

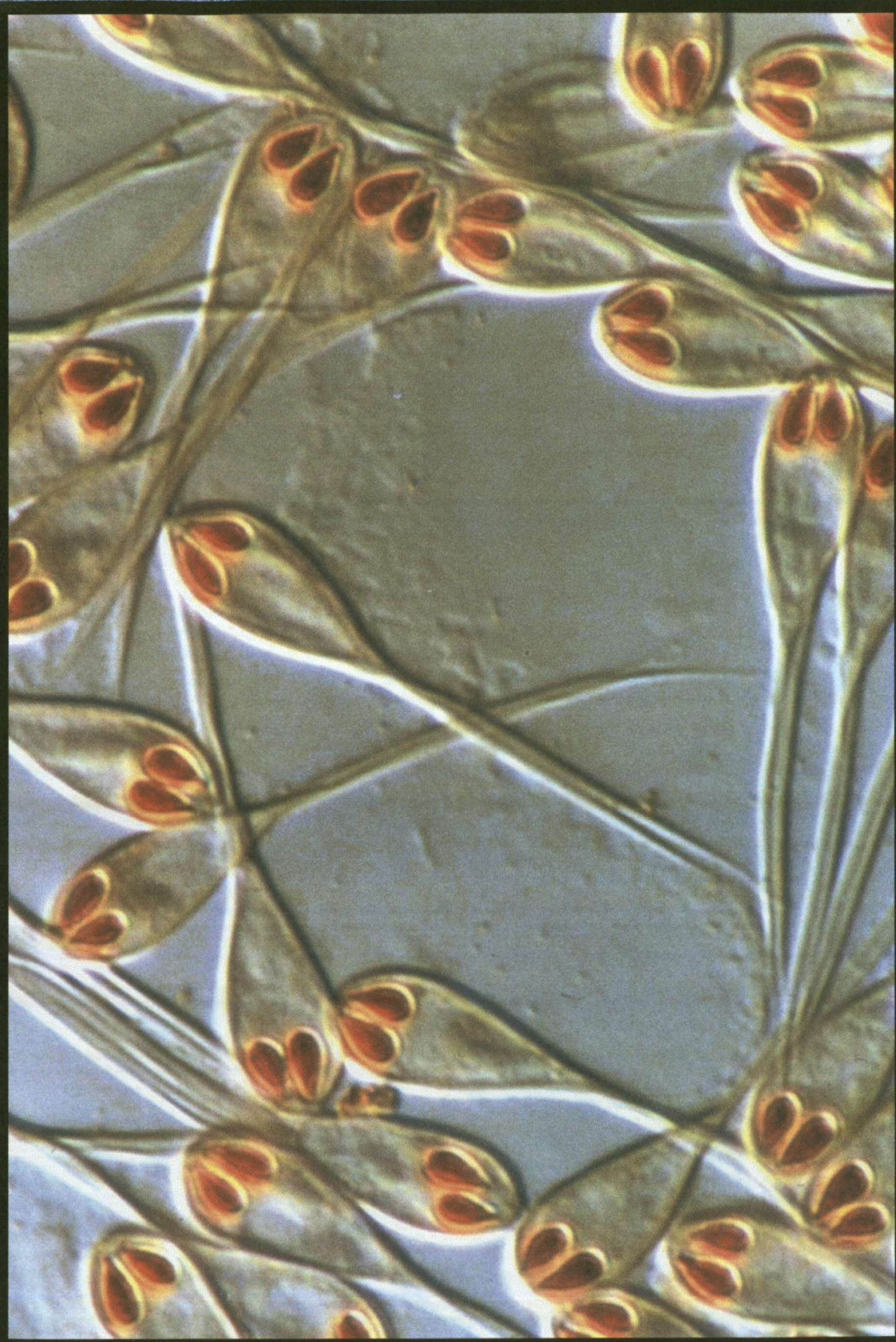
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**MYXOSPOREAN PARASITES
(MYXOZOA: MYXOSPOREA) INFECTING
FISHES IN THE OKAVANGO RIVER
SYSTEM, BOTSWANA**

by

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*Dissertation submitted in fulfilment of the requirements for the degree
Magister Scientiae in the Faculty of Natural and Agricultural Sciences
Department of Zoology and Entomology
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CHAPTER 1



Introduction

The Phylum Myxozoa Grassé, 1960 comprises an immensely diverse and intricate group of spore forming obligatory parasites, which have been intriguing scientists such as Thélohan (1892, 1895) and Gurley (1894) since the 19th century. First described during the 1830's, descriptions of new species and hosts have grown enormously through the years, as the pathogenic potential of these organisms was recognised (Bartholomew 1998). Today, 170 years later, there are well over 1300 species known throughout the world. The enormous species diversity and success of myxosporean parasites can most probably be attributed to the fact that they are able to infect just about any organ of the host that they parasitise. Although the majority of myxosporean parasites infect freshwater and marine teleosts, they have also been found in a few other vertebrate groups such as amphibians (Upton, Freed, Freed, McAllister & Goldberg 1992), elasmobranchs, myxines and lampreys (Lom & Dyková 1995). A number of myxosporean species have also been described from invertebrates such as a digenean (Overstreet 1976) as well as a freshwater bryozoan (Canning, Okamura & Curry 1996).

Myxosporeans are characterised by the formation of spores. These spores may vary greatly in size and shape and due to their small size and protozoan habits (Smothers, Von Dohlen, Smith & Spall 1994), myxosporeans have traditionally been classified in the Kingdom Protista. The characteristics of the spores have, however, always placed them in a unique position in this kingdom because they exhibit a degree of multicellularity and also contain nematocyst-like polar capsules (Lom & Dyková 1995), phenomena that are found in no other protistan group (Smothers *et al.* 1994). Furthermore, the Phylum Myxozoa had also until recently been considered to consist out of two classes, namely the Class Myxosporea Bütschli, 1882 and the Class Actinosporea Noble, 1980, with myxosporeans being mostly parasites of fish and actinosporeans mostly parasitising freshwater and marine oligochaetes (Kent, Margolis & Corliss 1994). An amazing discovery was made when Wolf and Markiw (1984) subsequently proved that extrapiscine development of a certain myxosporean takes place in an oligochaete alternate host, which acts as the site of development for the triactinomyxon stages that were previously attributed to the Class Actinosporea. Since this discovery a number of scientists have subsequently shown this alternating

life cycle for several myxosporean species. A few recent examples include El-Mansy and Molnar (1997), El-Mansy, Molnar and Székely (1998) and Molnar, El-Mansy, Székely and Baska (1998), all of which demonstrate actinosporean spores developing in oligochaetes, infecting fishes and after a complicated intrapiscine development producing myxosporean spores capable of infecting oligochaetes.

Current research on myxosporeans is thus centering on the interesting features of their biology, life cycle and especially their significance as pathogens in aquaculture industries (Lom & Dyková 1995). Some myxosporeans have an undeniable pathogenic incidence and can weaken or even kill the hosts they parasitise (Fomena, Marqués & Bouix 1993). *Myxobolus cerebralis* Hofer, 1903 is a well-known pathogenic myxosporean, causing "whirling disease" in salmonid fry (Lom & Dyková 1992) and has often caused extensive economic losses in trout industries throughout the world. Many myxosporean species are also known to cause large macroscopic 'cysts' or plasmodia and although in many cases not much host response is always elicited, the size of these plasmodia may result in a distortion of the organs of the host in which they occur.

In Africa approximately 100 species of myxosporeans are currently known to infect freshwater, brackish and marine fishes of which nine genera and 84 species are found in freshwater fishes. All of these species have been described from northern Africa with no valid species descriptions appearing from southern Africa. A fish farm in Cameroon recently revealed the presence of 10 myxosporean species that all held the potential to have serious pathogenic incidence in the fish stocks, weakening or even killing the hosts (Fomena *et al.* 1993). Since these pathogenic species had already been reported in Uganda (Baker 1963), Nigeria (Okaeme, Obiekezie & Lehman 1988) and even in the Middle East (Israel) (Landsberg 1985) it appears as if they are widely distributed throughout Africa. The available literature regarding African myxosporeans (see Chapter 2) reveals that the current known distribution of these parasites in Africa, merely reflects the location of scientists interested in them across the continent, rather than their actual distribution and biodiversity.

In southern Africa only a limited amount of work has been done on myxosporeans by authors such as Fantham (1919, 1930), Gilchrist (1924), Van Wyk (1968) and

Paperna, Hartely and Cross (1987). An indirect record of myxosporeans from Botswana was recorded by Peters (1971) (See Chapter 2). The present study on myxosporeans parasitising fish in Botswana is thus the first in a long time to be undertaken in southern Africa and the very first ever to be initiated in Botswana.

Botswana is a land locked country situated in southern Africa, surrounded by South Africa, Namibia, and Zimbabwe. Economically it is one of the strongest countries in Africa with its major source of income being from diamond mines and tourism. The people living in Botswana work largely on these diamond mines, in tourism industries or are involved in cattle farming. It might seem unexpected for a country falling mainly within the largest desert in the world, the Kalahari, with an average rainfall of 250-600 mm a year, that there is also a large proportion of the population dependant on fish for a living. This is because northwestern Botswana contains one of the world's largest inland deltas, formed by the Okavango River flowing in a southeasterly direction from Angola.

The fishes of the Okavango represent a valuable natural resource for the people of Botswana. In order to assure long-term survival for a sustainable fishery development it is essential to have thorough knowledge of the taxonomy, distribution, biology and ecology of the fish populations living in the Okavango. The effects of parasites and diseases on the fish populations also form an intricate part of this entire process. Scientists from the JLB Smith Institute of Ichthyology in Grahamstown, South Africa, conducted extensive surveys on the biology, ecology and taxonomy of the fish in the Okavango during the 1980's (Skelton 1993). No research has, however, been conducted on the presence, biodiversity and distribution of parasites infecting the fishes in the Okavango in Botswana. Mackenzie (1999) has suggested that there are good reasons to focus on parasites as indicators of the effects of pollutants on marine organisms. This could also be true for freshwater parasites since many species have delicate free living transmission stages, which are highly sensitive to environmental change. A reduction in their levels of infection will serve as early warning signs that changes are occurring. Alternately, other parasites are highly resistant and will respond to environmental change by increased levels of infection. This could essentially be used in determining the health status of the entire Okavango River and Delta.

In the light of this lack of knowledge on the fish parasite population in the Okavango, a project was proposed, under leadership of Prof. J. G. van As, from the Aquatic Parasitology Research Group, Department of Zoology and Entomology, University of the Free State, to investigate the presence, distribution and biodiversity of fish parasites in the Okavango River in Botswana. The project was initiated in 1997 and has already led to a number of scientific publications (Van As & Van As 1999, Smit, Davies & Van As 2000), a masters dissertation (Christison 1998) as well as a number of conference contributions (Christison & Van As 1999, Christison, Van As & Basson 1999, Christison, Reed, Smit, Basson & Jansen van Rensburg 1999, Jansen van Rensburg, Basson & Van As 1999, Reed & Van As 1999, Reed, Kruger, Van As & Basson 1999 and Van As, Van As & Basson 1999).

Due to the potential pathological nature of myxosporean fish parasites, the research into the biodiversity of these parasites infecting fishes in the Okavango forms an integral part of this larger project. The aims for this particular project involve the following:

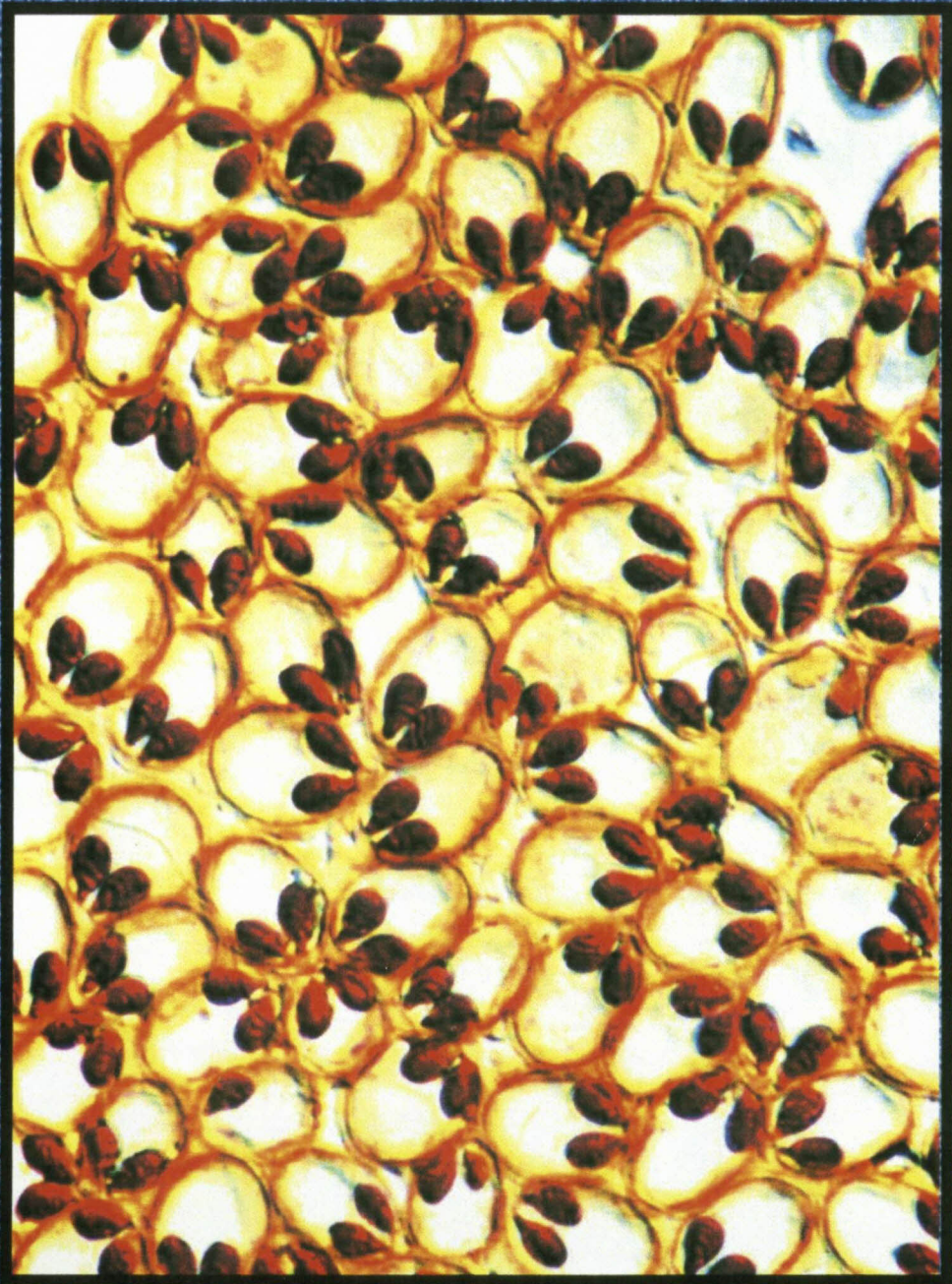
- *Investigate the available literature regarding African myxosporeans and compile a database of species occurring in freshwater fishes in Africa.*
- *Investigate the taxonomic status, species biodiversity and prevalence of myxosporean species in selected organs of the fishes occurring in the Okavango River system in Botswana.*
- *Establish a database of myxosporean parasites occurring on fishes in the region.*
- *Determine whether any myxosporean species infecting important commercial fishes may hold possible dangers for aquaculture industries.*

Following this short introduction to the myxosporeans (*Chapter 1*) a brief description of their biology, development, taxonomy and a review on the history of myxosporean research in Africa will be provided (*Chapter 2*). The importance of the Okavango River in Botswana will be discussed (*Chapter 3*) and will be followed by a description of the specific collection localities as well as the essential materials and methods used for this project (*Chapter 4*). Species from the genera *Henneguya* Thélohan, 1892 (*Chapter 4*) and *Myxobolus* Bütschli, 1882 (*Chapter 5*) collected

from the Okavango River in Botswana will be described, followed by a summary of the myxosporean/host relationships as well as the prevalence of these myxosporeans in Botswana (*Chapter 7*). A general discussion will follow (*Chapter 8*) after which a list of the literature cited for this project will be provided (*Chapter 9*) as well as the abstract and acknowledgements. *Appendix I* contains an essential glossary of terms used throughout the dissertation and *Appendix II* shows the permit for collection of fishes in Botswana.

from the Okavango River in Botswana will be described, followed by a summary of the myxosporean/host relationships as well as the prevalence of these myxosporeans in Botswana (*Chapter 7*). A general discussion will follow (*Chapter 8*) after which a list of the literature cited for this project will be provided (*Chapter 9*) as well as the abstract and acknowledgements. *Appendix I* contains an essential glossary of terms used throughout the dissertation and *Appendix II* shows the permit for collection of fishes in Botswana.

CHAPTER 2



The Phylum Myxozoa Grassé, 1960

The biology and characteristics of myxosporeans is very complex and unique. This chapter provides a background to the biology of the Phylum Myxozoa and also reviews the taxonomy as well as the history of myxosporean research in Africa.

BIOLOGY AND GENERAL CHARACTERISTICS

In the light of the discoveries that some myxosporeans have alternating actinosporean stages in the life cycle, Kent *et al.* (1994) propose to maintain the Phylum Myxozoa and suppress the Class Actinosporea, reducing the classes to one, namely Class Myxosporea, thus incorporating both life forms. Since this dissertation only deals with myxosporeans collected from fish hosts, the term myxosporean will be used throughout the dissertation.

Myxosporeans may be divided into two groups based on the site preference in the fish host where they occur. According to Lom and Dyková (1992) coelozoic species live in body cavities such as gall- or urinary bladders and histozoic species are found within various tissues. 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.

The formation of spores consequently indicates the infective stage of the myxosporean phase in the life cycle. The spore shapes of different species show remarkable variability and may range in size from 10-20 μ m. The same species inhabiting different organs in a single host may also show variation in size and occasionally in shape. The spores (Fig. 2.1) are of multicellular origin, surrounded by two, three or more shell valves and also contain one or more polar capsules. Next to the polar capsules is an amoeboid sporoplasm that is infective to the host. The shell valves join at a sutural plane that is either twisted or straight. These valves may have markings or be extended as pointed processes (Schmidt & Roberts 2000). The polar filaments may be described as hollow tubes, that are terminally closed and spirally twisted along their length, probably serving to attach to the hosts' intestinal surface

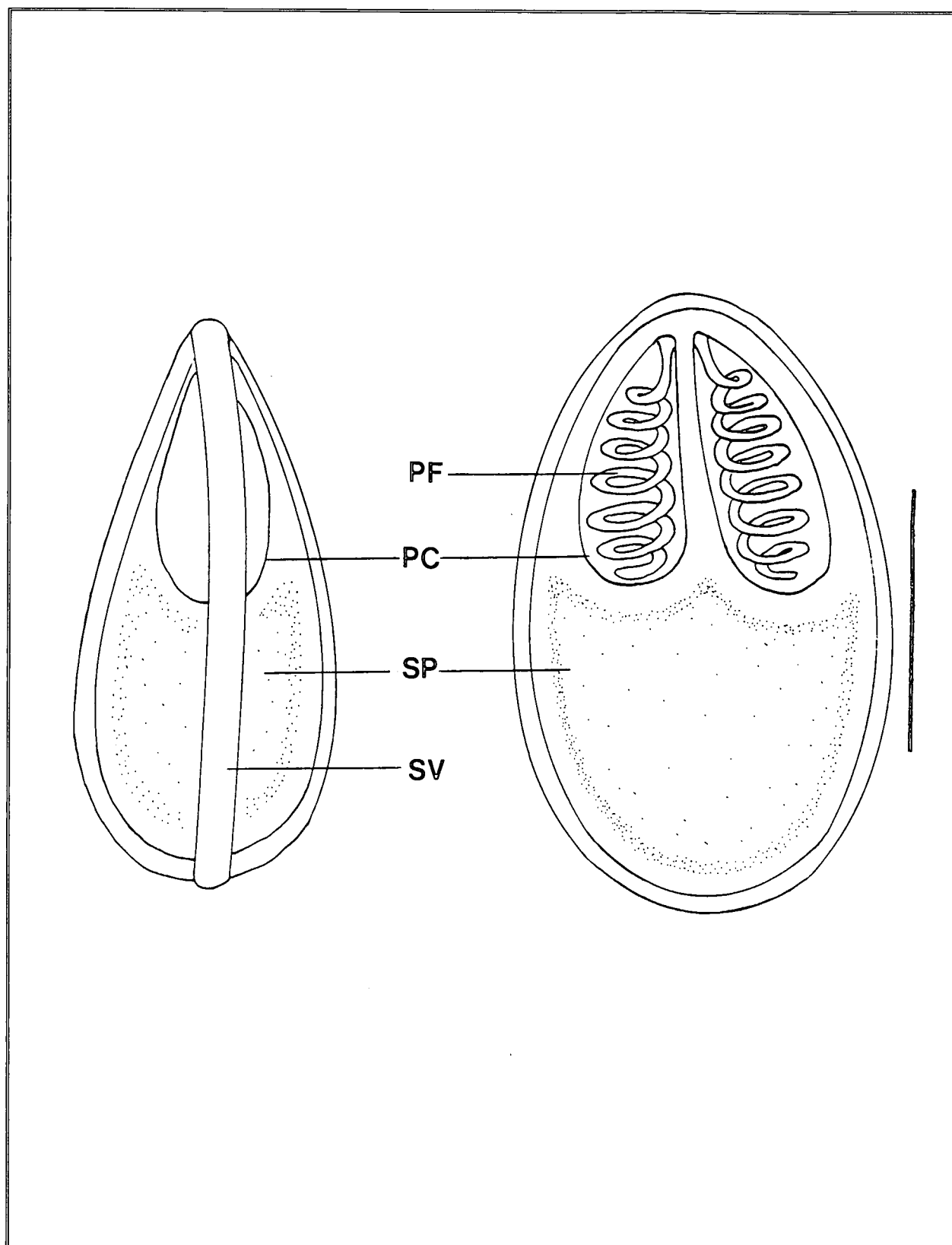


Figure 2.1: Diagrammatic representation of a myxosporean spore from the genus *Myxobolus* Butschli, 1882. **PC**-Polar capsule, **PF**-Polar filament, **SP**-Sporoplasm, **SV**-Shell valve. Scale bar: 10 μ m.

and helping to separate the shell valves in order to release the sporoplasm (Lom & Dyková 1992). The number of coils and configuration of the polar filaments are important taxonomic characteristics used in species classification.

