanc Marqués and Bouix, 1991	7.90	Sakiti, Blanc, Marqués and Bouix (1991)
Sphaerospora melenensis Fomena, Marqués and Bouix, 1993	7.91a, b	Fomena, Marqués and Bouix (1993)
Sphaerospora sangmelimaensis Fomena and Bouix, 1994	7.92a, b	Fomena and Bouix (1994)
Sphaerospora tilapiae Fomena, Marqué and Bouix, 1993	7.93a, b	Fomena, Marqués and Bouix (1993)
Thelohanellus assambai Fomena, Marqués, Bouix and Njiné, 1994	7.94	Fomena, Marqués, Bouix, and Njiné (1994)
Thelohanellus citharini Kostoïngue, Fall, Faye and Toguebaye, 1999	7.95	Kostoïngue, Fall, Faye and Toguebaye (1999)
Thelohanellus ndjamenaensis Kostoïngue, Fall, Faye and Toguebaye, 1999	7.96	Kostoïngue, Fall, Faye and Toguebaye (1999)
Thelohanellus niloticus, (Gurley, 1893)	No figure	Gurley (1893)
Thelohanellus sanageansis Fomena, Marqués, Bouix and Njiné,1994	7.97a, b	Fomena, Marqués, Bouix and Njiné (1994)
Thelohanellus valeti Fomena and Bouix, 1987	7.98a, b, c	Fomena and Bouix (1987)
Unicauda strongylura (Gurley, 1893), [syn. *Henneguya strongylura* (Gurley, 1893) Labbé,1899]	7.99a, b	Fomena and Bouix (1997)

Table 7.2. References to articles used for redrawing Africa marine myxosporean species. Species listed alphabetically.

Myxosporean species	Figure	Reference
Alatospora africana Shulman, Kovaleva and Dubina, 1979	7.100a, b	Shulman, Kovaleva and Dubina (1979)
Alatospora dracoidea Shulman, Kovaleva and Dubina, 1979	7.101a-d	Shulman, Kovaleva and Dubina (1979)
Alatospora contrariocapsularia Shulman, Kovaleva and Dubina, 1979	7.102a-g	Shulman, Kovaleva and Dubina (1979)
Alatospora parvicapsula Shulman, Kovaleva and Dubina, 1979	7.103a-c	Shulman, Kovaleva and Dubina (1979)
Alatospora samaroidea Shulman, Kovaleva and Dubina, 1979	7.104a-e	Shulman, Kovaleva and Dubina (1979)
Bibteria admiranda Kovaljova, Zubchenko and Krasin, 1983	7.105	Kpatcha, Diebakate and Toguebaye (1996a)
Ceratomyxa acanthuri Kpatcha, Diebakate, Faye and Toguebaye, 1996	7.106	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Ceratomyxa australis Gaevskaya and Kovaleva, 1979	7.107	Gaevskaya and Kovaleva (1979)
Ceratomyxa fistulariae Kpatcha, Diebakate, Faye and Toguebaye, 1996	7.108	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Ceratomyxa lagocephali Kpatcha, Diebakate, Faye and Toguebaye, 1996	7.109	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Ceratomyxa shulmani Dubina and Isakov, 1976	7.110	Dubina and Isakov (1976)
Ceratomyxa syacii Kpatcha, Diebakate, Faye and Toguebaye, 1996	7.111	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Ceratomyxa trachinocephali Kpatcha, Diebakate, Faye and Toguebaye, 1996	7.112	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Ceratomyxa trichuiri Kpatcha, Diebakate, Faye and Toguebaye, 1996	7.113	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Ceratomyxa truncata Thélohan, 1895	7.114	Kpatcha, Diebakate, Faye and Toguebaye (1996b)
Davisia donecae Gaevskaya and Kovaleva, 1979	7.115a, b	Gaevskaya and Kovaleva (1979)
Henneguya brachydeuteri Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	7.116	Kpatcha, Faye, Diebakate, Fall and Toguebaye (1997)
Henneguya joalensis Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	7.117	Kpatcha, Faye, Diebakate, Fall and Toguebaye (1997)

Table 7.2 continued. References to articles used for redrawing Africa marine myxosporean species. Species listed alphabetically.