MYXOSPOREAN DEVELOPMENT IN THE FISH HOST

(SUMMARISED FROM LOM & DYKOVÁ 1992)

While still within the spore, the two haploid nuclei of the sporoplasm fuse to form a synkaryon (Fig. 2.2A, B). If two uninucleate sporoplasms are present, both these and their nuclei fuse to form a zygote. The uninucleate amoebula arising from this fusion process is the only true 'protozoan' stage in the entire life cycle, because as further development takes place, the myxosporean becomes pluricellular. The development of this amoebula stage starts with growth and nuclear division, in which one of the daughter cells is enveloped by a sheet composed of cisternae of endoplasmic reticulum (Fig. 2.2C, D). This results in a secondary cell within the primary cell. From this primary cell or trophozoite, which encloses an inner secondary cell within a membrane bound vacuole, the organisation of all the subsequent extrasporogonic or sporogonic cycles are derived. The nucleus of the trophozoite, that is the vegetative nucleus, can produce many vegetative nuclei and the inner, generative cells, can also divide. These inner generative cells or secondary cells ensure the continuation of the next generation.

The further development of the trophozoites may follow one of two pathways, i. e., extrasporogonic development, that involves the proliferation of trophozoites in the hosts and which may result in heavy infections or sporogonic development that constitutes the development of the trophozoites to the eventual formation of the spores. The process of sporogonic development involves the plasmodia or trophozoites becoming encased within a fibroblast envelope and eventually appearing as large and often macroscopic structures often referred to as 'cysts'. According to Lom and Dyková (1995), sporogony of early and advanced stages in coelozoic species occurs simultaneously and in histozoic species, sporogony takes place in a synchronised way, so that all the spores reach maturity at the same time. The end result is a plasmodium packed full with mature spores.

The development of mature spores in the plasmodia or trophozoites may take place in one of two ways. In large plasmodial trophozoites spores may develop in pansporoblasts (Fig. 2.2G-J). Sporogenesis by means of pansporoblasts starts by the union of two generative cells (Fig. 2.2G), one of which, the pericyte, envelops the other, the sporogonic cell. The cell membranes persist and eventually the sporogonic cell is enclosed in a tightly fitting vacuole in the pericyte (Fig. 2.2H). The pericyte cell then divides, producing two cells of the pansporoblast envelope, which actively mediates the flow of nutrition to the developing sporogonic cell (Fig. 2.2I). Binary fission of the latter gives rise to the sporoblast cells, which include the valvogenic cells forming the spore shell valves, capsulogenic cells forming the polar capsules and sporogonic cells forming the sporoplasm (Fig. 2.2J-L). Pansporoblasts are mostly disporic, but occasionally these may be monosporic.

In some cases the development of spores may take place directly. In the case pseudoplasmodia in some genera with one vegetative nucleus, sporogony begins simply by the production of a number of cells sufficient to compose one or two spores within the pseudoplasmodium cell. During sporogenesis, sporoblast cells assume their predetermined roles, namely, valvogenic cells spreading thinly around the sporoplasmic and capsulogenic cells. The cell membrane is thickened from beneath with non-keratinous proteins and the cytoplasm shrinks into a dense mass and the cell becomes a shell valve.

LIFE CYCLE AND TRANSMISSION

A direct mode of transmission was always 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 undergoes autogamy to produce the only uninucleate stage in the life cycle. This cell then migrates to the final site of infection and eventually develops mature spores (Bartholomew 1998). According to Bartholomew (1998) this interpretation could not be demonstrated under laboratory conditions and had thus always been rather controversial.

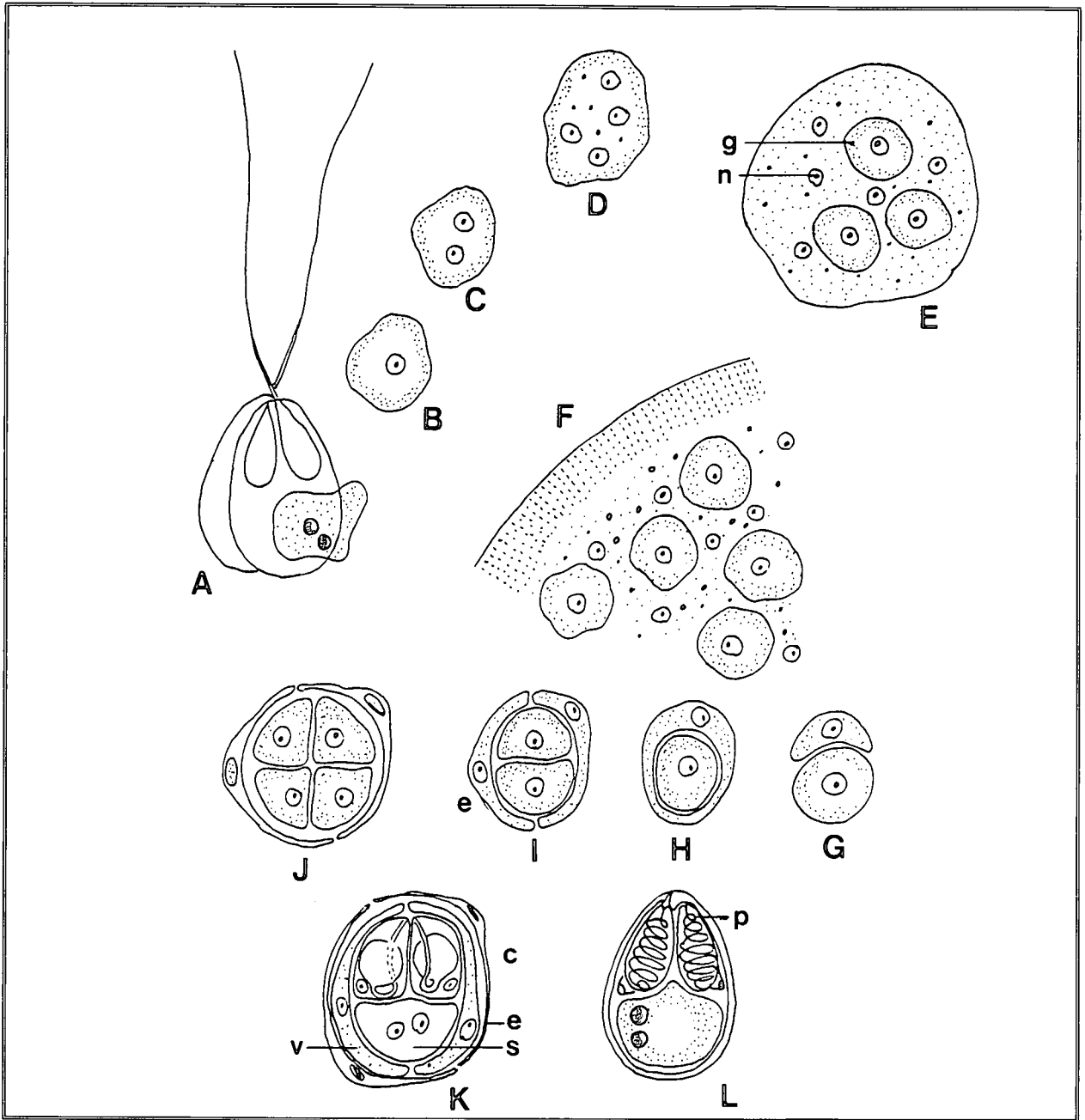


Figure 2.2: Diagram illustrating myxosporean development in the fish host for the genus *Myxobolus* Bütschli, 1882. **A**-Hatching of the sporoplasm, **B**-Sporoplasm after autogamy, **C**, **D**, **E**-growth and proliferation of the generative cells (**g**) and vegetative nuclei (**n**), **F**-Part of a mature polysporic plasmodium, **G**-**J**-Formation of pansporoblast arising from the union of a pericyte and sporogonic cell, **K**-Pansporoblast with a sporoblast **L**-Mature spore. **e**-pericyte degraded into a pansporoblast envelope, **v**-valvogenic cell, **c**-capsulogenic cell, **s**-sporoplasmic cell, **p**-polar filament [Redrawn from Lom & Dyková (1992)].

Wolf and Markiw (1984) were investigating the life cycle of *Myxobolus cerebralis* when they discovered that this particular myxosporean had an actinosporean (Fig. 2.3), parasitising an oligochaete, as an alternating life form. The importance of this discovery, as mentioned in Chapter 1, was that myxosporeans and actinosporeans had traditionally been classified together in the Phylum Myxozoa as two separate classes, thus the discovery that they are alternating life forms, has had far reaching effects.

The life cycle of *Myxobolus cerebralis*, according to Wolf and Markiw (1984) was proposed as presented in Figure 2.4. 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 branchial route. This is when the myxosporean phase begins. After three to four months the myxosporean stage is complete with mature spores 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 (Wolf & Markiw 1984).

The life cycle of PKX, an organism that causes Proliferative Kidney Disease (PKD) in salmonid fish which was identified as a myxosporean parasite (Kent & Hendrick 1985) was until recently unknown. Anderson, Canning and Okamura (1999) then discovered similarities between the 18S-rDNA sequence of myxosporeans infecting North American bryozoans and PKX, suggesting that several species of bryozoans act as hosts for PKX for at least part of its life cycle. Seasonal growth of bryozoans coincides with the outbreaks of PKD, while the widespread occurrence is also consistent with the development of PKD in fisheries receiving water from rivers, lakes and reservoirs.

The life cycle strategies of myxosporeans do not end here. Diamant (1997) reported a direct fish to fish transmission for a marine myxosporean. His reports indicated that the myxosporean is transmitted between fish via the ingestion of infected fish tissue and through water borne contamination.

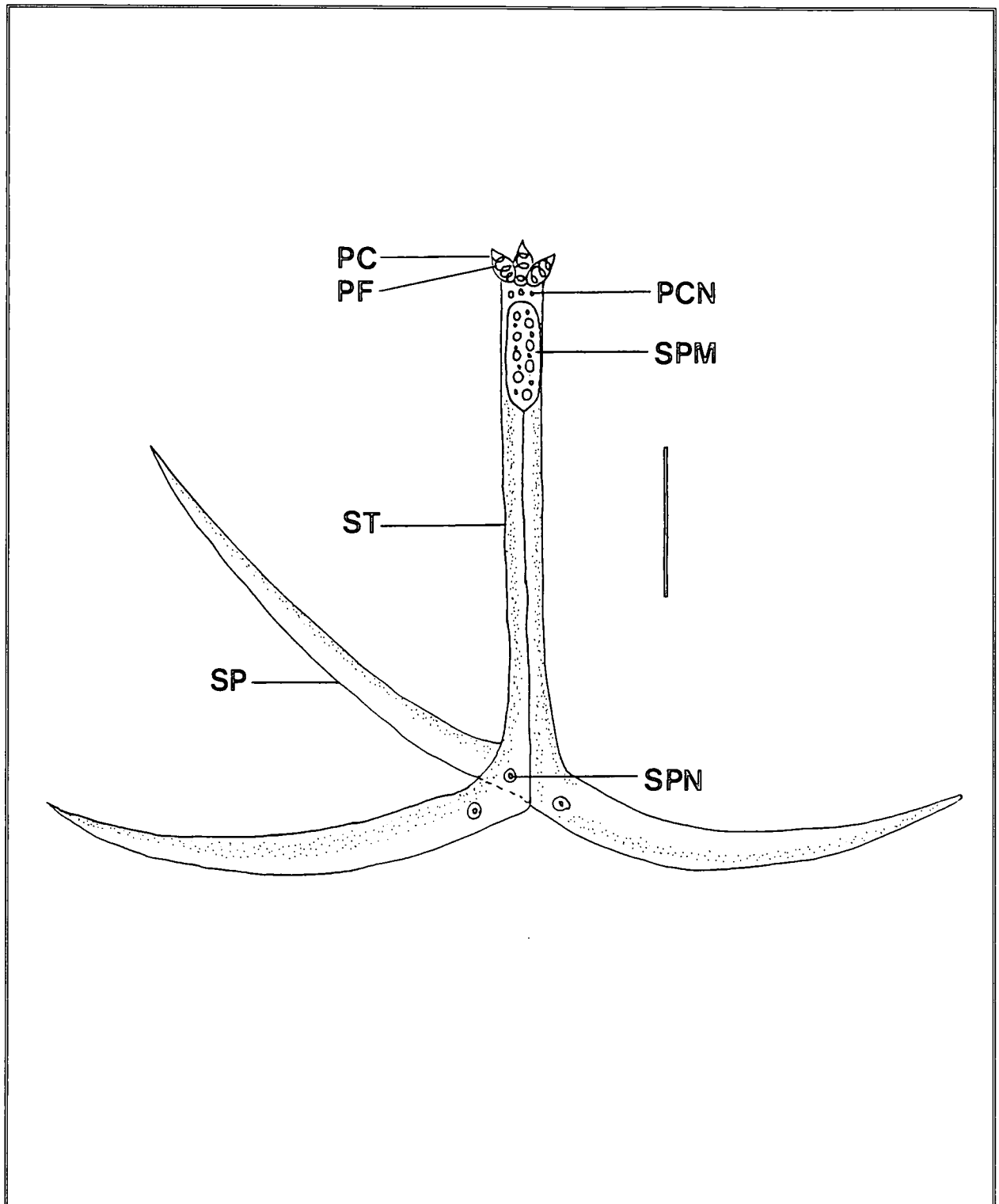


Figure 2.3: Schematic line drawing of a waterborne spore of the genus *Triactinomyxon* Stolc, 1899. **PC**-Polar capsules, **PF**-Polar filaments, **PCN**-Polar capsule nuclei, **SPM**-Sporoplasmic mass, **SP**-Spore process, **ST**-Style, **SPN**-Spore process nucleus [Redrawn from Xiao & Desser (1998)]. Scale bar: 10 μ m.

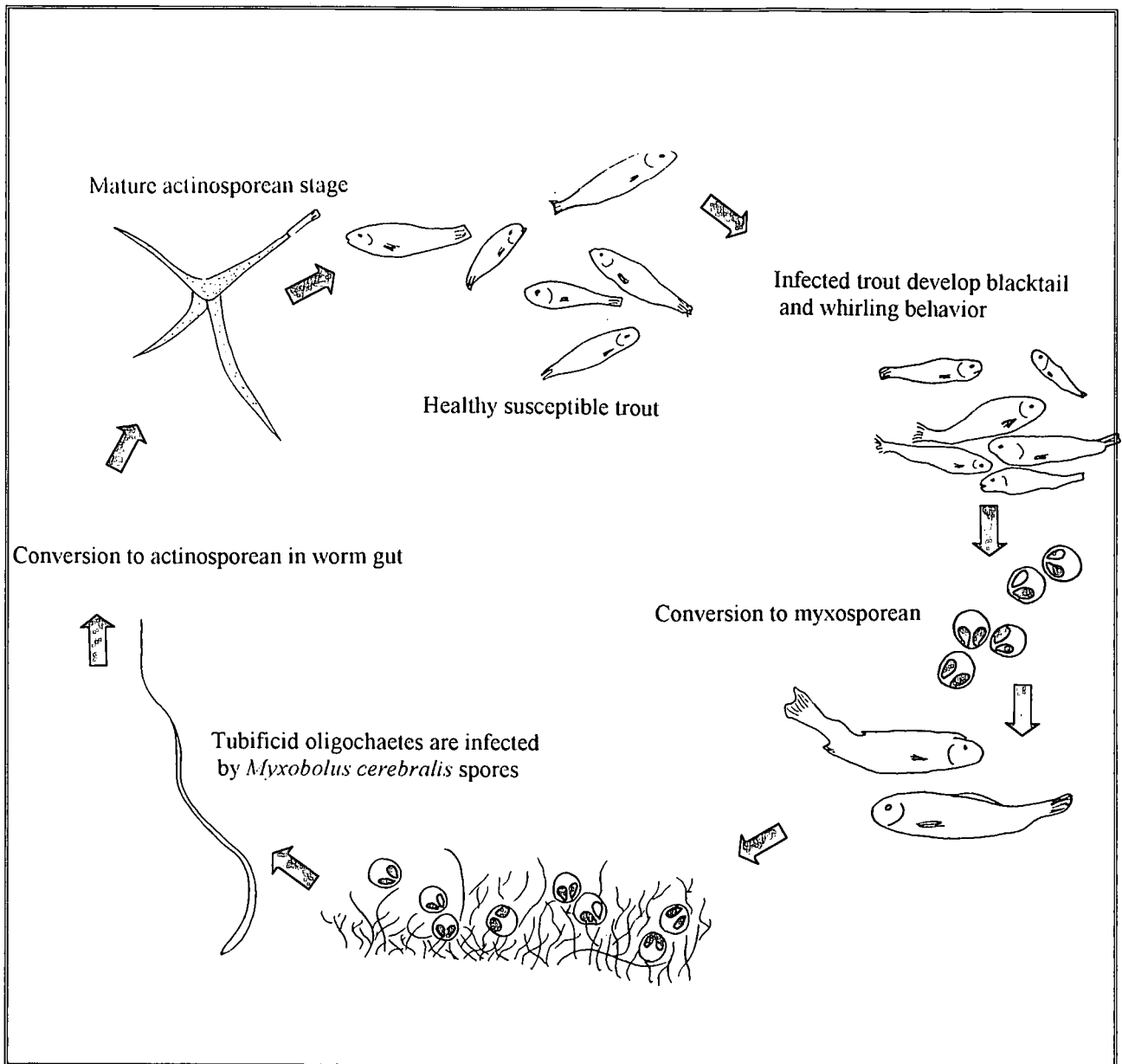


Figure 2.4: Diagram illustrating the life cycle of *Myxobolus cerebralis* Hofer 1903.

Clockwise from the bottom centre: Spores of *M. cerebralis* infect tubificid oligochaetes and initiate the actinosporean phase. At 12°C and 3 to 4 months later conversion to the actinosporean is nearly complete as multiple parasite plasmodia mature in the worm gut. Young salmonids ingest the worms or waterborne *Triactinomyxon* infects the fish via the gut or branchial route and the myxosporean phase begins. At 1 to 1.5 months the fish show signs of "whirling disease", at 3 to 4 months the myxosporean phase is complete with maturation in the cartilage of spores of *M. cerebralis* [Adapted from Wolf & Markiw (1984)]

PATHOLOGY

It appears as if, during their evolution, myxosporeans have struck a balanced host-parasite equilibrium because even though they are known to infect just about any organ of the hosts, relatively few are known to cause serious or fatal infections (Lom & Dyková 1995). Certain species do, however, directly damage their hosts by causing pathological changes, some decrease fitness by reducing fecundity and others reduce the market value of the fish (Bartholomew 1998). In most cases host reactions elicited are mostly cell and tissue reactions that are not necessarily aimed at the destruction of the host. If the parasite develops in an atypical site, a much more pronounced tissue response is provoked (Lom & Dyková 1995).

Unfortunately myxosporean infections have often been the cause of serious economical losses in fish aquaculture industries. Reasons for myxosporean parasites causing problems in culture situations could be, as with most other fish parasites, that the fish are kept in artificial habitats and usually in large numbers, consequently raising their stress levels and thus making them more susceptible to disease. Several well-known or infamous diseases in fish farming and aquaculture facilities are attributed to myxosporean infections.

A very widespread disease such as salmonid “whirling disease”, which is caused by *Myxobolus cerebralis*, has been known for many decades to cause great damage to the culture of rainbow trout in many countries in Europe and subsequently in North America. Originally described from Germany, the disease was first reported in the USA in the late 1950's and has since spread to 21 states housing trout populations (Bergesen & Anderson 1997). The parasite is found within the cartilage of the fish, where it results in a very serious disease of the skeleton, causing deformation of the cartilage and a subsequent whirling behavior in the fish (Hoffman 1963).

Proliferative Kidney Disease (PKD), infecting rainbow trout in North America and Europe, has resulted in annual losses of £640 000 in the United Kingdom alone (Lom & Dyková 1992). The parasite is found within the kidney interstisium, from where it penetrates into the tubular lumen where it starts sporogenesis, without ever producing mature spores. Visible symptoms include a bulging abdomen due to hypertrophic kidneys as well as anemia (Lom & Dyková 1992).

Davies, Andrews, Upton & Matthews (1998) reported that gobies infected with a myxosporean from the genus *Kudoa* Meglitsch, 1947 experienced muscle loss while the fish were still alive. This is unusual because myxosporeans from the genus *Kudoa* are typically histozoic parasites of teleost fish that are associated with post-mortem myoliquefaction of the tissue. The subsequent result of such myxosporean infections, is a reduction of the market value of infected fish products (Moran, Whitaker & Kent 1999).

TAXONOMY

The taxonomy of myxosporeans has been under scrutiny for almost as long as the group has been discovered. Increased interest in myxosporeans, combined with ever improving technology has resulted in dramatic taxonomic changes taking place over the past 15 years (Bartholomew 1998).

As mentioned previously, myxosporeans have traditionally been classified together with other protozoans in the Kingdom Protista. Phylum Myxozoa, comprising the classes, Myxosporea and Actinosporea with myxosporeans parasitising fish and other cold-blooded vertebrates and actinosporeans mostly parasitising freshwater and marine oligochaetes (Kent *et al.* 1994). Although actinosporeans were originally described at the turn of the 20th century (Bartholomew 1998), they do not represent nearly as many described species as the myxosporeans. The reason for this is most probably due to the fact that myxosporean parasites of fish were investigated to a much greater extent as a result of the importance of fish in fish farms and aquaculture situations throughout the world.

The taxonomy of myxosporeans is based almost exclusively on the morphology of the spores, due to difficulty in distinguishing different vegetative stages of various species. The Class Myxosporea is divided into two orders, based on different spore characteristics, i.e the Bivalvulida Shulman, 1959 (spores with two shell valves and one to four polar capsules) and Multivalvulida Shulman, 1959 (spores with three to seven shell valves and one to seven polar capsules) (Lom & Dyková 1995). The entire class consists out of three suborders, 17 families and 48 genera (See Table 2. 1, compiled from Lom & Dyková 1992).

Table 2.1: Classification of the Class Myxosporea Bütschli, 1881 [Compiled from Lom & Dyková (1992)]

Phylum:	Myxozoa Grassé, 1960
Class:	Myxosporea Bütschli, 1881
Order:	Bivalvulida Shulman, 1959
Suborder I:	Sphaeromyxina Lom and Noble, 1984
Family:	Sphaeromyxidae Lom and Noble, 1984
Genus:	<i>Sphaeromyxa</i> Thélohan, 1892
Suborder II:	Variisporina Lom and Noble, 1984
Family:	Myxidiidae Thélohan, 1892
Genus:	<i>Myxidium</i> Buetschli, 1882
	<i>Zschokkella</i> Auerbach, 1910
	<i>Coccomyxa</i> Léger and Hesse, 1907
Family:	Ortholineidae Lom and Noble, 1984
Genus:	<i>Ortholinea</i> Shulman, 1962
	<i>Neomyxobolus</i> Chen and Hsieh, 1960
	<i>Triangula</i> Chen and Hsieh, 1984
Family:	Sinuolineidae Shulman, 1959
Genus:	<i>Sinuolinea</i> Davis, 1917
	<i>Davisia</i> Laird, 1953
	<i>Myxoproteus</i> Doflein, 1898 (syn. <i>Conispora</i> Sankurathri, 1977)
	<i>Bipteria</i> Kovaleva, Zubchenko and Krasin, 1983
	<i>Paramyxoproteus</i> Wierzbicka, 1986
	<i>Neobipteria</i> Kovaleva, Gaevskaya and Krasin, 1986
	<i>Shulmania</i> Kovaleva, Zubchenko and Krasin, 1983
	<i>Noblea</i> Kovaleva, 1989
Family:	Fabesporidae Naidenova and Zaika, 1969
Genus:	<i>Fabespora</i> Naidenova and Zaika, 1969
Family:	Ceratomyxidae Doflein, 1899
Genus:	<i>Leptotheca</i> Thélohan, 1895
	<i>Ceratomyxa</i> Thélohan, 1892
	<i>Meglitschia</i> Kovaleva, 1988
Family:	Sphaerosporidae Davis, 1917
Genus:	<i>Sphaerospora</i> Thélohan, 1892 (syn. <i>Podospora</i> Chen and Hsieh, 1984)
	<i>Hoferellus</i> Berg, 1898 (syn. <i>Mitraspora</i> Fujita, 1912)
	<i>Wardia</i> Kudo, 1919
	<i>Palliatius</i> Kovaleva and Dubina, 1979
	<i>Myxobilatus</i> Davis, 1944
Family:	Chloromyxidae Thélohan, 1892
Genus:	<i>Chloromyxum</i> Mingazzini, 1890
	<i>Caudomyxum</i> Bauer, 1948

Table 2.1 continued: Classification of the Class Myxosporea Bütschli, 1881 [Compiled from Lom & Dyková (1992)].

	<i>Agarella</i> Dunkerly, 1915
Family:	Auerbachiiidae Evdokimova, 1973
Genus:	<i>Auerbachia</i> Meglitsch, 1960
	<i>Globospora</i> Lom, Noble and Laird, 1975
Family:	Alatosporidae Shulman, Kovaleva and Dubina, 1979
Genus:	<i>Alatospora</i> Shulman, Kovaleva and Dubina, 1979
	<i>Pseudoalatospora</i> Kovaleva and Gaevskaya, 1983
Family:	Parvicapsulidae Shulman, 1953
Genus:	<i>Parvicapsula</i> Shulman, 1953
Suborder III:	Platysporina Kudo, 1919
Family:	Myxobolidae Thélohan, 1892
Genus:	<i>Myxobolus</i> Bütschli, 1882 (syn. <i>Myxosoma</i> Thélohan, 1892; <i>Lentospora</i> Plehn, 1905; <i>Facieplatycauda</i> Wyatt, 1979 and <i>Rudicapsula</i> Kalvati and Narasimhamamurti, 1984)
	<i>Phlogospora</i> Quadri, 1962
	<i>Laterocaudata</i> Chen and Hsieh, 1984
	<i>Henneguya</i> Thélohan, 1892
	<i>Hennegoides</i> Lom, Tonuthai and Dyková, 1991
	<i>Tetrauronema</i> Wu, Wang and Jiang, 1988
	<i>Thelohanelius</i> Kudo, 1933
	<i>Neothelohanelius</i> Das and Haldar, 1986 (syn. <i>Lomosporus</i> Gupta and Khera, 1988)
	<i>Neohenneguya</i> Tripathi, 1953
	<i>Trigonosporus</i> Hoshina, 1952
Order:	Mutivalvulida Shulman, 1959
Family:	Trilosporidae Shulman, 1959
Genus:	<i>Trilospora</i> Noble, 1939
	<i>Uncapsula</i> Davis, 1924 (syn. <i>Pileispora</i> Naidenova and Zaika, 1970; <i>Parapilei spora</i> Naidenova and Zaika, 1970)
Family:	Kudoidae Meglitsch, 1960
Genus:	<i>Kudoa</i> Meglitsch, 1947 (syn. <i>Tetraspina</i> Xie and Chen, 1988)
Family:	Pentacapsulidae Naidenova and Zaika, 1970
Genus:	<i>Pentacapsulidae</i> Naidenova and Zaika, 1970
Family:	Hexacapsulidae Shulman, 1959
Genus:	<i>Hexacapsula</i> Arai and Matsumoto, 1953
Family:	Septemcapsulidae Hsieh and Chen, 1984
Genus:	<i>Septemcapsula</i> Hsieh and Chen, 1984

According to Tripathi (1948), the first classification of myxosporeans was given by Thélohan (1892, 1895) and was, as it is today, based largely on spore characteristics. Various authors such as Gurley (1894) and Doflein (1899, 1901) viewed their ideas after Thélohan. Auerbach (1910) produced a monograph in which he discussed the three main groups of the cnidosporidia, namely the "myxosporidien, actinosporidien

and the microsporidien". In this monograph Auerbach provided a comprehensive taxonomic and literature review on the three groups compiling the cnidosporidians.

Approximately two years later in 1912 Parisi also provided a classification system and based it solely on spore characteristics, dividing the suborders according to the microhabitat of the parasite. This classification system was not accepted by Kudo (1920), who then provided his own version, which he later modified in 1933. According to Tripathi (1948), Kudo divided the order Myxosporidia into suborders and families based on the following:

- Suborders were separated according to the relation of the sutural axis to the greatest diameter of the spore.
- Different characteristics were used for families such as habitat (coelozoic or histozoic), number of polar capsules, position of polar capsules and presence or absence of polar capsules.

Tripathi (1948) provided his own classification system also based on spore characteristics. He concentrated on the two different types of spores that are found, namely, those spores that have one to four polar capsules together or near the anterior end of the spore and those that have two widely separated polar capsules, one at each end. These characters were, according to him, suitable for separating sub-orders. For the separation of families he decided to use the number of polar capsules.

After a number of years Lom and Noble (1984) provided a revision of the classification of the Class Myxosporea, following the main lines proposed by Levine, Corliss, Cox, Deroux, Grain, Honigberg, Leedale, Loeblich, Lom, Lynn, Merinfeld, Page, Polyansky, Sprague, Vávra and Wallace (1980) who incorporated Schulman's (1966) system for the class Myxosporea. According to Lom and Noble (1984) the Class Myxosporea along with the class Actinosporea had, at that time together become widely recognized as an independent Phylum Myxozoa.

During the same year Wolf and Markiw (1984) provided the evidence that salmonid "whirling disease" may be caused by an actinosporean produced in an oligochaete. As already mentioned, experimental results indicated that instead of being separate

classes in the Phylum Myxozoa, that some myxosporeans and actinosporeans are actually alternating life forms of a single organism.

After the discovery of the alternating life forms of some myxosporeans and actinosporeans, Kent *et al.* (1994) proposed a taxonomic and nomenclatural revision for the protistan Phylum Myxozoa. Since they had established indisputable evidence that confirmed the existence of a two-host life cycle for some myxosporeans, it was necessary to revise their classification, thus Kent *et al.* (1994) proposed, amongst others, the following:

- Firstly to maintain the Phylum Myxozoa, to suppress the class Actinosporea, reducing the myxosporean classes to one.
- To conditionally retain the remaining actinosporean stages, until the alternate myxosporean stages are identified and to refer to the oligochaete host, in which actinosporean development occurs as the alternate host for myxosporeans.

The taxonomic implications of discovering that many myxosporeans and actinosporeans may be alternating stages in a single life cycle resulted in some serious re-thinking of the classification system. This was, however, not the end of the taxonomic troubles for the group. Myxosporeans had still been considered to fall within the Sub-Kingdom Protozoa until Smothers *et al.* (1994) provided molecular evidence that myxosporeans are in actual fact metazoans. Thus, although myxosporeans have protozoan habits and size, they also exhibit a degree of multicellularity and cell differentiation which is found in no other protistan group (Smothers *et al.* 1994). Examples of these complexities included the similarities between polar capsules and cnidarian nematocysts (Weill 1938), as well as cellular differentiation, with the desmosome-like structures between shell valve cells in which they appear to be some primitive non-cnidarian animal lineage (Grassé & Lavette 1978).

In order to try and establish some sort of answer regarding these uncertainties of myxosporean origins, Smothers *et al.* (1994) determined the sequences of small-subunit (18S) ribosomal RNA's (rRNAs) for five myxosporean species in three different genera to solve the phylogenetic position according to molecular evidence.

The results indicated the position of the myxosporeans as metazoan lineages were entirely supported by both parsimony and neighbor-joining analysis (Fig. 2.5). They also found no evidence that myxosporeans and cnidarians share a recent, common, evolutionary history, but that the origins appear to date later in metazoan phylogeny, more closely to the appearance of bilateral animals.

Also working on the phylogeny of myxosporeans, Siddall, Martin, Bridge, Desser and Cone (1995) proposed that the revisions to the systematics of the myxosporeans was not yet complete, stating that the phylum be abandoned because its origins do lie in a group of parasitic cnidarians. Their analysis of the full-length 18S rRNA genes from 23 taxa resulted in a single most-parsimonious cladogram. In this cladogram three myxosporean genera were found to be a monophyletic sister group to a cnidarian parasite. Analysis of the partial sequences returned two most parsimonious trees, again with the myxosporeans as a sister group to the cnidarian parasite and with an overall unlikely paraphyletic relationship for the phylum Cnidaria. Analysis of the data set which combined characters from aligned partial sequences as well as morphological characters resulted in two equally parsimonious cladograms, that supported a monophyletic Phylum Cnidaria within which the myxosporeans were a sister group to the cnidarian parasite. The final analysis resulted in a single tree, which also includes the monophyletic Cnidaria with the myxosporeans as a sister group. In conclusion, Siddall *et al.* (1995) suggested that the existence of a planula stage or a free-swimming medusoid should not be ruled out, since sexuality had already been documented amongst the myxosporeans.

Discoveries in the past century regarding the biology and life cycles of myxosporeans have revealed many unanswered questions that need to be addressed. There is thus still much to be done regarding the sorting of the taxonomy of myxosporeans. Bartholomew (1998) recorded that several independent phylogenetic analyses by a number of scientists have indicated that myxosporeans have roots within the animal kingdom, but although protozoan affinities are no longer defended, the precise relationship of myxosporeans with the other metazoan groups still remains to be controversial.

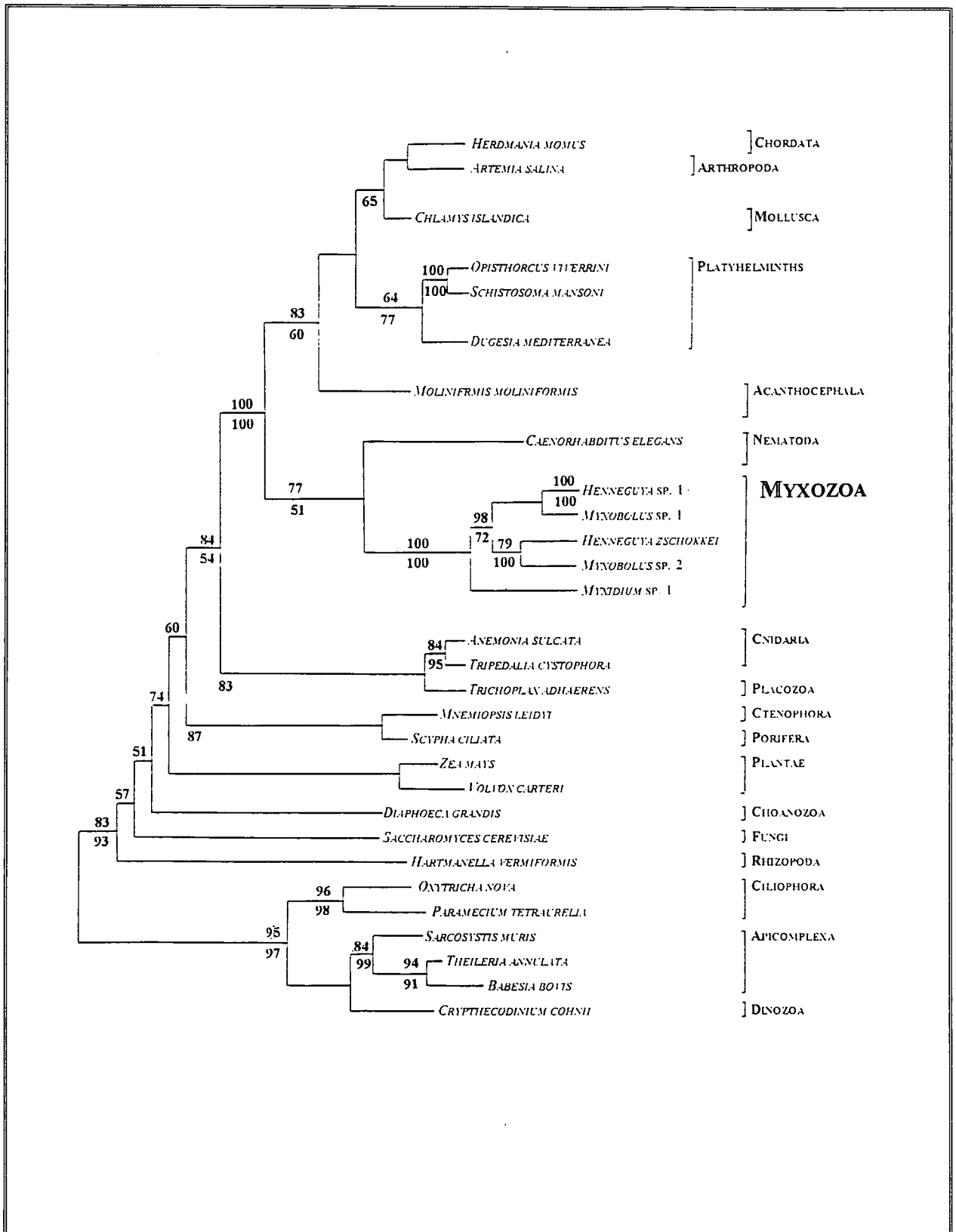


Figure 2.5: Phylogenetic position of myxosporeans amongst representative eukaryote groups as inferred from 18S ribosomal RNA sequences [Redrawn from Smothers, Von Dohlen, Smith & Spall (1994)]

THE HISTORY OF MYXOSPOREAN RESEARCH IN AFRICA

Myxosporean research in Africa dates back to the late 19th century with authors such as Gurley (1893) being one of the earliest records referring to the continent. Having approximately 100 myxosporean species known from freshwater, brackish and marine fishes throughout the African continent and of which approximately 84 infect primarily freshwater fishes (Table 2.2) (Fomena & Bouix 1997), this number is continuously growing. When comparing this number to the more than 1300 species described throughout the world, 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. To date research has been carried out in the following countries: Benin, Burkina-Faso, Cameroon, Chad, Egypt, Ghana, Morocco, Nigeria, Senegal, Tunisia, Uganda and even a very limited number in South Africa (Fomena & Bouix 1997) (Fig. 2.6).

Early in the twentieth century, Fantham (1919) recorded various marine myxosporeans from the south coast of South Africa. In his observations he recorded species from the genus *Myxidium* Bütschli, 1882 in the bile of a number of the intertidal rock pool fishes. He also mentioned a species from the genus *Hoferellus* Berg, 1898 that was found in the kidney of intertidal pool fishes. Most of his work was done at St. James Bay and Kalk Bay situated on the south coast of South Africa.

At the same time of Fantham's research, Gilchrist (1924) was investigating the occurrence of a myxosporean infecting the Cape sea fish or 'snoek'. He described a species infecting the muscles of this fish as *Chloromyxum thyristes* Gilchrist, 1924 and recorded the flesh of the fishes infected with this myxosporean, becoming soft and liquid resulting in the phenomenon been known as 'pap snoek'. This species has subsequently been relocated in the genus *Kudoa* and is now *Kudoa thyristes* (Gilchrist, 1924).

Fantham (1930) again recorded some myxosporeans from the same marine environments as before, but in addition he also investigated some freshwater fish in the northern parts of South Africa. He described *Leptotheca obovalis* Fantham, 1930, *Sphaerspora subelegans* Fantham, 1930, *Myxidium cortutum* Fantham, 1930,

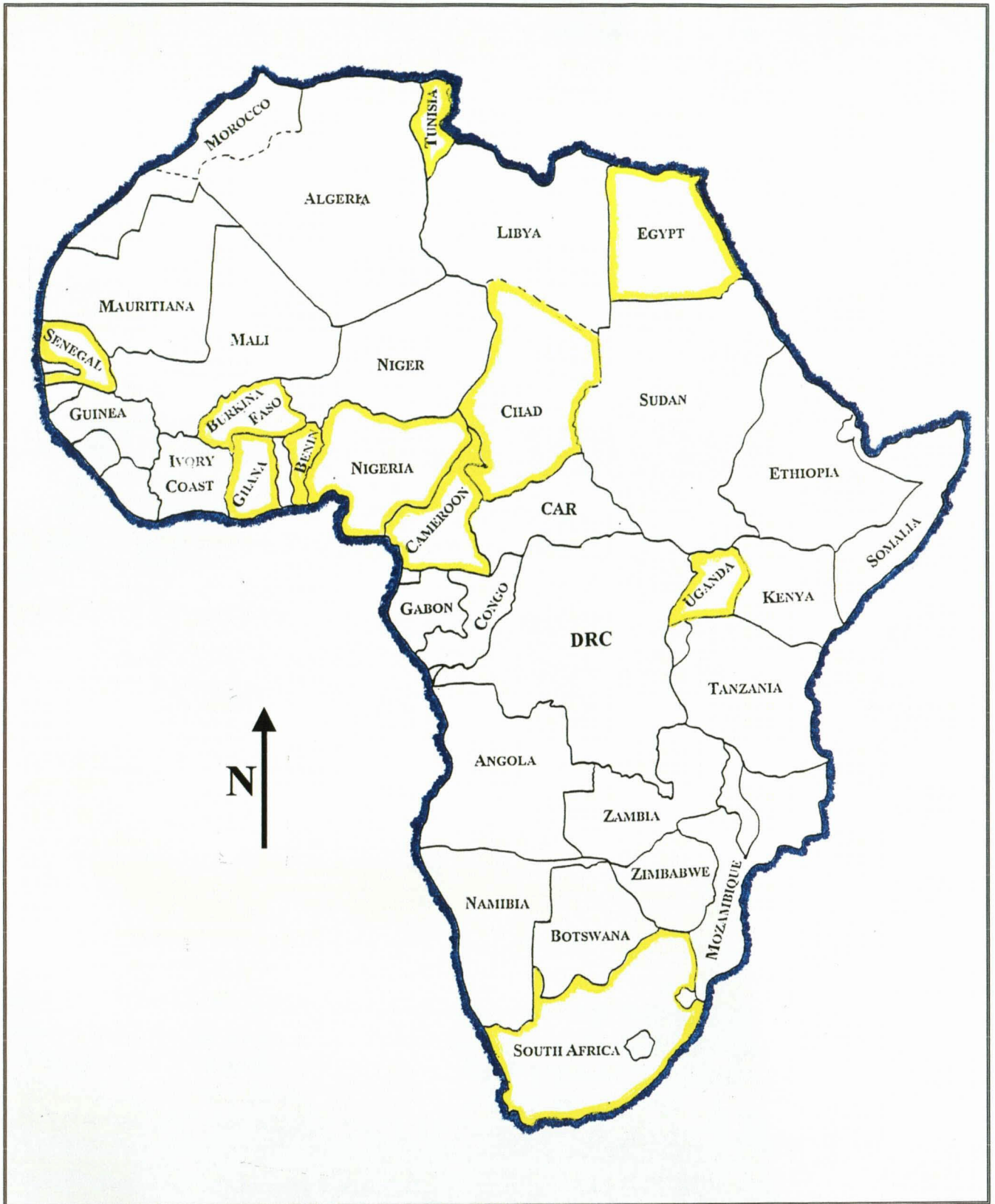


Figure 2.6: Map of Africa illustrating the countries where most myxosporean research has been conducted (**DRC**-Democratic Republic of the Congo, **CAR**-Central African Republic)

M. pagelli Fantham, 1930, *M. parvoviforme* Fantham, 1930, *Sphaeromyxa arcuata* Fantham, 1930, *S. curvula* Fantham, 1930 and *Myxobolis ovoidalis* Fantham, 1930 from a number of marine intertidal fish species. He also noted the presence of some *Myxobolus* Bütschli, 1882 species in a few barbel as well as in *Cyprinus carpio*. Insufficient information and illustrations make it difficult to re-identify the species he described.