Myxosporean species	Figure	Reference
Henneguya. kayarensis Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	7.118	Kpatcha, Faye, Diebakate, Fall and Toguebaye (1997)
Henneguya lutjani Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	7.119	Kpatcha, Faye, Diebakate, Fall and Toguebaye (1997)
Henneguya. mbourensis Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	7.120	Kpatcha, Faye, Diebakate, Fall and Toguebaye (1997)
Henneguya ouakamensis Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	7.121	Kpatcha, Faye, Diebakate, Fall and Toguebaye (1997)
Henneguya priacanthi Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	7.122	Kpatcha, Faye, Diebakate, Fall and Toguebaye (1997)
Henneguya yoffensis Kpatcha, Faye, Diebakate, Fall and Toguebaye, 1997	7.123	Kpatcha, Faye, Diebakate, Fall and Toguebaye (1997)
Kudoa boopsi Kpatcha, Diebakate, Faye and Toguebaye, 1999	No figure	Kpatcha, Diebakate, Faye and Toguebaye (1999)
Kudoa thyristes (Gilchrist, 1924)	7.124a, b	Lom and Dyková (1992)
Leptotheca elongata Thélohan, 1895	7.125	Kpatcha, Diebakate and Toguebaye (1996a)
Leptotheca lutjani Kpatcha, Diebakate and Toguebaye, 1996	7.126	Kpatcha, Diebakate and Toguebaye (1996a)
Leptotheca pegusae Kpatcha, Diebakate and Toguebaye, 1996	7.127	Kpatcha, Diebakate and Toguebaye (1996a)
Myxidium abudefdufi Kpatcha, Diebakate and Toguebaye, 1996	7.128	Kpatcha, Diebakate and Toguebaye (1996a)
Myxidium elopsi Kpatcha, Diebakate and Toguebaye, 1996	7.129	Kpatcha, Diebakate and Toguebaye (1996a)
Myxidium giganteum Doflein, 1898	7.130	Kpatcha, Diebakate and Toguebaye (1996a)
Myxidium gigantissimum Dubina and Isakov, 1976	7.131	Dubina and Isakov (1976)
Myxobolus bizerti Bahri and Marques, 1996	7.132	Bahri and Marques (1996)
Myxobolus episquamalis Egusa, Maeno and Sorimachi, 1990 (possible junior synomym of *M. exiguus*)	7.133	Bahri and Marques (1996)
Myxobolus exiguus Thélohan, 1985	7.134	Bahri, Marques, Coste, Bouix and Hassine (1995)
Myxobolus goreensis Fall, Kpatcha, Diebakate and Toguebaye, 1997	7.135	Fall, Kpatcha, Diebakate, Faye and Toguebaye (1997)
Myxobolus hannensis Fall, Kpatcha, Diebakate and Toguebaye, 1997	7.136	Fall, Kpatcha, Diebakate, Faye and Toguebaye (1997)
Myxobolus hani Faye, Kpatcha, Diebakate, Fall and Toguebaye, 1999	7.137	Faye, Kpatcha, Diebakate, Fall and Toguebaye (1999)
Myxobolus ichkeulensis Bahri and Marques, 1996	7.138	Bahri and Marques (1996)
Myxobolus mugilis Negm-Eldin, Govedich and Davies, 1999	7.139	Negm-Eldin, Govedich and Davies (1999)
Myxobolus mülleri Bütschli, 1882	7.140	Fall, Kpatcha, Diebakate, Faye and Toguebaye (1997)
Myxobolus raibauti Fall, Kpatcha, Diebakate and Toguebaye, 1997	7.141	Fall, Kpatcha, Diebakate, Faye and Toguebaye (1997)
Myxobolus spinacurvatura Maeno, Sorimachi, Ogawa and Egusa, 1990	7.142	Bahri and Marques (1996)
Ortholinea basma Ali, 2000	7.143	Ali (2000)
Palliatus mirabilis Shulman, Kovaleva and Dubina, 1979	7.144	Shulman, Kovaleva and Dubina (1979)
Palliatus grandis Shulman, Kovaleva and Dubina, 1979	7.145	Shulman, Kovaleva and Dubina (1979)
Palliatus indecorus Shulman, Kovaleva and Dubina, 1979	7.146	Shulman, Kovaleva and Dubina (1979)
Sphaeromyxa balbiani Thélohan, 1892	7.147	Kpatcha, Diebakate and Toguebaye (1996a)
Unicapsula marquesi Diebakate, Fall, Faye and Toguebaye, 1999	7.148	Diebakate, Fall, Faye and Toguebaye (1999)
Zschokkella mugilidae Kpatcha, Diebakate and Toguebaye, 1996	7.149	Kpatcha, Diebakate and Toguebaye (1996a)