The next thirty years passed without any apparent publications appearing on myxosporeans in Africa. The first paper to appear after this time was that of Baker (1963) who worked in Uganda, not on myxosporeans but on the blood parasites of fishes in Lake Victoria. Whilst investigating the blood parasites of these fishes he came across some myxosporean infections in the internal organs. From this material he was able to describe three myxosporeans from the genus *Myxobolus*.

Van Wyk (1968) recorded the presence of salmonid whirling disease in trout farms in the Cape Province in South Africa and three years later, Fahmy, Mandour and El-Naffar (1971) described *Myxobolus niloticus* Naffar, 1971 from *Labeo niloticus*, from the Nile River in Assuit, Egypt.

The only publication from southern Africa during the seventies was that of Peters (1971), commenting on Boulenger (1911) who published a brief note on an anabantid from the Okavango River showing a mouth brooding habit. 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 apparently look like eggs, and discovered that they were in actual fact a myxosporean infection.

In Nigeria, Abolarin (1971a) described the pathological effects of a new species of myxosporean infecting the West African catfish. This species, *Hennegyua clariae* Abolarin, 1971, appeared to be one of the first records of this genus in Africa. In this paper Abolarin also provided a review of the genus *Hennegyua* Thélohan, 1882 and later that same year, Abolarin (1971b) recorded a preliminary study of myxosporeans

from Nigerian fishes. In this paper he reported the same species described by Gurley (1893), suggesting only that the species should be moved to another genus. Siau (1971) also described several new species from Benin.

In 1973, Paperna surveyed the presence of some myxosporeans in Ghana and East Africa. No new species were described, but a list of myxosporeans found infecting the examined fishes was provided. In 1974, Abolarin described a new species, *Myxobolus tilapiae* Abolarin, 1974, from three fish species in Nigeria. A year later, Fahmy, Mandour and El- Naffar (1975), published the results of a survey conducted by them, on the myxosporeans collected from the River Nile at Assuit province, Egypt. To end this very productive decade of the seventies, Schulman, Kovaleva and Dubina (1979) described some marine myxosporeans found infecting fishes along the Atlantic coast of northern Africa.

Myxosporean research in North Africa had clearly begun to take shape by the 1980's. Fomena, Bouix and Birgi (1985) investigated the occurrence of myxosporeans in Cameroon and in their first paper regarding this investigation, they described approximately 10 new myxosporean species from the genus *Myxobolus*. During the following year Fomena and Bouix (1986) concentrated on species from the genus *Myxidium*. Fishes belonging to four families were found infected with five new species from the genus *Myxidium*. In three years these authors contributed substantially to the knowledge on the distribution and occurrence of myxosporeans in freshwater fishes in Cameroon.

With the expansion of tilapia cultures in Egypt during the 1980s, Faisal and Shalaby (1987) investigated myxosporean species from the genus *Myxobolus* that were most commonly associated with disease conditions in wild *Oreochromis niloticus*. At the same time in South Africa, Paperna *et al.* (1987) investigated the ultrastructure of the plasmodium of *Myxidium giardi* Cépède, 1906 and its attachment to the epithelium of the urinary bladder of the eel *Anguilla mossambica*.

Concentrating on myxosporean infections in cultured estuarine catfish, *Chrysichthys nigrodigitatus*, in Nigeria, Obiekezie and Enyenihi (1988), described *Henneguya chrysichthys* Obiekezie and Enyenihi, 1988 from the gills of this fish and also

histopathologically examined the host reactions elicited by the infection. Increased interest in the infections of cultured fish in North Africa led to myxosporean species being described by Ashmawy, Abu-Elwafa, Imam and El-Otifi (1989) from Egypt. These included two species from the genus *Myxobolus* and two from the genus *Henneguya* infecting both *Tilapia* and *Clarias* spp. in the Nile River in the Behera Province, Egypt.

Interest in myxosporean parasites in African fish increased dramatically during the 1990's, with research becoming more detailed, involving not only mere species descriptions, but pathological effects and ultrastructural aspects of infections. The 1990's began with an investigation of myxosporeans in cultured *Tilapia* in Nigeria. Obiekezie and Okaeme (1990) identified 10 species from the genus *Myxobolus*, of which six were reported for the first time from Nigerian fishes including two new species. Sakiti, Blanc, Marqués and Bouix (1991) described six new species from the genus *Myxobolus* and also recorded the presence of three other known species from the same genus in Lake Nokoue, Benin.

Obiekezie and Schmahl (1993) described the ultrastructure of the parasite-host interface of *Henneguya laterocapsulata* Landsberg, 1987 infecting cultured hybrid African catfish from Nigeria. Fomena *et al.* (1993) examined *Oreochromis niloticus* from a fish farm in Cameroon and revealed the presence of 10 myxosporean species from the genera *Myxobolus* and *Sphaerospora* Thélohan, 1892 of which four were recorded as new species.

Also in Cameroon, Fomena and Bouix (1994) described a further six new species from freshwater teleosts. During the same year, the first myxosporean publication from Chad appeared. Kostoingue and Toguebaye (1994) surveyed 242 Chadian freshwater fish belonging to 35 genera and identified seven *Myxobolus* species, of which three were reported as being new species. Alyain, Soheir, El-Menyawe and Mahmoud (1994) revised some protozoan infections in Nile Catfish in Upper Egypt, including a number of myxosporeans species, which had previously been recorded from Egypt.

Mazen (1994) recorded the pathological effects of *Myxobolus heterosporus* (Baker, 1963) on the eye of the fish *Oreochromis niloticus*, which is an economically important fish species in many African countries. Ghaffar, Aziz, El-Shahawi and Naas (1994) published light and electron micrographs of a *Myxobolus* sp. infecting *O. niloticus* and *Oreochromis aureus* in the Nile River. Ghaffar, El-Shahawi and Naas (1995) also reported on myxosporeans infecting other economically important fish species in the Nile River at Giza Governorate, Egypt.

The recent publications from Egypt as well as from other countries suggested that the focus of research has moved to economically important fish species. Scientists in these countries had apparently recognized the economical importance of myxosporeans and thus the need to investigate their presence in important aquaculture fish species.

Kpatcha, Diebakate and Toguebaye (1996) examined 1630 fish belonging to 37 families and 51 genera caught off the coast of Senegal in West Africa. From these they established the presence of nine myxosporean species of which five were reported to be new. During the same year Kpatcha, Diebakate, Faye and Toguebaye (1996) also described various new myxosporean species from the genus *Ceratomyxa* Thélohan, 1895 from a number of marine fishes caught along the coast of Senegal. Bahri and Marqués (1996) recorded four species from the genus *Myxobolus* from *Mugil cephalus* in the Ichkeul Lagoon in northern Tunisia.

Fomena and Bouix (1996a, b) described new species from the genus *Henneguya* from freshwater fishes in Cameroon and in the following year produced a very valuable key to the myxosporeans infecting freshwater fishes in Africa (Fomena and Bouix 1997). Paperna (1997) provided an overview of a few myxosporeans infecting fishes from common families, such as Cichlidae, Cyprinidae and Mugilidae from various African countries. He also discussed the geographic range, taxonomy, life cycle, biology and pathology of myxosporeans in Africa.

Kostoïngue, Faye and Toguebaye (1998) described new myxosporean species from the genera *Myxidium* and *Myxobolus* from freshwater fishes in Chad. Ali (1998) provided light and electron micrographs of *Chloromyxum vanasi* Ali, 1998 infecting

the Nile catfish. During the following year, Faye, Kpatcha, Diebakate, Fall and Toguebaye (1999) published on myxosporean gill infections in fishes from Senegal and also described a new species from the genus *Myxobolus*. Diebakate, Fall, Faye and Toguebaye (1999) described *Unicapsula marquesi* Diebakate, Fall, Faye and Toguebaye, 1999 from the gills of *Polydactylus quadrifilis* from the Senegalese coast in West Africa. Kostoingue, Fall, Faye and Toguebaye (1999) again described three new myxosporean species from Chad and Kpatcha, Diebakate, Faye and Toguebaye (1999) also provided light and electron microscopy of a new species, *Kudoa boopsi* Kpatcha, Diebakate, Faye and Toguebaye, 1999 a gill parasite of *Boops boops* from the coast of Senegal.

Interest in myxosporean parasites through the years in Africa has not been confined to fish hosts. Upton *et al.* (1992) investigated testicular myxosporidiasis in the flat-backed toad from Cameroon. In another publication, McAllister and Freed (1996) discovered a new host and geographic record for *Myxidium lesminteri* Delvinquier, Markus and Passmore, 1992 in the stripe-burrowing frog, *Tomopterna cryptotis*, in Namibia. This was one of the few papers to appear from southern Africa through the decades.

Table 2.2: Myxosporeans infecting freshwater fish in Africa. Species are arranged in alphabetical order [Compiled from Fomena & Bouix (1997)]

Species	Fish species	Organ	Country	Reference
GENUS THELOHANELLUS KUDO, 1933				
<i>Thelohanellus assambai</i> Fomena, Marqués, Bouix & Njiné, 1994	<i>Labeo</i> sp	Gills & Fins	Cameroon	Fomena, Marqués, Bouix, & Njiné (1994)
<i>Thelohanellus citharini</i> Kostoingue, Fall, Faye & Toguebaye, 1999	<i>Citharinus citharinus</i>	Heart	Chad	Kostoingue, Fall, Faye & Toguebaye (1999)*
<i>Thelohanellus niloticus</i> , (Gurley, 1893)	<i>Labeo niloticus</i>	Skin	Nile River (Egypt)	Gurley (1893)
<i>Thelohanellus sanageansis</i> Fomena, Marqués, Bouix & Njiné 1994	<i>Labeo</i> sp	Gills & fins	Cameroon	Fomena, Marqués, Bouix, & Njiné (1994)
<i>Thelohanellus valeti</i> Fomena & Bouix, 1987	<i>Barbus aspilus</i> , <i>B. jae</i>	Operculum & stomach wall	Nyong Basin (Cameroon)	Fomena & Bouix (1987)
GENUS MYXIDIUM BÜTSCHLI, 1882				
<i>Myxidium birgi</i> Fomena & Bouix, 1986	<i>Aphyosemion splendopleure</i>	Gall Bladder	Mouanko (Cameroon)	Fomena & Bouix (1986)
<i>Myxidium bouixi</i> Siau, 1971	<i>Synodontis ansorgii</i>	Gall bladder	Porto Nova Lagoon (Benin)	Siau (1971)
<i>Myxidium brienomyri</i> Fomena & Bouix, 1986	<i>Brienomyrus brachyistus</i>	Gall Bladder	Nyong Basin (Cameroon)	Fomena & Bouix (1986)
<i>Myxidium camerounensis</i> Fomena & Bouix, 1986	<i>Neolebias ansorgei</i>	Gall Bladder	Mouanko (Cameroon)	Fomena & Bouix (1986)
<i>Myxidium distichodi</i> Kostoingue, Faye & Toguebaye, 1998	<i>Distichodus engycephalus</i>	Gall bladder	Chad	Kostoingue, Faye & Toguebaye (1998)*
<i>Myxidium latesi</i> Kostoingue, Faye & Toguebaye, 1998	<i>Lates niloticus</i>	Gall bladder	Chad	Kostoingue, Faye & Toguebaye (1998)*
<i>Myxidium mendehei</i> Fomena & Bouix, 1994	<i>Barbus guirali</i> , <i>B. martorelli</i>	Kidneys	Nyong Basin (Cameroon)	Fomena & Bouix (1994)
<i>Myxidium nyongensis</i> Fomena & Bouix, 1986	<i>Barbus aspilus</i> , <i>B. jae</i> , <i>B. guirali</i> , <i>B. martorelli</i> , <i>B. camptacanthus</i>	Gall bladder	Nyong & Sangana Basins (Cameroon)	Fomena & Bouix (1986)
<i>Myxidium petrocephali</i> Fomena & Bouix, 1986	<i>Petrocephalus simus</i>	Gall bladder	Nyong basin (Cameroon)	Fomena & Bouix (1986)
<i>Myxidium schalli</i> Ghaffer, Shahawi & Naas, 1995	<i>Synodontis schall</i>	Gall bladder	Giza Governorate (Egypt)	Ghaffer, El-Shahawi & Naas (1995)
GENUS SPHAEROSPORA THELOHAN, 1892				
<i>Sphaerospora melenensis</i> Fomena, Marqués & Bouix, 1993	<i>Oreochromis niloticus</i>	Kidneys	Yaounde (Cameroon)	Fomena, Marqués & Bouix (1993)
<i>Sphaerospora sangmelimaensis</i> Fomena & Bouix, 1994	<i>Petrocephalis simus</i> , <i>Brienomyrus brachyistus</i> , <i>Hepsetus odoe</i>	Kidneys	Nyong & Lobo Basins (Cameroon)	Fomena & Bouix (1994)
<i>Sphaerospora tilapiae</i> Fomena, Marqué & Bouix, 1993	<i>Oreochromis niloticus</i>	Kidneys & spleen	Yaounde Cameroon	Fomena, Marqués & Bouix (1993)

Table 2.2 continued: Myxosporeans infecting freshwater fish in Africa. Species are arranged in alphabetical order [Compiled from Fomena & Bouix (1997)].

Species	Fish species	Organ	Country	Reference
GENUS MYXOBILATUS DAVIS, 1944				
<i>Myxobilatus accessobrachialis</i> Obiekezie & Okaeme, 1987	<i>Heterobranchius bidorsalis</i>	Accessory breathing organ	New Busa (Nigeria)	Obiekezie & Okaeme (1987)
<i>Myxobilatus synodontis</i> Siau, 1971	<i>Synodontis ansorgii</i>	Gills	Djassin (Benin)	Siau (1971)
GENUS MYXOBOLUS BUTSCHLI, 1882				
<i>Myxobolus africanus</i> Fomena, Bouix & Birgi, 1985	<i>Hepsetus odoe</i>	Gills	Nyong, Sanaga Basins (Cameroon)	Fomena, Bouix & Birgi (1985)
<i>Myxobolus agolus</i> Landsberg, 1985	<i>Oreochromis aureus</i> × <i>O. niloticus</i> , <i>O. niloticus vulcani</i>	Kidneys & spleen	Israel	Landsberg (1985)
	<i>Sarotherodon galilaeus</i> , <i>Oreochromis niloticus</i> , <i>Tilapia guinensis</i>	Kidneys & spleen	Cross River State & New Busa (Nigeria)	Obiekezie & Okaeme (1990)
	<i>Oreochromis niloticus</i>	Kidneys & spleen	Yaounde (Cameroon)	Fomena, Marqués & Bouix (1993)
	<i>Hemichromis fasciatus</i>	Gills	Yaounde (Cameroon)	Fomena, Bouix & Birgi (1985)
<i>Myxobolus amieti</i> Fomena, Bouix & Birgi, 1985	<i>Ctenopoma nanum</i>	Gills, eyes & muscles	Nyong Basin (Cameroon)	Fomena, Bouix & Birgi (1985)
<i>Myxobolus beninensis</i> Sakiti, Blanc, Marqués & Bouix, 1991	<i>Sarotherodon melanotheron</i>	Gills	Lake Nokou (Benin)	Sakiti, Blanc, Marqués & Bouix (1991)
<i>Myxobolus bilongi</i> Fomena, Marqués, Bouix & Njiné, 1994	<i>Labeo</i> sp.	Gills & fins	Cameroon	Fomena, Marqués, Bouix & Njiné (1994)
<i>Myxobolus brachysporus</i> (Baker, 1963)	<i>Tilapia esculenta</i> , <i>T. variabilis</i>	Spleen	Lake Victoria (Uganda)	Baker (1963)
	<i>Oreochromis niloticus</i> , <i>Sarotherodon galilaeus</i> , <i>Tilapia guinensis</i> , <i>O. niloticus</i> × <i>S. galilaeus</i>	Kidneys & spleen	Cross River State (Nigeria)	Obiekezie & Okaeme (1990)
	<i>Oreochromis niloticus</i>	Kidneys & spleen	Yaounde (Cameroon)	Fomena, Marqués & Bouix (1993)
<i>Myxobolus burkinei</i> Kabré, Sakiti, Marqués & Sawadogo, 1995	<i>Labeo coubie</i>	Gills & fins	Burkina Faso	Kabré, Sakiti, Marqués & Sawadogo (1995)
<i>Myxobolus camerounensis</i> Fomena, Marqués & Bouix, 1993	<i>Oreochromis niloticus</i>	Gills, eyes & muscles	Yaounde (Cameroon)	Fomena, Marqués & Bouix (1993)
<i>Myxobolus chariensis</i> Kostoingue, Faye & Toguebaye, 1998	<i>Brycinus macrolepidotis</i>	Gills	Chad	Kostoingue, Faye & Toguebaye (1998)*
<i>Myxobolus citharinopsi</i> Kostoingue, Faye & Toguebaye, 1998	<i>Citharinops distichoides</i>	Gills	Chad	Kostoingue, Faye & Toguebaye (1998)*
<i>Myxobolus clarii</i> Mandour, Galal & Abed, 1993	<i>Clarias lazera</i>	Testis	Assuit (Egypt)	Mandour, Galal & Abed (1993)
<i>Myxobolus comoei</i> Kabré, Sakiti, Marqués & Sawadogo, 1995	<i>Clarias angullaris</i>	Gills	Comoe & Kompienga Dam (Burkina Faso)	Kabré, Sakiti, Marqués & Sawadogo (1995)

Table 2.2 continued: Myxosporeans infecting freshwater fish in Africa. Species are arranged in alphabetical order [Compiled from Fomena & Bouix (1997)].

Species	Fish species	Organ	Country	Reference
<i>Myxobolus dahomeyensis</i> Siau, 1971	<i>Synodontis ansorgii</i>	Ovaries	Porto Novo (Benin)	Siau (1971)
	<i>Sarotherodon melanotheron</i> , <i>Tilapia zillii</i> , <i>Oreochromis niloticus</i> , <i>O. mossambicus</i> × <i>O. niloticus</i>	Ovaries	Lake Nokoue (Benin)	Sakiti, Blanc, Marqués & Bouix (1991)
<i>Myxobolus distichodi</i> Kostoïngue and Toguebaye, 1994	<i>Distichodus engycephalus</i>	Gills, liver & intestine	Ndjamena & Maïlo (Chad)	Kostoïngue & Toguebaye (1994)
<i>Myxobolus dossoui</i> Sakiti, Blanc, Marqués & Bouix, 1991	<i>Tilapia zillii</i> , <i>Hemichromis fasciatus</i> , <i>Oreochromis mosambica</i> × <i>O. niloticus</i>	Gills	Lake Nokoue (Benin)	Sakiti, Blanc, Marqués & Bouix (1991)
<i>Myxobolus equatorialis</i> Landsberg, 1985	<i>Oreochromis aureus</i> × <i>O. niloticus</i> ,	Spleen	Israel	Landsberg (1985)
	<i>Oreochromis niloticus</i> , <i>Sarotherodon galilaeus</i> ,	Kidneys & spleen	New Busa (Nigeria)	Obiekezie & Okaeme (1990)
	<i>Oreochromis niloticus</i>	Kidneys & spleen	Yaounde (Cameroon)	Fomena, Marqués & Bouix (1993)
<i>Myxobolus exiguus</i> Thélohan, 1895	<i>Abramis brama</i> , <i>Chondrostoma nasus</i> , <i>Mugil capito</i> ,	Gills & various organs	Eurasia	Thélohan (1895)
	<i>Mugil cephalis</i> , <i>M. auratus</i>	Scales	Tunisia	Siau (1978)
<i>Myxobolus fotoi</i> Fomena, Marqués & Bouix, 1993	<i>Oreochromis niloticus</i>	Gills	Yaounde (Cameroon)	Fomena, Marqués & Bouix (1993)
<i>Myxobolus galileaus</i> Landsberg, 1985	<i>Sarotherodon galilaeus</i>	Kidneys & spleen	Israel	Landsberg (1985)
	<i>Oreochromis niloticus</i> , <i>Sarotherodon galilaeus</i> , <i>O. niloticus</i> × <i>S. galileaus</i> , <i>Tilapia guineensis</i>	Kidneys, eyes & spleen	Cross River State & New Busa (Nigeria)	Obiekezie & Okaeme (1990)
	<i>Sarotherodon galilaeus</i>	Gills & intestine	Ndjamena, Maïlo, Mara (Chad)	Kostoïngue & Toguebaye (1994)
<i>Myxobolus heterosporus</i> Baker, 1963	<i>Tilapia esculenta</i> , <i>T. variabilis</i> , <i>Oreochromis niloticus</i>	Liver, kidneys & spleen	Lake George (Uganda)	Baker (1963)
	<i>Tilapia zillii</i> , <i>Sarotherodon melanotheron</i> , <i>Hemichromis fasciatus</i>	Gills & viscera	Lake Nokoue (Benin)	Sakiti, Blanc, Marqués & Bouix (1991)
	<i>Oreochromis niloticus</i>	Kidneys & spleen	Yaounde (Cameroon)	Fomena, Marqués & Bouix (1993)

Table 2.2 continued: Myxosporeans infecting freshwater fish in Africa. Species are arranged in alphabetical order [Compiled from Fomena & Bouix (1997)].

Species	Fish species	Organ	Country	Reference
<i>Myxobolus homeosporus</i> Baker, 1963	<i>Tilapia esculenta</i> , <i>T. variabilis</i>	Muscles	Lake Victoria (Uganda)	Baker (1963)
	<i>Oreochromis niloticus</i>	Cornea	New Busa (Nigeria)	Obiekezie & Okaeme (1990)
	<i>Tilapia variabilis</i> , <i>T. zillii</i> , <i>Oreochromis niloticus</i> , <i>Sarotherodon galilaeus</i>	Ectoparasitic	Lake Victoria (Uganda)	Paperna (1973)
	<i>Sarotherodon galilaeus</i>	Ectoparasitic	Lake Volta (Ghana)	Paperna (1973)
<i>Myxobolus hydrocyni</i> Kostoingue & Toguebaye, 1994	<i>Hydrocynis forskali</i>	Gills	Maïlao (Chad)	Kostoingue & Toguebaye (1994)
<i>Myxobolus israelensis</i> Landsberg, 1985	<i>Oreochromis niloticus</i> × <i>O. aureus</i> , <i>Sarotherodon galilaeus</i> , <i>O. niloticus vulcani</i>	Kidneys & spleen	Israel	Landsberg (1985)
	<i>Oreochromis niloticus</i> , <i>Sarotherodon galilaeus</i> , <i>Oreochromis niloticus</i> × <i>O. aureus</i> , <i>Tilapia guineensis</i>	Kidneys & spleen	New Busa (Nigeria)	Obiekezie & Okaeme (1990)
	<i>Oreochromis niloticus</i>	Kidneys & spleen	Yaounde (Cameroon)	Fomena, Marqués & Bouix (1993)
<i>Myxobolus kainjiae</i> Paperna, 1973	<i>Haplochromis niloticus</i> , <i>H. elegans</i>	Ovaries	Lake George (Uganda)	Paperna (1973)
	<i>Oreochromis niloticus</i> , <i>Sarotherodon galilaeus</i>	Ovaries	New Busa (Nigeria)	Obiekezie & Okaeme (1990)
<i>Myxobolus kriebeinsis</i> Fomena & Bouix, 1994	<i>Brycinus longipinnis</i>	Skin, eyes & kidneys	Lobe and Sanaga Basin (Cameroon)	Fomena & Bouix (1994)
<i>Myxobolus mailaensis</i> Kostoingue, Faye & Toguebaye, 1998	<i>Synodontis gambiensis</i>	Kidneys	Chad	Kostoingue, Faye & Toguebaye (1998)*
<i>Myxobolus maraensis</i> Kostoingue, Faye & Toguebaye, 1998	<i>Citharinus citharinus</i>	Gills	Chad	Kostoingue, Faye & Toguebaye (1998)*
<i>Myxobolus ndjamenaensis</i> Kostoingue, Faye & Toguebaye, 1998	<i>Citharinus citharinus</i>	Kidneys	Chad	Kostoingue, Faye & Toguebaye (1998)*
<i>Myxobolus nilei</i> Faisal & Shalaby, 1987	<i>Oreochromis niloticus</i>	Gills, skin, eyes, kidneys & pancreas	Egypt	Faisal & Shalaby (1987)
<i>Myxobolus niloticus</i> Fahmy, Mandour & El-Naffar, 1971	<i>Labeo niloticus</i>	Fins	Assuit (Egypt)	Fahmy, Mandour & El-Naffar (1971)
<i>Myxobolus njinei</i> Fomena, Bouix & Birgi, 1985	<i>Barbus campthacanthus</i> , <i>B. guirali</i> , <i>B. batesii</i> , <i>B. martorelli</i>	Gills	Nyong and Sanaga Basins, (Cameroon)	Fomena, Bouix & Birgi (1985)
<i>Myxobolus nkolyaensis</i> Fomena & Bouix, 1994	<i>Barbus jae</i>	Gills	Nyong Basin, (Cameroon)	Fomena & Bouix (1994)

Table 2.2 continued: Myxosporeans infecting freshwater fish in Africa. Species are arranged in alphabetical order [Compiled from Fomena & Bouix (1997)].

Species	Fish species	Organ	Country	Reference
<i>Myxobolus nyongana</i> Fomena, Bouix & Birgi, 1985	<i>Barbus aspilus</i> , <i>B. jae</i> , <i>B. camphacanthus</i> , <i>B. guirali</i> , <i>B. martorelli</i>	Gills	Nyong Basin (Cameroon)	Fomena, Bouix & Birgi (1985)
	<i>Sarotherodon melanotherodon</i>	Gills	Lake Nokoue (Benin)	Sakiti, Blanc, Marqués & Bouix (1991)
	<i>Alestes dentex</i> , <i>Labeo parvus</i>	Gills & eyes	Maïlao (Chad)	Kostoïngue & Toguebaye (1994)
<i>Myxobolus oloi</i> Fomena & Bouix, 1994	<i>Barbus aspilus</i> , <i>B. guirali</i> , <i>B. camptacanthus</i>	Gills kidneys & heart	Nyong & Sangana Basins (Cameroon)	Fomena & Bouix (1994)
<i>Myxobolus polycentropsi</i> Fomena, Bouix & Birgi, 1985	<i>Polycentropsis abbreviata</i>	Gills	Mouanko (Cameroon)	Fomena, Bouix & Birgi (1985)
	<i>Tilapia zillii</i>	Gills	Lake Nokoue (Benin)	Sakiti, Blanc, Marqués & Bouix (1991)
<i>Myxobolus sarigi</i> Landsberg, 1985	<i>Oreochromis niloticus</i> × <i>O. aureus</i> , <i>Sarotherodon galilaeus</i> , <i>O. niloticus</i>	Kidneys & spleen	Israel	Landsberg (1985)
	<i>Oreochromis niloticus</i> <i>Sarotherodon galilaeus</i> , <i>O. niloticus</i> × <i>S. galilaeus</i>	Kidneys & spleen	New Busa (Nigeria)	Obiekezie & Okaeme (1990)
	<i>Oreochromis niloticus</i>	Kidneys & spleen	Yaounde (Cameroon)	Fomena, Marqués & Bouix (1993)
<i>Myxobolus sarotherodoni</i> Sakiti, Blanc, Marqués & Bouix, 1991	<i>Sarotherodon melanotheron</i>	Gills	Lake Nokoue (Benin)	Sakiti, Blanc, Marqués & Bouix (1991)
<i>Myxobolus stenosis</i> Paperna, 1973	<i>Synodontis schall</i>	Gills	Uganda	Paperna (1973)
	<i>Synodontis clarias</i>	Kidneys	Ndjamena, Maïlao, Mara (Chad)	Kostoïngue & Toguebaye (1994)
	<i>Synodontis schall</i>	Gills	Mara (Chad)	Fomena, Bouix & Birgi (1985)
<i>Myxobolus synodonti</i> Fomena, Bouix & Birgi, 1985	<i>Synodontis batesii</i>	Stomach wall	Nyong Basin (Cameroon)	Fomena, Bouix & Birgi (1985)
<i>Myxobolus tilapiae</i> Abolarin, 1974	<i>Tilapia zillii</i> , <i>Oreochromis niloticus</i> , <i>Sarotherodin galilaeus</i>	Gills & Fins	Nigeria	Abolarin (1974)
	<i>Oreochromis niloticus</i>	Gills, kidneys & spleen	Yaounde (Cameroon)	Fomena, Marqués & Bouix (1993)
<i>Myxobolus zillei</i> Sakiti, Blanc Marqués & Bouix, 1991	<i>Tilapia zillii</i>	Gills	Lake Nokoue (Benin)	Sakiti, Blanc, Marqués & Bouix (1991)
	<i>Lates niloticus</i>	Gills & intestine	Ndjamena & Maïlao (Chad)	Kostoïngue & Toguebaye (1994)
GENUS UNICAUDA DAVIS, 1944				
<i>Unicauda strongylura</i> (Gurley, 1893), [syn. <i>Henneguya strongylura</i> (Gurley, 1893) Labbé, 1899]	<i>Synodontis schall</i>	Unknown	Nile Egypt	Gurley (1893), Labbé (1899)

Table 2.2 continued: Myxosporeans infecting freshwater fish in Africa. Species are arranged in alphabetical order [Compiled from Fomena & Bouix (1997)].

Species	Fish species	Organ	Country	Reference
GENUS <i>HENNEGUYA</i> THELOHAN, 1892				
<i>Henneguya bopeleti</i> Fomena & Bouix, 1987	<i>Chrysichthys nigrodigitatus</i>	Gills	Nyong Basin (South Cameroon)	Fomena & Bouix (1987)
<i>Henneguya branchialis</i> Ashmawy, Abu-Elwafa, Imam & El-Otifi, 1989	<i>Clarias lazera</i>	Gills & intestine	Giza Governorate (Egypt)	Ashmawy, Abu-Elwafa, Imam & El-Otifi (1989)
<i>Henneguya camerounensis</i> Fomena and Bouix, 1987	<i>Synodontis batesii</i> , <i>Eutropius multioeniatus</i>	Gills	Nyong & Lobo Basins (Cameroon)	Fomena & Bouix (1987)
<i>Henneguya chrysichthys</i> Obiekezie & Enyenihi, 1988	<i>Chrysichthys nigrodigitatus</i>	Gills	Cross River Estuary (Nigeria)	Obiekezie & Enyenihi (1988)
<i>Henneguya clariae</i> Abolarin, 1971	<i>Clarias lazera</i>	Gills	Nigeria	Abolarin (1971)
<i>Henneguya ctenopoma</i> Fomena & Bouix, 1996	<i>Ctenopoma nanum</i>	Gills	Nyong Basin (Cameroon)	Fomena & Bouix (1996)
<i>Henneguya laterocapsulata</i> Landsberg, 1987	<i>Clarias lazera</i>	Body	Israel	Landsberg (1987)
	<i>C. lazera</i> × <i>Heterobranchus bidorsalis</i>	Unkown	Nigeria	Obiekezie & Schmahl (1993)
<i>Henneguya malapteruri</i> Fomena & Bouix, 1996	<i>Malapterurus electricus</i>	Skin & muscles	Dibang (Cameroon)	Fomena & Bouix (1996)
<i>Henneguya ntementis</i> Fomena & Bouix, 1996	<i>Brienomyrus brachyistius</i>	Kidneys, spleen & gall-bladder wall	Ebolowa (Cameroon)	Fomena & Bouix (1996)
<i>Henneguya nyongensis</i> Fomena & Bouix, 1996	<i>Marcusenius moori</i>	Gills & Muscles	Nyong Basin (Cameroon)	Fomena & Bouix (1996)
<i>Henneguya odzai</i> Fomena & Bouix, 1996	<i>Marcusenius moori</i>	Gills	Odza II (Cameroon)	Fomena & Bouix (1996)
GENUS <i>KUDOJA</i> MEGLITSCH, 1947				
<i>Kudoja eleotrisi</i> Siau, 1971	<i>Eleotris kribensis</i>	Gills	Djassin (Benin)	Siau (1971)
GENUS <i>CHLOROMYXUM</i> MINGAZZINI, 1890				
<i>Chloromyxum birgii</i> Fomena & Bouix, 1994	<i>Barbus aspilus</i> , <i>B. martorelli</i> , <i>Amphilius longirostris</i>	Gall bladder	Nyong & Lobo Basins (Cameroon)	Fomena & Bouix (1994)
<i>Chloromyxum vanasi</i> Ali, 1998	<i>Bagras bayad</i>	Gall bladder	Nile River (Egypt)	Ali (1998)

* References added since 1997

Table 2.2 continued: Myxosporeans infecting freshwater fish in Africa. Species are arranged in alphabetical order [Compiled from Fomena & Bouix (1997)].

Species	Fish species	Organ	Country	Reference
GENUS HENNEGUYA THELOHAN, 1892				
<i>Henneguya bopeleti</i> Fomena & Bouix, 1987	<i>Chrysichthys nigrodigitatus</i>	Gills	Nyong Basin (South Cameroon)	Fomena & Bouix (1987)
<i>Henneguya branchialis</i> Ashmawy, Abu-Elwafa, Imam & El-Otifi, 1989	<i>Clarias lazera</i>	Gills & intestine	Giza Governorate (Egypt)	Ashmawy, Abu-Elwafa, Imam & El-Otifi (1989)
<i>Henneguya camerounensis</i> Fomena and Bouix, 1987	<i>Synodontis batesii</i> , <i>Eutropius multioeniatus</i>	Gills	Nyong & Lobo Basins (Cameroon)	Fomena & Bouix (1987)
<i>Henneguya chrysichthys</i> Obiekezie & Enyenihi, 1988	<i>Chrysichthys nigrodigitatus</i>	Gills	Cross River Estuary (Nigeria)	Obiekezie & Enyenihi (1988)
<i>Henneguya clariae</i> Abolarin, 1971	<i>Clarias lazera</i>	Gills	Nigeria	Abolarin (1971)
<i>Henneguya ctenopoma</i> Fomena & Bouix, 1996	<i>Ctenopoma nanum</i>	Gills	Nyong Basin (Cameroon)	Fomena & Bouix (1996)
<i>Henneguya laterocapsulata</i> Landsberg, 1987	<i>Clarias lazera</i>	Body	Israel	Landsberg (1987)
	<i>C. lazera</i> × <i>Heterobranchus bidorsalis</i>	Unkown	Nigeria	Obiekezie & Schmahl (1993)
<i>Henneguya malapteruri</i> Fomena & Bouix, 1996	<i>Malapterurus electricus</i>	Skin & muscles	Dibang (Cameroon)	Fomena & Bouix (1996)
<i>Henneguya ntementis</i> Fomena & Bouix, 1996	<i>Brienomyrus brachyistius</i>	Kidneys, spleen & gall-bladder wall	Ebolowa (Cameroon)	Fomena & Bouix (1996)
<i>Henneguya nyongensis</i> Fomena & Bouix, 1996	<i>Marcusenius moori</i>	Gills & Muscles	Nyong Basin (Cameroon)	Fomena & Bouix (1996)
<i>Henneguya odzai</i> Fomena & Bouix, 1996	<i>Marcusenius moori</i>	Gills	Odza II (Cameroon)	Fomena & Bouix (1996)
GENUS KUDOA MEGLITSCH, 1947				
<i>Kudoa eleotrisi</i> Siau, 1971	<i>Eleotris kribensis</i>	Gills	Djassin (Benin)	Siau (1971)
GENUS CHLOROMYXUM MINGAZZINI, 1890				
<i>Chloromyxum birgii</i> Fomena & Bouix, 1994	<i>Barbus aspilus</i> , <i>B. martorelli</i> , <i>Amphilius longirostris</i>	Gall bladder	Nyong & Lobo Basins (Cameroon)	Fomena & Bouix (1994)
<i>Chloromyxum vanasi</i> Ali, 1998	<i>Bagras bayad</i>	Gall bladder	Nile River (Egypt)	Ali (1998)

* References added since 1997

CHAPTER 3



The Okavango River and Delta, Botswana

The Okavango River and Delta system is a vast inland wetland situated in the far northwestern corner of Botswana. The entire region is composed of approximately 15 000 km² of waterways, floodplains, islands and forests. Internationally it represents one of the largest inland water systems in the world and is relatively ecologically unperturbed (Merron & Bruton 1986). The origin of this unique system lies in the southern slopes of the Angolan Highlands (Fig. 3.1), which form a series of headwater streams and rivers, that eventually give rise to the Okavango River. Initially, the streams flow in a south and southeasterly direction and then gather to form a large mainstream, the Cubango, which turns eastwards shortly after reaching the Angola-Namibia border (Merron 1991). A second major branch of the system, the Cuito, also rises in Angola and joins the main stream before it flows across and forms the western boundary of the Caprivi strip (Merron 1991). These two rivers subsequently join to form the mighty Okavango River, flowing along Namibia's northern border, before crossing the Caprivi strip and flowing over the Popa Falls into northwestern Botswana (Balfour 1996).

Situated in the middle of the oldest desert in the world, the Kalahari, this is the only wetland of its kind that forms an inland delta and is one of the few river systems in the world that are visible from space (Fig. 3.4A). Once the Okavango River has crossed into Botswana, the river takes on three distinct forms (Bailey 1998) (Fig. 3.2). The first of which is a region known as the panhandle where the river slows its pace and begins its meandering through a 100-km strip of wetland. The panhandle is formed as the river is channeled by the Gomare Fault, which forms the southern most extremity of the Great African Rift Valley of East Africa (Balfour 1996). Once the river spills over the Gomare Fault, into a region where the land subsided millions of years ago, the river spreads out and takes on the appearance of a delta, splitting into a web of channels and islands (Bailey 1998). Upon entering the perennial swamp, the mainstream splits into three distributary systems i.e., Thoage, Nqoga and Jao.

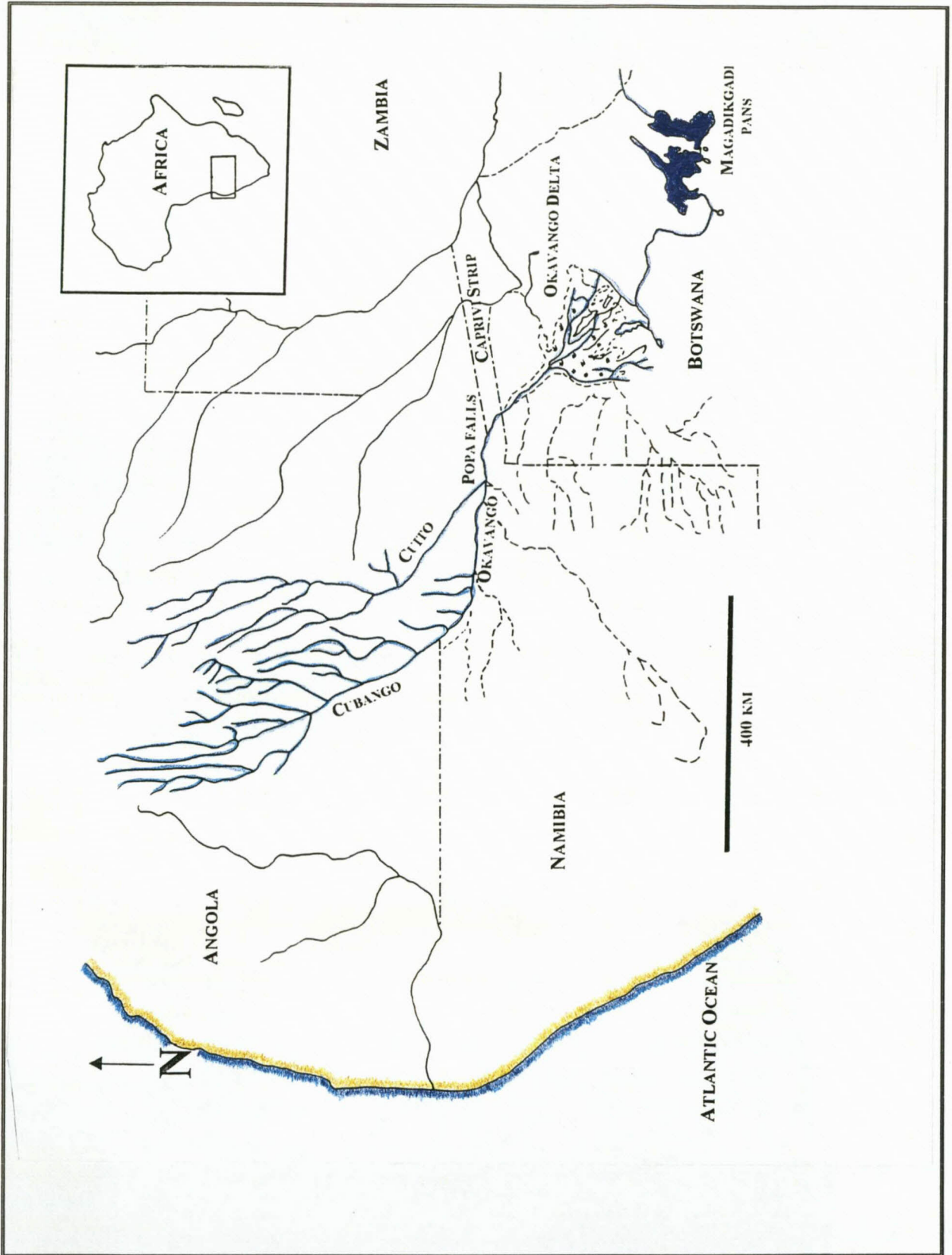


Figure 3.1: Map of the Okavango River and Delta drainage system showing the two main tributaries, the Cubango and the Cuito [Adapted from Skelton, Bruton, Merron & Van der Waal (1985)]

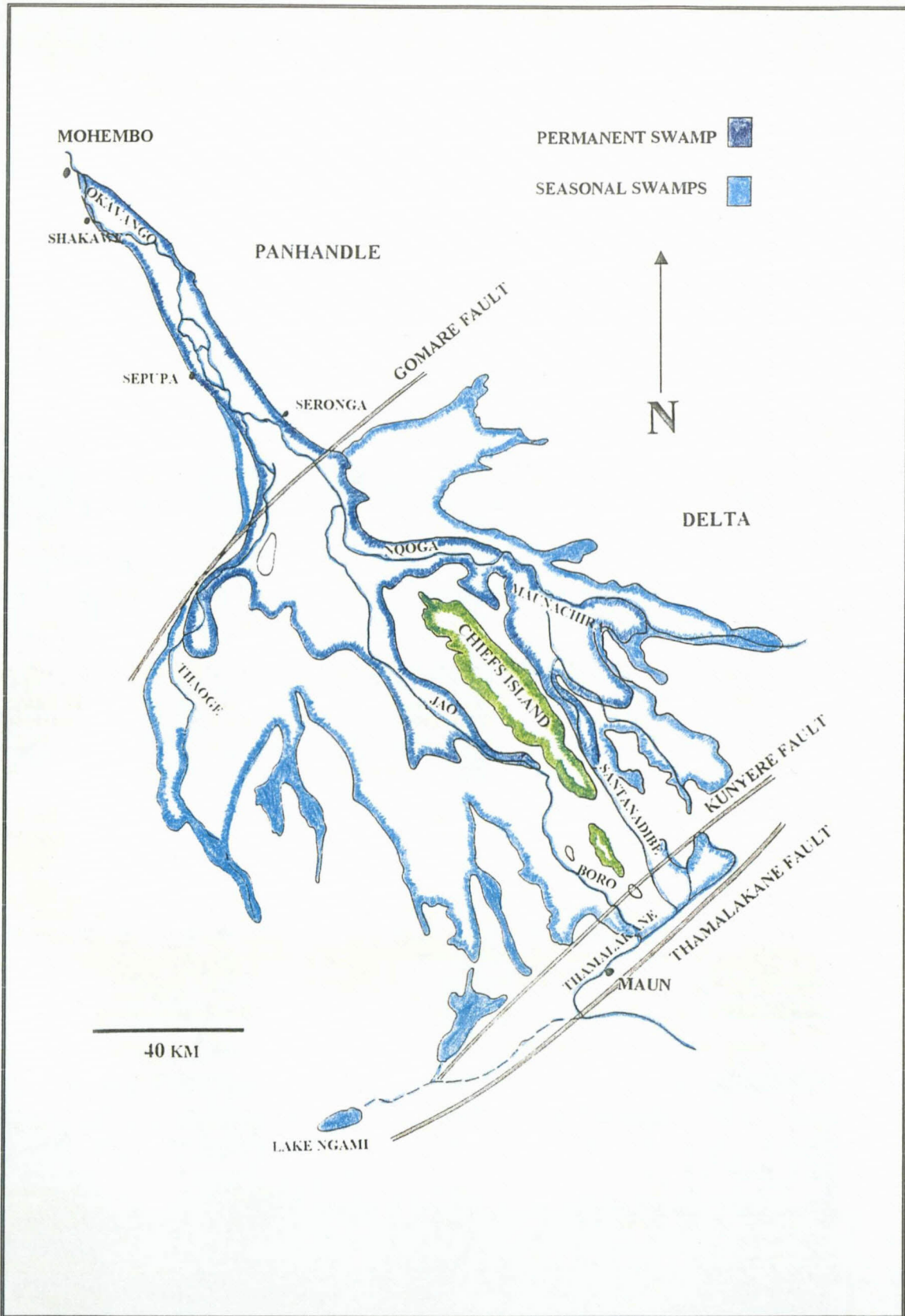


Figure 3.2: Map of the Okavango River and Delta in Botswana showing the panhandle, delta, faults and main distributary rivers [Adapted from Skelton, Bruton, Merron & Van der Waal (1985)].

The Thoage is the western most distributary, while the Nqoga extends along the Moanachira and Kwai Rivers and the Jao, being the primary distributary in the central delta (Merron 1991). At the southeast end of the Okavango Delta, the main drainage channels, the Boro and Santandadibe Rivers reunite along the Thamalakane Fault to form the southwestward-flowing Thamalakane River (Merron 1991).

The Okavango Delta region can subsequently 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 a 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 Okavango wetland also has two distinct gradients, a slightly more gentle one in the panhandle region (1m: 5570m) and a slightly steeper one on the alluvial fan or delta region (1m: 3400m). The change in gradient is as a result of the Gomare Fault and is due to the loss of confinement of the flood plain, which results in the wide dispersal of the sediment load and hence a steepening of the gradient (McCarthy, Barry, Bloem, Ellery, Heister, Merry, Rüter & Sternberg 1997).

The Okavango River is also subject to annual cycles of flooding and draining and may range in area from 15 000 km² in the flood season to 6000 to 8000 km² in the dry season (Cambell 1983). The flood waters from the Angolan Highlands reach the northern panhandle in January and take approximately six months to move through the entire Delta, reaching the southern drainage rivers in June (Merron 1991). This slow pattern of inundation is largely due to the gentle gradient. Although local rainfall can influence hydrological conditions, the magnitude and duration of the annual flood is determined mainly by headwater catchment in the Angolan Highlands. The rate of water flow of the Okavango River measured at the Water affairs monitoring station at Mohembo for 1984, 1998, 1999 and 2000 is shown in Figure 3.3. This illustrates the variation in the rate of water flow from year to year. On average the annual flood brings with it 11 billion cubic meters of water passing through the panhandle region (Bailey 1998).

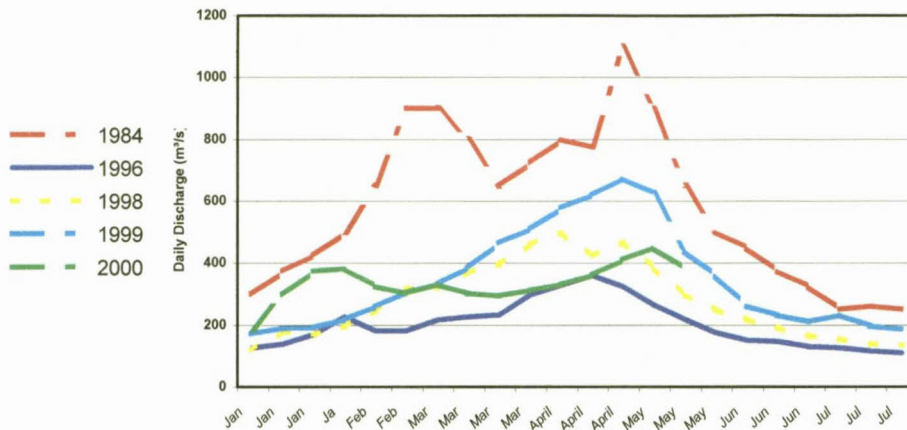


Figure 3.3: Powerserve flood graph illustrating the rate of water flow of the Okavango River measured at the Water affairs monitoring station at Molembo for 1984, 1996, 1998, 1999, 2000.

Botswana is generally a dry country with an average annual rainfall of only between 250 mm in the south and 650 mm in the north (Merron 1991). Although the rainfall in the region of the delta is much less than in the catchment area, the rains that fall between November and April contribute a further 5 billion cubic meters to the annual flood (Bailey 1998). This enormous area covered by the Okavango Delta provides a multitude of habitats for the very diverse fish fauna occurring in the region. Merron (1987) distinguished five major ecotones in the Okavango system, based on the availability of surface water. These ecotones included:

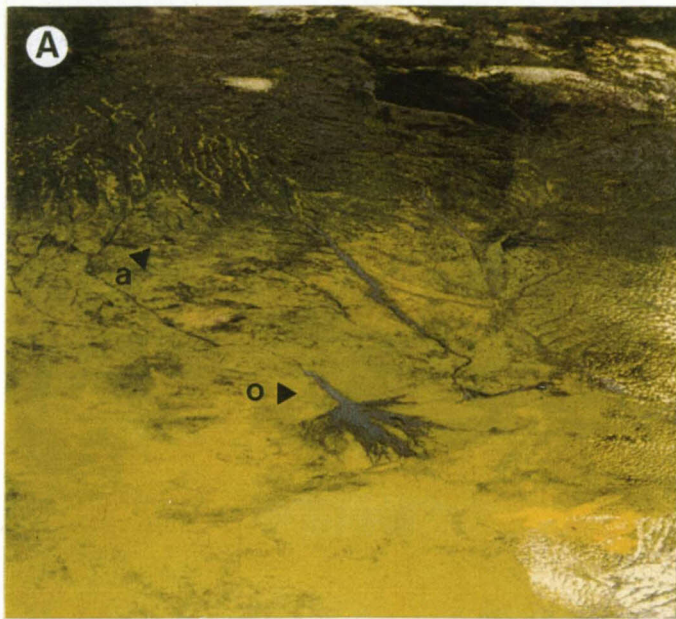
- A riverine section in Namibia (Fig. 3.4B)
- A riverine 'panhandle' stretching from Shakawe in the north to Seronga in the south (Fig. 3.4C)
- An upper permanent swamp, which includes many of the habitat types, found in the riverine 'panhandle' (Fig. 3.4D)
- A lower seasonally inundated swamp (Fig. 3.4E)
- The drainage rivers (Fig. 3.4F)
- Additionally, another important ecotone would be the sump lakes or salt pans that occasionally run dry such as Lake Ngami and Lake Xao.

This multitude of habitat types allow the fish fauna of the Okavango to contain distinct communities of fish that may be separated from each other by the physical characteristics of the different habitats in which they co-evolved (Merron 1991). The relatively stable ecotones such as the riverine section, riverine panhandle and permanent swamp allow a diverse and biotically interdependent fish community to develop, while the fluctuating seasonal swamp and drainage river ecotones are characterised by a less diverse fish community (Merron 1991). Furthermore, floodplain fish populations are often characterised by a dependence on the natural, annual flood cycle for their survival (Lowe-McConnel 1975). Merron (1991) suggests that the floods are important in periodically connecting the water bodies on the floodplain to the river, which facilitates essential ecological functions such as the movement, and spawning of many of the fish species.

Figure 3.4

Photographs illustrating the five major ecotones in the Okavango as distinguished by Merron (1987).

- A: Photograph showing an aerial view of the Okavango River and Delta region from space (NORAD Satellite photograph, CSIR) (a-Angolan Highlands, o-Okavango River system)
- B: Popa Falls, a riverine section of Okavango River in Namibia
- C: A section of the riverine panhandle, between Shakawe and Seronga
- D: The upper permanent swamp of the Okavango Delta
- E: Aerial view of the lower seasonally inundated swamp of the Okavango River and Delta
- F: Flood water reaching the Thamalakane drainage river at the southern most point of the Okavango Delta.



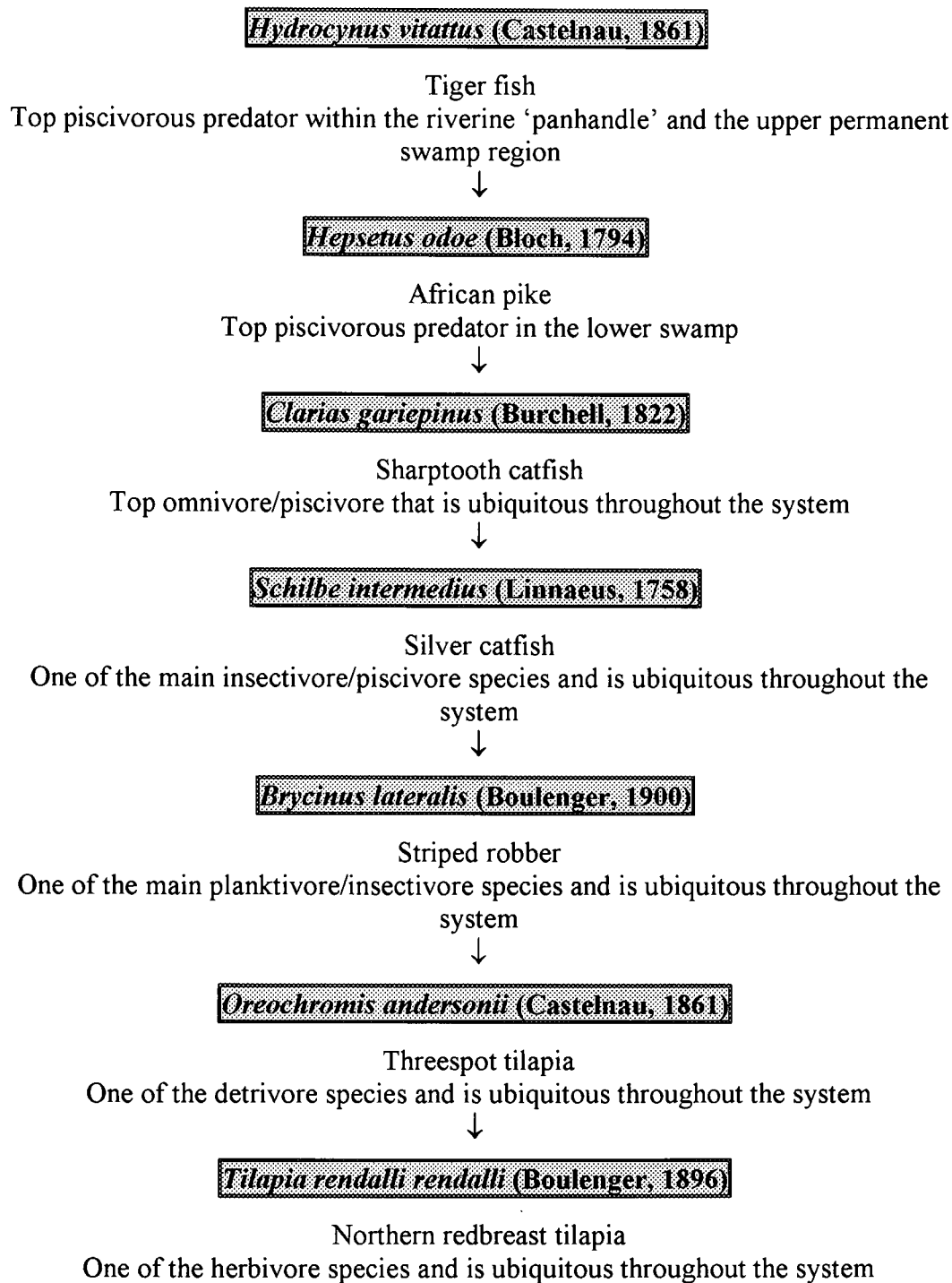
By inundating low lying regions, the floodwaters result in the conversion of terrestrial plant and animal matter into food for fish and other aquatic organisms and also provide a safe nursery site for fish larvae and juveniles during early stages of development (Bruton & Jackson 1983).

The rise and fall of the annual flood is thus one of the most important driving forces of the Okavango. It is intimately associated with the habits of the fishes and also assists in their distribution as well as the clearing of blockages in the system caused by, for example, floating beds of papyrus (Skelton, Bruton, Merron & Van der Waal 1985).

Within the Okavango River and Delta itself, the major factor determining the distribution of the fishes appears to be the various habitat preferences, with the physical barriers playing only a minor role. Skelton *et al.* (1985) revealed that there are at present approximately 88 species of fish inhabiting the Okavango drainage system with about 68 species occurring in Botswana (Table. 3.1).

Reporting on the broad distribution of the Okavango fish species Ladiges (1964) and Poll (1966, 1967) divided the Angolan fish fauna into five zoogeographic regions: Zaire Basin, Zambezi, Angolan (coastal rivers excluding the Cunene), the Okavango and the Cunene. Although there is considerable overlap in the distribution of species between these regions, the fish fauna occurring in the Zambezi, Okavango and Cunene is most similar (Bell-Cross 1968). According to Skelton *et al.* (1985) of the fish species recorded from the Okavango, 77 are also found in the Upper Zambezi and at least 43 in the Cunene. The similarity in the fish fauna of these rivers indicate that there was most probably a number of direct links in the drainage evolution of these river systems (Bell-Cross 1968).

The fish population throughout the Okavango system in Botswana is a predator driven system, with two top predators occurring in different parts of the swamp. The trophic levels amongst the fish populations are as follows:



Many of the fish species living in the Okavango have adaptations that allow them to survive in their specific habitats. The tiger fish, *Hydrocynus vitattus*, which is a predatory characin, distributed throughout Africa, is the top predator in the Okavango

upper swamp region. According to Bruton (1984), this species is not found in the lower swamp where *Hepsetus odoe*, the African pike is the top predator. As noted by Bell-Cross (1966), *Hydrocynus vittatus* is not found in water that recedes at the end of the rainy season to such an extent that they are cut off from permanent water bodies. Furthermore, it is possible that increasing turbidity of the water in the lower swamp regions, drainage rivers and sump lakes is another reason for the absence of this visual predator (Bruton 1984).

Hepsetus odoe, an endemic African freshwater fish, which belongs to the nonspecific family Hepsetidae, prefers the quiet backwaters and is common in the floodplains throughout the system (Merron, Holden & Bruton 1990). These fish have adapted to the changing environmental conditions, brought about by the annual flood cycle. They construct a foam nest for guarding their young and to provide an oxygen rich environment for them to grow (Merron 1991).

The sharptooth catfish, *Clarias gariepinus*, partakes in massive feeding migrations in the upper parts of the Okavango Delta, between October and November. This pack-hunting phenomenon is initiated by the receding water levels, which force the smaller fish species into the mainstream river channels. According to Merron (1987), these catfish runs are ecologically significant since their response is an indicator of the fluctuating water levels. Not only *C. gariepinus* species partake in this but also *Clarias ngamensis* with dramatic changes in the diets of these *Clarias* species being noted during these runs (Merron 1991).

The threespot tilapia, *Oreochromis andersonii*, exhibits considerable phenotypic plasticity. According to Merron (1991), fish from seasonally inundated areas show a smaller mean size, egg size and larger number of eggs relative to fish in the perennially flooded areas. The size at sexual maturity is also smaller and it is evident that these different reproductive characteristics exhibited by *O. andersonii* are dependent on the degree of water retention by the different habitats.

Apart from various life strategy adaptations, it is also known that the morphology of fishes is closely related to the habitats in which they prefer to live (Lyon 1993). According to this author, fish with similar morphological characteristics occupy

similar habitats. In the Okavango system he was able to recognise a significant vertical separation of habitat types including, the substratum – (where mud feeders are found), the benthic habitat – (where bottom feeders are found), the pelagic habitat – (where midwater feeders are found) and finally, the surface feeders. The author also recognised a horizontal separation of habitats, which included the mainstream environment and the floodplain lagoons.

Lyon (1993) found that fish with forked to lunate tails (Fig. 3.5A), such as *Hydrocynus vittatus*, tended to occur in the mainstream, whereas weaker swimmers have truncate or more blunt tails and occur in lagoon type habitats (Fig. 3.5B). Surface feeders such as Johnston's topminnow *Aplocheilichthys johnstoni* have a rounded abdomen and flattened dorsal profile (Fig. 3.5C), allowing them to feed near the surface without exposing themselves to predators. Furthermore fish occurring in the midwater habitat such as mormyrids and cichlids have relatively deep bodies and tend to be compressed laterally (Fig. 3.5D), which means they have narrow bodies relative to their height. Finally substratum fish tend to have broad depressed bodies (Fig. 3.5E & F), such as *Clarias gariepinus*.

The fishes of the Okavango River system in Botswana are not only ecologically important to the function of the entire system, but are also a very valuable resource for people living in and around the river. Fish provide a free, high protein supplement to the diet of many subsistence people and also form an important recreational and commercial fishery (Merron 1993). During the 1980's increased demand for fish resulted in a marked escalation in fishing effort (Merron 1993). As a result, fish species that play an important part in the food chain such as *Hydrocynus vittatus*, *Hepsetus odoe*, *Clarias gariepinus*, *Oreochromis andersonii* and *Tilapia rendallii* may be at risk of exploitation (Merron 1991).

Dangers other than over-fishing include the incorrect use of insecticides. During the mid-1970's large-scale aerial spraying of the Okavango using the insecticide endosulfan was initiated in the fight against the tsetse fly, the carrier of deadly sleeping sickness in man.

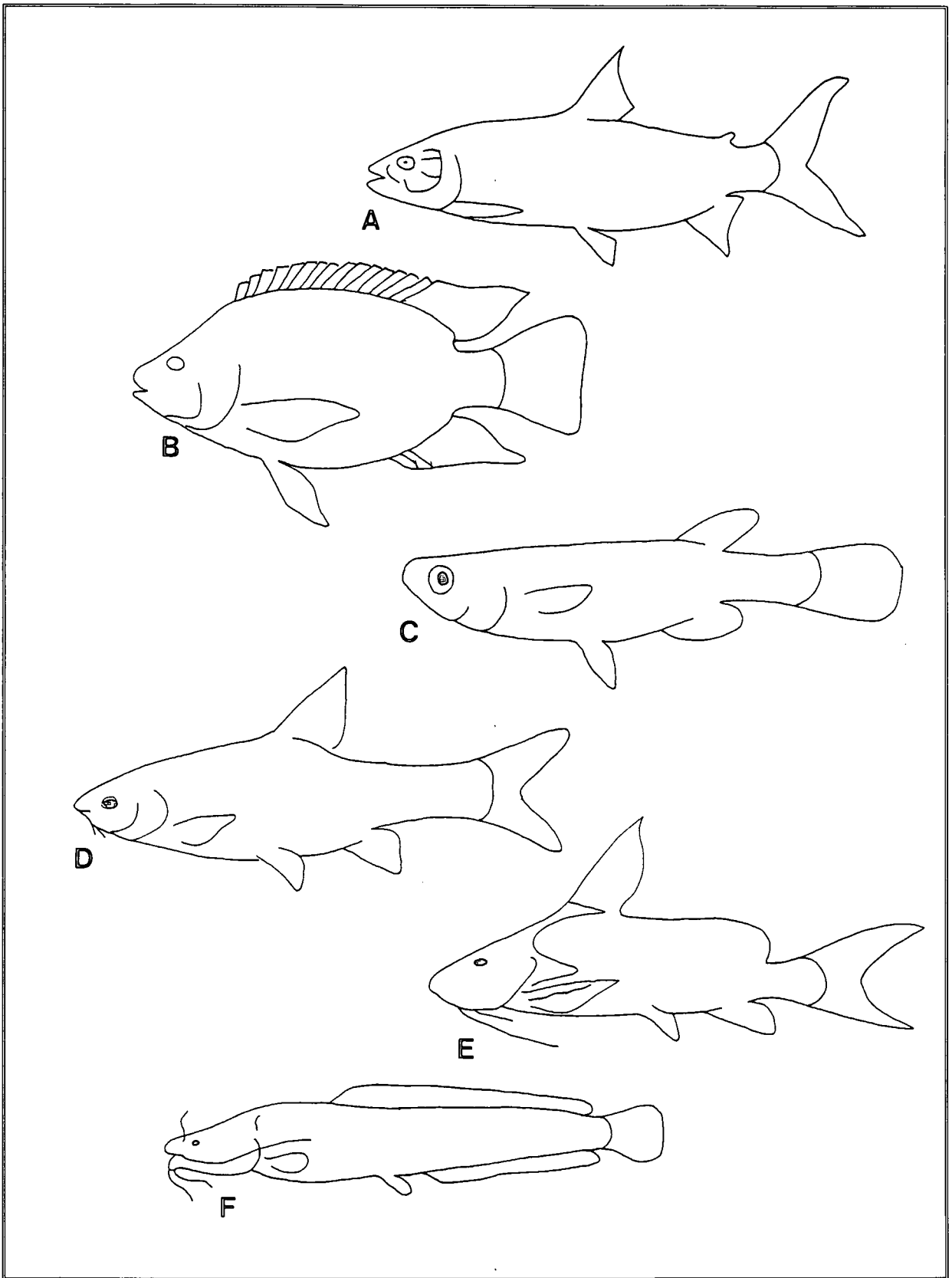


Figure 3.5: Body forms of Okavango fishes. **A**-Mainstream inhabitant, **B**-Lagoon inhabitant, **C**-Surface feeder, **D**-Midwater inhabitant, **E** & **F**-Substratum inhabitant [Redrawn from Lyon (1993)]

According to Merron (1992), the advantage of this aerial spraying was that it allowed rapid mortalities of the flies as well as the ability to control large areas more effectively than before. The main disadvantage is, however, that it blankets many non-target organisms, such as the fish populations.

There are unfortunately a number of threats facing the Okavango ecosystem (Skelton *et al.* 1985). These include, as already mentioned, insecticide spraying, but also encroachment of cattle onto the seasonal floodplain as well as pollution and erosion caused by outboard-powered boats. In addition, increased recreational fishing pressure, decreased fertilization of the water by game populations, disruption of natural food webs by removal of crocodiles and other predators. However, the most serious threats are those that will cause alterations to the flood regime. Significant advances in the understanding of the complex and dynamic Okavango fish fauna was made by Merron (1987). The aims of his findings were to formulate additional fisheries recommendations designed to increase the yield of fish to local fishermen, while at the same time ensuring that the biotic diversity and essential ecological processes were maintained.

If the demand for fish in the Okavango in Botswana continues to grow throughout the next millenium it will be essential to determine the presence of economically important fish parasites. As mentioned in Chapters 1 and 2, myxosporean parasites of fish have had serious effects on various economically important fish industries throughout the world. The determination of the distribution and biodiversity of myxosporean species infecting Okavango fishes is thus immensely important, especially since this region holds the potential for establishing a fishing industry. Once the biodiversity of myxosporean species has been determined, it would be possible to predict which species might hold a threat to the fish populations in deteriorating conditions, both in the wild and in captivity.

Table 3.1: Fish species inhabiting the Okavango River system in Botswana (adapted from Skeilton, Bruton, Merron & Van der Waal 1985) divided into families.

Species	Common name
MORMYRIDAE	
<i>Hippopotamyrus ansorgii</i> (Boulenger, 1905)	Slender stonebasher
<i>Hippopotomyrus discorhynchus</i> (Peters, 1852)	Zambezi parrotfish
<i>Marcusenius macrolepidotis</i> (Peters, 1852)	Bulldog
<i>Mormyrus lacerda</i> Castenau, 1861	Western bottlenose
<i>Petrocephalis catostoma</i> (Günther, 1866)	Churchill
<i>Pollimyrus castelnaui</i> (Boulenger, 1911)	Dwarf stonebasher
CHARACIDAE	
<i>Brycinus lateralis</i> (Boulenger, 1900)	Stripped robber
<i>Hydrocynus vittatus</i> (Castelnaui, 1861)	Tigerfish
<i>Micralestes acutidens</i> (Peters, 1852)	Silver robber
<i>Rhabdalestes maunensis</i> (Fowler, 1935)	Okavango robber
HEPSETIDAE	
<i>Hepsetus odoe</i> (Bloch, 1794)	African pike
DISTICHODONTIDAE	
<i>Hemigrammocharax machadoi</i> Poll, 1967	Dwarf citharine
<i>Hemigrammocharax multifasciatus</i> Boulenger, 1923	Multibar citharine
<i>Nannocharax macropterus</i> Pellegrin, 1925	Broadbar citharine
CYPRINIDAE	
<i>Barbus afrovernayi</i> Nichols & Boulton, 1927	Spottail barb
<i>Barbus barnardi</i> Jubb, 1965	Blackback barb
<i>Barbus barotseensis</i> Pellingrin, 1920	Barotse barb
<i>Barbus bifrenatus</i> Fowler, 1935	Hyphen barb
<i>Barbus eutaenia</i> Boulenger, 1904	Orangefin barb
<i>Barbus fasciolatus</i> Günther, 1868	Red barb
<i>Barbus haasianus</i> David, 1936	Sicklefin barb
<i>Barbus kerstenii</i> Peters, 1868	Redspot barb
<i>Barbus miolepis</i> Boulenger, 1902	Zigzag barb
<i>Barbus lineomaculatus</i> Boulenger, 1903	Line-spotted barb
<i>Barbus multilineatus</i> Worthington, 1933	Copperstripe barb
<i>Barbus paludinosus</i> Peters, 1852	Straightfin barb
<i>Barbus poechii</i> Steindachner, 1911	Dashtail barb
<i>Barbus radiatus</i> Peters, 1853	Beira barb
<i>Barbus thamalakanensis</i> Fowler, 1953	Thamalakane barb

Table 3.1 continued: Fish species inhabiting the Okavango River system in Botswana (adapted from Skelton, Bruton, Merron & Van der Waal 1985) divided into families.

Species	Common name
<i>Barbus unitaeniatus</i> Günther, 1866	Longbeard barb
<i>Coptostomabarbus wittei</i> David & Poll, 1937	Upjaw barb
<i>Labeo cylindricus</i> Peters, 1852	Redeye labeo
<i>Labeo lunatus</i> Jubb, 1963	Upper Zambezi labeo
<i>Mesobola brevianalis</i> (Boulenger, 1908)	River sardine
<i>Opsaridium zambezense</i> (Peters, 1852)	Barred minnow
CLAROTEIDAE	
<i>Parauchenoglanis ngamensis</i> Boulenger, 1911	Zambezi grunter
SCHILBEIDAE	
<i>Schilbe intermedius</i> (Linneus, 1758)	Silver catfish
AMPHILIDAE	
<i>Leptoglanis rotundiceps</i> (Hilgendorf, 1905)	Spotted sand catlet
CLARIDAE	
<i>Clarias gariepinus</i> (Burchell, 1822)	Sharptooth catfish
<i>Clarias lithiocephalus</i> Boulenger, 1898	Smoothhead carfish
<i>Clarias ngamensis</i> Castelnau, 1861	Blunttooth catfish
<i>Clarias theodorae</i> Weber, 1897	Snake catfish
<i>Clarias stappersii</i> Boulenger, 1915	Blotched catfish
MOCHORIDAE	
<i>Chiloglanis fasciatus</i> Pellegrin, 1936	Okavango suckermouth
<i>Synodontis leopardinus</i> Pellegrin, 1914	Leopard squeaker
<i>Synodontis macrostigma</i> Boulenger, 1911	Large spot squeaker
<i>Synodontis nigromaculatus</i> Boulenger, 1905	Spotted squeaker
<i>Synodontis thamalakanensis</i> Fowler, 1935	Bubblebarb squeaker
<i>Synodontis vanderwaali</i> Skelton & White, 1990	Finetooth squeaker
<i>Synodontis woosnami</i> Boulenger, 1911	Upper Zambezi squeaker
CYPRINODONTIDAE	
<i>Aplocheilichthys hutereaui</i> (Boulenger, 1913)	Mesh-scaled topminnow
<i>Aplocheilichthys johnstoni</i> (Günther, 1893)	Johnston's topminnow
<i>Aplocheilichthys katangae</i> (Boulenger, 1912)	Stripped topminnow
CICHLIDAE	
<i>Hemichromis elongatus</i> (Guichenot, 1861)	Banded jewelfish
<i>Oreochromis andersonii</i> (Castelnau, 1861)	Threespot tilapia
<i>Oreochromis macrochir</i> (Boulenger, 1912)	Greenhead tilapia
<i>Pharyngochromis acuticeps</i> (Steindagner, 1866)	Zambezi happy
<i>Pseudocrenilabrus philander</i> (Weber, 1897)	Southern mouthbrooder
<i>Sargochromis carlottae</i> (Boulenger, 1905)	Rainbow happy

Table 3.1 continued: Fish species inhabiting the Okavango River system in Botswana (adapted from Skelton, Bruton, Merron & Van der Waal 1985) divided into families.

Species	Common name
<i>Sargochromis codringtonii</i> (Boulenger, 1908)	Green happy
<i>Sargochromis giardi</i> (Pellegrin, 1903)	Pink happy
<i>Sargochromis greenwoodi</i> (Bell-Cross, 1975)	Greenwood's happy
<i>Sargochromis gracilis</i> Greenwood, 1984	Slender happy
<i>Serranochromis altus</i> Winemiller & Kelso-Winemiller, 1990	Humpback largemouth
<i>Serranochromis angusticeps</i> (Boulenger, 1907)	Thinface largemouth
<i>Serranochromis longimanus</i> (Boulenger, 1911)	Longfin largemouth
<i>Serranochromis macrocephalus</i> (Boulenger, 1899)	Purpleface largemouth
<i>Serranochromis robustus jallae</i> (Günther, 1864)	Nembwe
<i>Serranochromis thumbergi</i> (Castelnau, 1861)	Brownspot largemouth
<i>Tilapia rendalli rendalli</i> (Boulenger, 1896)	Northern redbreast tilapia
<i>Tilapia ruweti</i> (Poll & Thys van den Audenaerde, 1965)	Okavango tilapia
<i>Tilapia sparrmanii</i> Smith, 1840	Banded tilapia
ANABANTIDAE	
<i>Microctenopoma intermedium</i> (Pellegrin, 1920)	Blackspot climbing perch
<i>Ctenopoma multispine</i> Peters, 1844	Many spined climbing perch
MASTACEMBELIDAE	
<i>Aethiomastacembelus frenatus</i> (Boulenger, 1901)	Long tail spiny eel

151 367 47

Table 3.1 continued: Fish species inhabiting the Okavango River system in Botswana (adapted from Skelton, Bruton, Merron & Van der Waal 1985) divided into families.

Species	Common name
<i>Sargochromis codringtonii</i> (Boulenger, 1908)	Green happy
<i>Sargochromis giardi</i> (Pellegrin, 1903)	Pink happy
<i>Sargochromis greenwoodi</i> (Bell-Cross, 1975)	Greenwood's happy
<i>Sargochromis gracilis</i> Greenwood, 1984	Slender happy
<i>Serranochromis altus</i> Winemiller & Kelso-Winemiller, 1990	Humpback largemouth
<i>Serranochromis angusticeps</i> (Boulenger, 1907)	Thinface largemouth
<i>Serranochromis longimanus</i> (Boulenger, 1911)	Longfin largemouth
<i>Serranochromis macrocephalus</i> (Boulenger, 1899)	Purpleface largemouth
<i>Serranochromis robustus jallae</i> (Günther, 1864)	Nembwe
<i>Serranochromis thumbergi</i> (Castelnau, 1861)	Brownspot largemouth
<i>Tilapia rendalli rendalli</i> (Boulenger, 1896)	Northern redbreast tilapia
<i>Tilapia ruweti</i> (Poll & Thys van den Audenaerde, 1965)	Okavango tilapia
<i>Tilapia sparrmanii</i> Smith, 1840	Banded tilapia
ANABANTIDAE	
<i>Microctenopoma intermedium</i> (Pellegrin, 1920)	Blackspot climbing perch
<i>Ctenopoma multispine</i> Peters, 1844	Many spined climbing perch
MASTACEMBELIDAE	
<i>Aethiomastacembelus frenatus</i> (Boulenger, 1901)	Long tail spiny eel

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CHAPTER 4



Materials and Methods

FIELDWORK

Fieldwork for this research project was conducted in the Okavango River and Delta in Botswana during June and July in both 1998 and 1999. Collections during 1998 were concentrated in the riverine panhandle where fully equipped field laboratories were set up at two strategic localities. The first of which was at Xaro (Fig. 4.1A) near the beginning of the panhandle and the second at Guma Lagoon, which is situated at the beginning of the delta. Collections during 1999 also took place in the riverine panhandle, but were subsequently concentrated in the delta region. A large mobile field laboratory barge (Fig. 4.1C & D) was constructed and used to travel from the panhandle into the delta region. This barge contained a fully equipped field laboratory and sleeping quarters, allowing sampling to take place in isolated areas, impossible to reach by land. The specific localities collected from in 1998 and 1999 were as follows:

PANHANDLE LOCALITIES

XARO MAINSTREAM- This habitat was characterised by relatively fast flowing, clear water with little vegetation other than the marginal papyrus banks. Mainstream habitats such as this predominate in the panhandle and as well as in the main distributary rivers.

LLOYDS LAGOON (Fig. 4.1B)-This was a lagoon formed by an inlet situated just off the mainstream. Mainstream lagoons such as this are open secluded bodies of water with quite a lot of vegetation such as water lilies. Hardly any dead plant material could be seen lying on the bottom of this lagoon. These lagoons have a very slow, continuous exchange of fresh water, which is filtered through the papyrus beds from the mainstream.

MOKORO LAGOON-Also a mainstream lagoon with similar characteristics to Lloyds Lagoon. This lagoon was, however, much more isolated from the mainstream with only a very narrow entrance, packed full with papyrus.

XARO BACKWATERS and MOHEMBO BACKWATERS (Fig. 4.1E)-These localities were situated in the panhandle and may be described as bodies of water totally isolated from the mainstream. Backwater habitats such as these are generally associated with mainstream environments and are permanent bodies of water that are isolated to such an extent that they exhibit no flow of water. Large amounts of decaying plant material could also be seen lying on the bottom of these backwater localities.

MOHEMBO FLOODPLAINS- This locality may be described as a shallow floodplain pool separated from the mainstream environment when the water levels are low.

DELTA LOCALITIES

GUMA LAGOON- This lagoon is a permanent, large, deep open body of water connected to the mainstream by a long narrow channel. Large amounts of dead fermenting plant material could be seen lying on the bottom of this lagoon.

ETSATSTA MAINSTREAM (Fig. 4.1F)-This mainstream environment is situated at the beginning of the upper permanent swamp and shows the same characteristics as Xaro Mainstream.

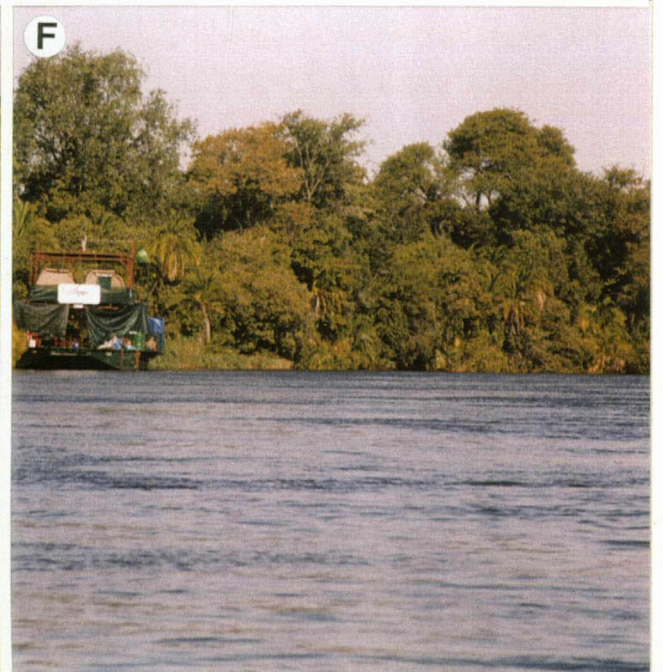
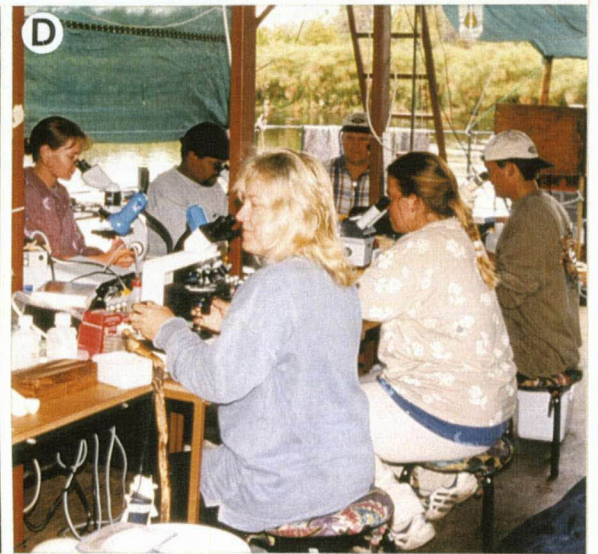
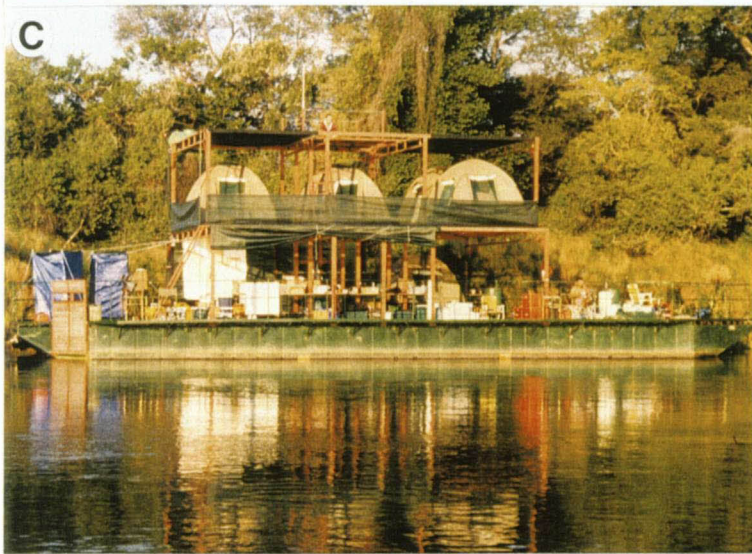
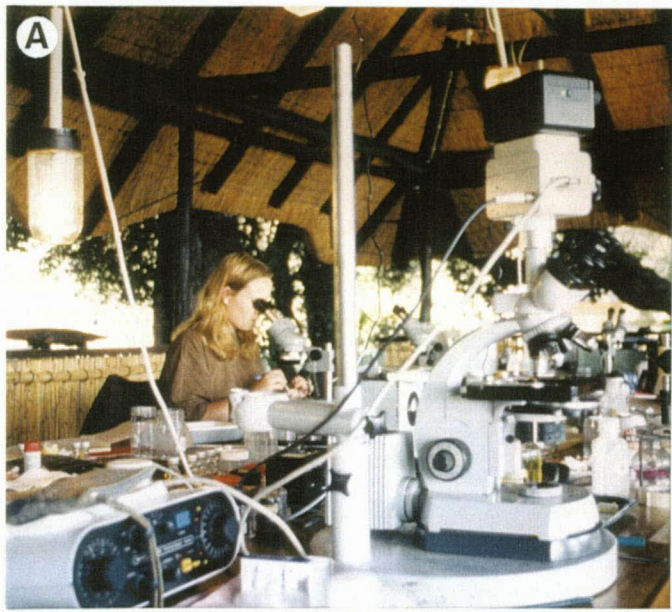
THOAGE LAGOON- Shows the same characteristics as Guma Lagoon, but is situated much closer to the mainstream and is not as deep. Decaying plant material could be seen lying on the bottom of this lagoon.

DUBA LAGOON- This lagoon is also similar to Guma Lagoon, but is situated further south, almost in the centre of the permanent swamp.

Figure 4.1

Photographs illustrating the mobile field laboratories of the Aquatic Parasitology laboratory as well as several of the collection localities

- A:** Field laboratory during 1998 at Xaro Camp in the panhandle
- B:** Lloyds Lagoon collection locality during 1998 in the panhandle
- C:** "Nembwe" the mobile field laboratory barge used during 1999
- D:** Field laboratory set up on "Nembwe"
- E:** Mohembo Backwaters collection locality during 1999 in the panhandle
- F:** Etsatsta Mainstream collection locality during 1999



COLLECTION OF FISH HOSTS

A permit for the collection of fish in Botswana has been included in Appendix II. Fish species were collected from the localities described above using a number of different methods. These methods were predetermined according to the type of habitat in which sampling was to take place.

HAND NETS- Small hand nets were used when collecting juvenile or small-sized fish species from mostly floodplain and backwater pools (Fig. 4.2A). These hand held nets had a very small mesh size and thus enabled the collection of small fish. Whilst the collectors wore waders or gumboots, the hand nets were plunged into the pools and pulled through the water as fast as possible to try and capture the elusive tiny fish.

SEIN NETS- A sein net, with relatively small mesh size, was used to collect small fish specimens in the larger floodplain pools and backwaters, where the volume of water was too high to use the conventional hand nets. Two workers were required to use the sein net. In most cases it was necessary to wear waders, while the two people concerned, placed on opposite sides of the net, dragged it across a section of the entire floodplain pool (Fig. 4.2B).

CAST NETS- Cast nets were used to collect fish in areas where small shoals of fish were visible. These areas were mostly in larger floodplain pools as well as smaller lagoons and secluded lagoons just off the mainstream (Fig. 4.2C). Cast nets were placed across one shoulder of the worker and then cast over the water, in order to spread the nets full diameter. Weights placed along the circumference allow the net to sink to the bottom very quickly, consequently trapping unwary fish.

GILL NETS- A series of gill nets, ranging in mesh size from 70 mm to 150mm, was used to collect fish in the large lagoons (Fig. 4.2D). The nets were positioned in the late afternoon and left in the water over night. Early the next morning they were removed. This was to ensure that most of the fish trapped in the nets would still be alive.

ROD AND LINE- It was necessary to apply conventional rod and line methods for some of the larger predatory fish species occurring in the mainstream and surrounding lagoons (Fig. 4.2E & F).

EXAMINATION OF FISHES

Fishes collected by the various methods described were taken back to the mobile field laboratories where they were kept alive in aerated aquaria containing fresh river water. Fish species collected were identified with the aid of Skelton (1993) which allowed fast identification of the fish. All fishes collected were measured in millimeters (mm) from the tip of the snout to the tips of the caudal fin and all measurements of fishes collected were illustrated in the table of results as follows:

AVERAGE (MINIMUM – MAXIMUM)

If less than five individuals of a certain species were examined, their lengths have all been recorded, for example 23, 56, 43, 44. Fish species name authors have only been included for those fish species examined for the purpose of this research project. In any references to other fish species from literature, the authors have been omitted.

The skin, gill operculum, eyes and fins of the fish were examined, using a dissection microscope, for any external signs of myxosporean plasmodia. Some of the larger fish species were anesthetized using benzocaine before they were subject to further examination. Once dissected, the gills, gill arch and buccal cavities were examined, using a dissection microscope. Any other organs showing obvious signs of possible myxosporean infections were also examined.

In the case of detecting a possible myxosporean infection, a squash preparation of the tissue concerned was made. To prepare a squash preparation, a piece of tissue, approximately 5mm³, was crushed between a microscope coverslip and glass slide. The temporary preparation was then viewed at between 10X – 40X magnification, using a compound light microscope in order to determine the presence of any myxosporean spores.

Figure 4.2

Photographs illustrating collection methods used to collect fishes

- A:** Collecting small fish using a hand net
- B:** Collection of fish using a sein net
- C:** Collection of fishes using a cast net
- D:** Collection of fish using a series of gill nets
- E, F:** Collecting fish using a rod and line



PRESERVATION OF MYXOSPOREAN SPORES

The standard techniques when working with myxosporeans requires the observation of live spores, but due to the isolated collection localities mature myxosporean spores found in plasmodia were 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.

Permanent preparations were made by impregnating smears from organs infected with myxosporeans with silver nitrate. To prepare these slides, infected organs such as gills were smeared across a microscope slide, in order to spread the spores apart. This slide was then left to dry and 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 mounting media (Eukitt).

HISTOLOGY

Gill arches containing large numbers of plasmodia were fixed in 10 % buffered neutral formalin and sent to the Department of Anatomical Pathology in the Faculty of Medicine at the University of the Free State for histological sectioning. The sections were cut at 4 μm and were stained with Harris' Haematoxylin and counter stained with Eosin. Sections were viewed and photographed using a Zeiss Axiophot Photomicroscope at magnifications varying between 10X to 100X (oil immersion).

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 0.5 μm 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. 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. Then a drop of spores was placed on the surface of the coverslip containing the Polylysin. The spores were allowed to settle to the surface of the coverslip.

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 critical 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 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 removed from 10% buffered neutral formalin and rinsed in a 1:1 solution of phosphate buffer and 10 % buffered neutral formalin for approximately 30 seconds. The tissue was then placed in pure phosphate buffer after which it was post-fixed in 1% osmium tetroxide for approximately 2 hours. 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. The rest of the dehydration continued as follows:

- 50 % ethanol – leave for 15 minutes
- 70 % ethanol – leave for 15 minutes
- 90 % ethanol – leave for 15 minutes
- 100 % ethanol – leave for 15 minutes (repeat 3X)

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 2-3 μ m 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 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 then 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. Methods applied at the UFS were basically the same as the above-mentioned method.

MEASUREMENT OF MYXOSPOREAN SPORES

All of the spores measured were fixed in 10% buffered neutral formalin and were measured according to the guidelines provided by Lom and Arthur (1989) (Fig. 4.3). According to these authors, 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. Spore width is measured perpendicular to the length, in the plane of the suture. The units for measurements are all provided in micrometers (μm) and are presented in the descriptions of the species collected as follows:

MINIMUM-MAXIMUM (AVERAGE \pm STANDARD DEVIATION, NUMBER OF SPORES MEASURED)

Polar capsule measurements are presented as follows:

MINIMUM-MAXIMUM (AVERAGE \pm STANDARD DEVIATION, NUMBER OF SPORES MEASURED) (LEFT)
 \times MINIMUM-MAXIMUM (AVERAGE \pm STANDARD DEVIATION, NUMBER OF SPORES MEASURED) (RIGHT)

INFECTION LEVELS

Levels of infestation for the number of plasmodia per host are presented in Chapter 7 and were recorded as follows:

Number of plasmodia per fish host	Index
1-10	X
10-30	XX
30-100	XXX
100-500	XXXX
500+	XXXXX

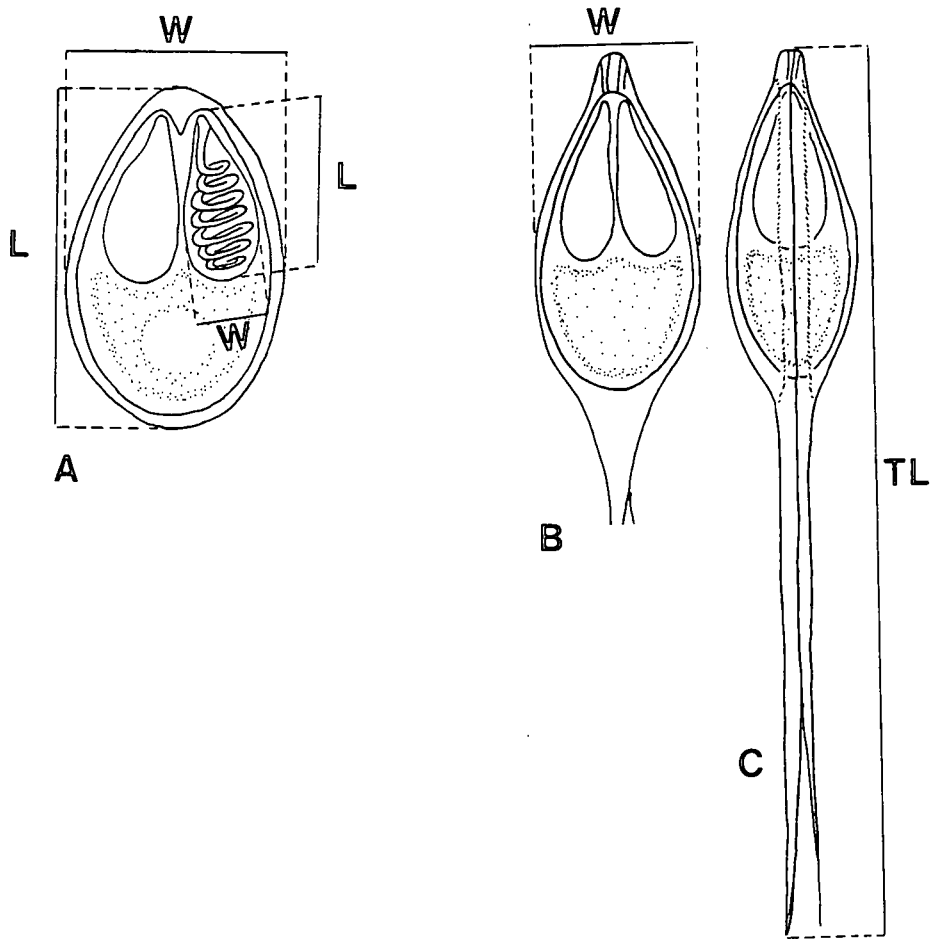


Figure 4.3: Methods of measuring myxosporean spores of the genera *Myxobolus* Butschli, 1882 (A) and *Henneguya* Thélohan 1892 (B & C) using the guidelines as illustrated by Lom and Arthur (1989). Polar capsule measurement is indicated in A. L-Length of the spore, W-width of the spore, TL-total length of *Henneguya* spores [Redrawn from Lom and Arthur (1989)]

In the case of high infection levels on the gills of readily collected fish species, the number of plasmodia were counted, with the gill arches numbered from number one to four as illustrated in Figure 4.4. The prevalence of each myxosporean infection in each fish species was calculated as a percentage as follows:

NUMBER OF INFECTED FISH

TOTAL NUMBER OF FISH EXAMINED × 100 = PREVALENCE (%)

MYXOSPOREAN MATERIAL

All myxosporean material collected from Botswana has been deposited in the collection of the Aquatic Parasitology Research Group at the Department of Zoology and Entomology, University of the Free State, Bloemfontein.

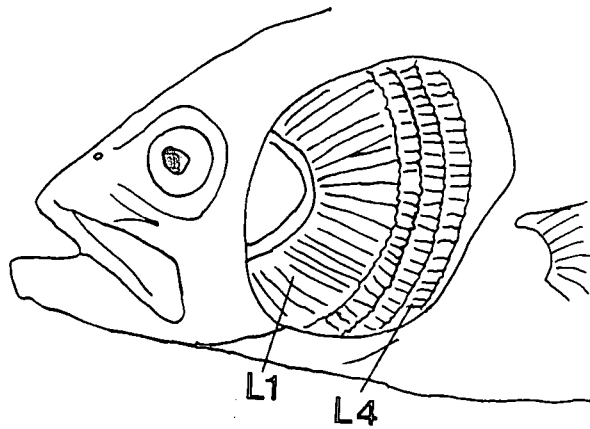


Figure 4.4: Diagram illustrating the numbering of gill arches L1-L4-Left hand gills numbered from 1 to 4, the same applies to the right gills.

CHAPTER 5



The genus *Henneguya* Thélohan, 1892

The genus *Henneguya* was created in 1892 by Thélohan and has since grown in size to more than 120 known species distributed throughout the world. Thirteen of these species have been described from Africa. Fomena and Bouix (1987, 1996a, b), contributed substantially to the knowledge on the distribution of this genus by describing seven of the 13 African *Henneguya* species from water bodies in Cameroon. Abolarin (1971a), Landsberg (1987), Obiekezie and Enyenihi (1988) as well as Ashmawy *et al.* (1989) and Kostoingue *et al.* (1999) described the remainder of these species. Included in the paper of Fomena and Bouix (1996a) was the description of two *Henneguya* species that were not allocated names. One of these was later described as *Henneguya ctenpomae* Fomena & Bouix 1996 by Fomena & Bouix (1996b). Since the remaining unnamed species resembles, in some ways, one of the species found in the Okavango fishes, it has been included in Table 5.1 (which provides a summary of all the known African *Henneguya* species infecting freshwater fish, type hosts and localities). This *Henneguya* species will subsequently be referred to as *Henneguya* sp. 1. *Henneguya* species described from Israel have also been included because a number of them have been recorded in Africa.

Myxosporeans of the genus *Henneguya* are characterised by having rounded, ellipsoid or spindle-shaped spores that are biconvex in sutural view (Fig. 5.1). The spores have two smooth shell valves with an extended caudal projection and two polar capsules, which may sometimes be very elongated (Lom & Dyková 1992). Most species are found histozoically in freshwater fish, but are occasionally also found parasitising marine fish (Lom & Dyková 1992). Two branchial forms have been recorded to infect fishes (Fomena & Bouix 1996a). The intralamellar (intercapillary) form develops within the blood capillaries and is not considered pathogenic and the interlamellar form develops amongst the basal epithelial cells of the lamellae and is highly pathogenic.

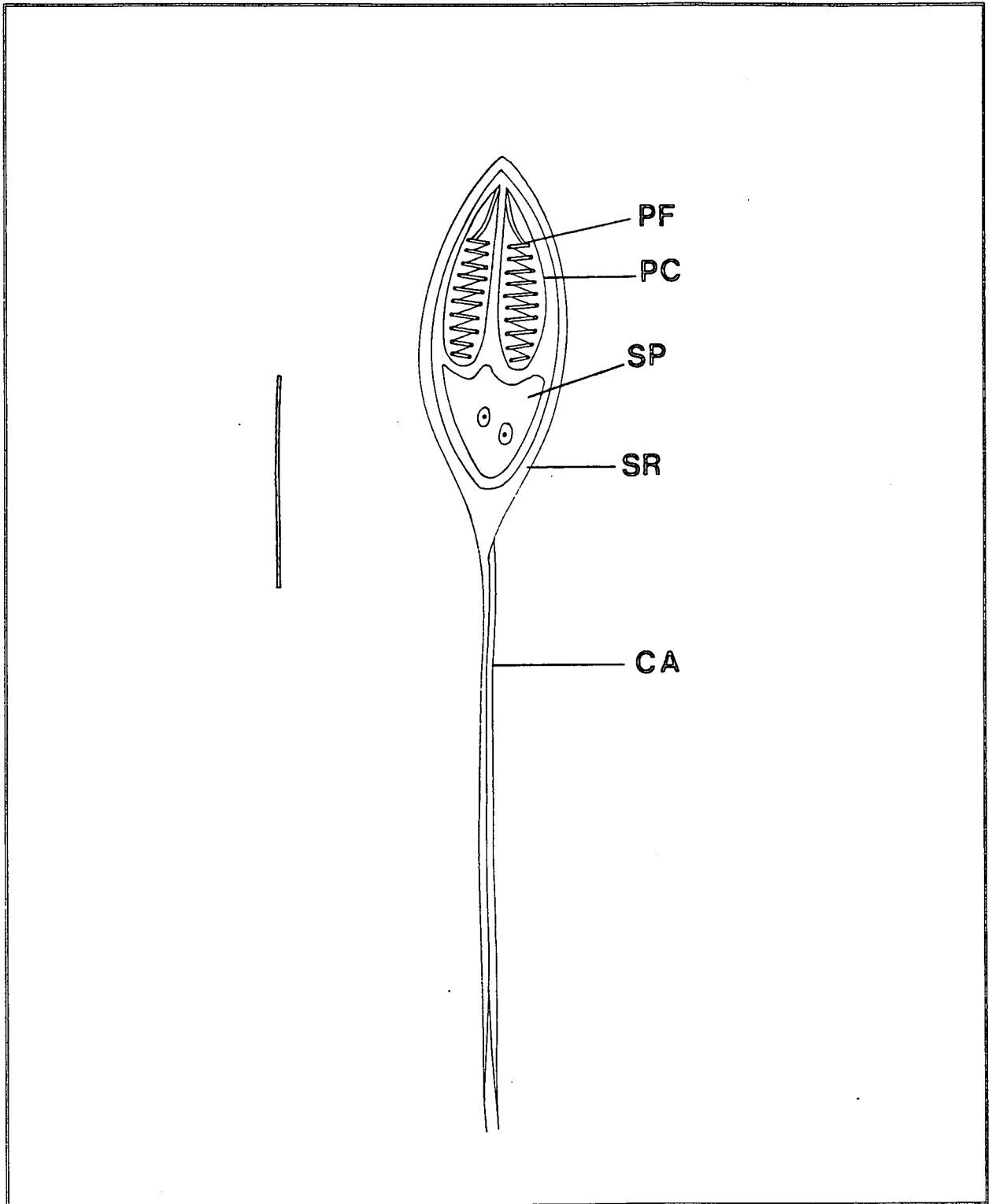


Figure 5.1: Line drawing of a *Henneguya suprabranchialis* Landsberg, 1987 spore illustrating specific morphological characteristics of *Henneguya* Thélohan, 1892 species [Redrawn from Landsberg (1987)]. PF-Polar filament, PC-Polar capsules, SP-Sporoplasm, SR-Sutural ridge, CA-Caudal appendages. Scale Bar: 10 μ m.

In Africa, limited knowledge on the pathological effects of *Henneguya* species is available, with most publications involving species descriptions that sometimes briefly mention pathological effects caused by the new species. In order to compare the myxosporeans from the genus *Henneguya* found infecting Okavango fishes, a brief description of the known African *Henneguya* species will be provided. This will be followed by a detailed description of the *Henneguya* species found infecting Okavango fishes.

Table 5.1: Compendium summarising the African species from the genus *Henneguya* Thélohan, 1892 infecting freshwater fish.

<i>HENNEGUYA BOPELETI</i> FOMENA & BOUX, 1987	
<p>Type host: <i>Chrysichtys nigrodigitatus</i></p> <p>Locality: Cameroon</p> <p>Location: Gills</p> <p>Figure: 5.2 A</p>	
REMARKS	
<p>This species is characterised by rounded plasmodia, which are found in the secondary gill lamellae of the host, varying in size from 192-450µm×116-303µm in diameter. The spores are ovoid in valvular view with two relatively long caudal appendages separated from their base. Two polar capsules of equal size are found in the anterior half of the spore and seven coils are visible in the polar filament.</p>	
MEASUREMENTS	
<p>Total length: 41-48µm</p> <p>Spore body length: 15-19µm</p> <p>Spore width: 5.5-7µm</p> <p>Polar capsules: 7-9µm (L)×1.5-2.5µm (W)</p>	
<p>Reference: Fomena & Bouix (1987)</p>	

Table 5.1 continued: Compendium summarising the African species from the genus *Henneguya* Thélohan, 1892 infecting freshwater fish.

<i>HENNEGUYA BRANCHIALIS</i> ASHMAWY, ABU-ELWAFI, IMAM & EL-OTIFI, 1989	
Type host: <i>Clarias lazera</i>	
Country: Nile River (Egypt)	
Location: Gills	
Figure: 5.2 B	
REMARKS	
The plasmodia are found in between the bases of the gill filaments and the tips of the secondary respiratory organ. The spores are elongated and fusiform with two identically elongated polar capsules that lie parallel to one another.	
MEASUREMENTS	
Caudal appendage length: 15.5-23.5 µm	
Spore body length: 12.5-17.5µm	
Spore width: Unknown	
Polar capsules: 6-8.5µm (L)×1.5-3µm (W).	
Reference: Ashmawy, Abu-Elwafi, Imam & El-Otifi (1989)	
<i>HENNEGUYA CAMEROUNENSIS</i> FOMENA & BOUX, 1987	
Type host: <i>Synodontis batesii</i>	
Country: Cameroon	
Location: Gills	
Figure: 5.2 C	
REMARKS	
Polysporous plasmodia are found within the primary and secondary gill filaments. The spore body is ovoid in valvular view with two pyriform shaped polar capsules present in the anterior halve of the spore body. Two smooth shell valves are present with two caudal appendages that are occasionally fused.	
MEASUREMENTS	
Total length: 13.5-21.5µm	
Spore body length: 9-11µm	
Spore width: Unknown	
Polar capsules: 4.5-6.5µm (L)×1-2µm (W)	
Reference: Fomena & Bouix (1987)	

Table 5.1 continued: Compendium summarising the African species from the genus *Henneguya* Thélohan, 1892 infecting freshwater fish.

<i>HENNEGUYA CHRYSICHTHYI</i> OBIKEZIE & ENYENIHI, 1988	
<p>Type host: <i>Chrysichtys nigrodigitatus</i></p> <p>Country: Nigeria</p> <p>Location: Gills</p> <p>Figure: 5.2 D</p>	
REMARKS	
<p>The polysporous whitish plasmodia are found predominantly on the primary gill filaments, between the secondary gill lamellae. The plasmodia tend to occur mostly near the tips of the filaments and are oval to broadly round, tapering to one end. The mature spores have an ovoid spore body in valvular view with the anterior end of the spore body bluntly pointed. The two shell valves are smooth and each taper to a long pointed tail and two polar capsules of unequal size are situated in the anterior half of the spore.</p>	
MEASUREMENTS	
<p>Total length: 27-32µm</p> <p>Spore body length: 13.7-16µm</p> <p>Spore width: 4.6-6.3µm</p> <p>Larger polar capsules: 4.5-5.5µm (L)×1-1.5µm (W)</p> <p>Smaller polar capsules: 4-4.5µm (L)×1.5-2µm (W)</p>	
<p>Reference: Obiekezie & Enyenihi (1988)</p>	
<i>HENNEGUYA CLARIAE</i> ABOLARIN, 1971	
<p>Type host: <i>Clarias lazera</i></p> <p>Locality: River Niger, Samaru Dam, Shika Stream (Nigeria)</p> <p>Location: Gills</p> <p>Figure: 5.2 E</p>	
REMARKS	
<p>The mature plasmodia of this species are found in the primary gill filaments and occasionally in the gill arch, opercular depressions and the gill rakers of <i>C. lazera</i>. The plasmodia might be as large as four millimeters in diameter. The caudal appendages appear to be fused and the spore body is elliptical in shape and contains two polar capsules in the anterior half. The polar capsules are mostly of equal length, but occasionally some spores have one polar capsule shorter and fatter than the other. An iodophilous vacuole is present in the sporoplasm of the spore. No sutural ridge or line was visible to the author.</p>	
MEASUREMENTS	
<p>Total length: 45-105µm</p> <p>Spore body length: 17.5-28.5µm</p> <p>Spore width: 5.5-8.5µm</p> <p>Polar capsules: 5-13.5µm (L)×2.5-3.5µm (W).</p>	
<p>Reference: Abolarin (1971a)</p>	

Table 5.1 continued: Compendium summarising the African species from the genus *Henneguya* Thélohan, 1892 infecting freshwater fish.

<i>HENNEGUYA CTENOPOMAE</i> FOMENA & BOUX, 1996	
Type host: <i>Ctenopoma nanum</i>	
Country: Cameroon	
Location: Gills	
Figure: 5.2 F	
REMARKS	
The mature spores are ovoid in valvular view and have a rounded anterior half with the posterior half of the spore slightly more tapered to form a blunt point. Two short caudal appendages extend from the shell valves and two polar capsules situated in the anterior half of the spore body.	
MEASUREMENTS	
Total length: 17-25µm	
Spore body length: 13-17µm	
Spore width: 8-10.5µm	
Polar capsules: 5-5.5µm (L)×2-3µm (W).	
Reference: Fomena & Bouix (1996b)	

<i>HENNEGUYA FUSIFORMIS</i> KOSTOINGUE, FALL, FAYE & TOGUEBAYE, 1999	
Type host: <i>Clarias anguillaris</i>	
Locality: Chad	
Location: Gills	
Figure: 5.3 A	
REMARKS	
The plasmodia of this species are ovoid and whitish in colour, measuring 0.25-2.5 mm. The spores are fusiform in frontal view and contain two equally sized, pyriform shaped polar capsules, one located behind the other. Within the polar capsules the polar filaments coils 5 to 6 times. A large quantity of sporoplasm occupies half of the spore and the caudal appendage is equal in length and divergent, curving outwards.	
MEASUREMENTS	
Total length: 59-61µm	
Spore body length: 29-33 µm	
Spore width: 5-7µm	
Polar capsules: 5-6µm (L)×3-4µm (W)	
Reference: Kostoingue, Fall, Faye & Toguebaye (1999)	

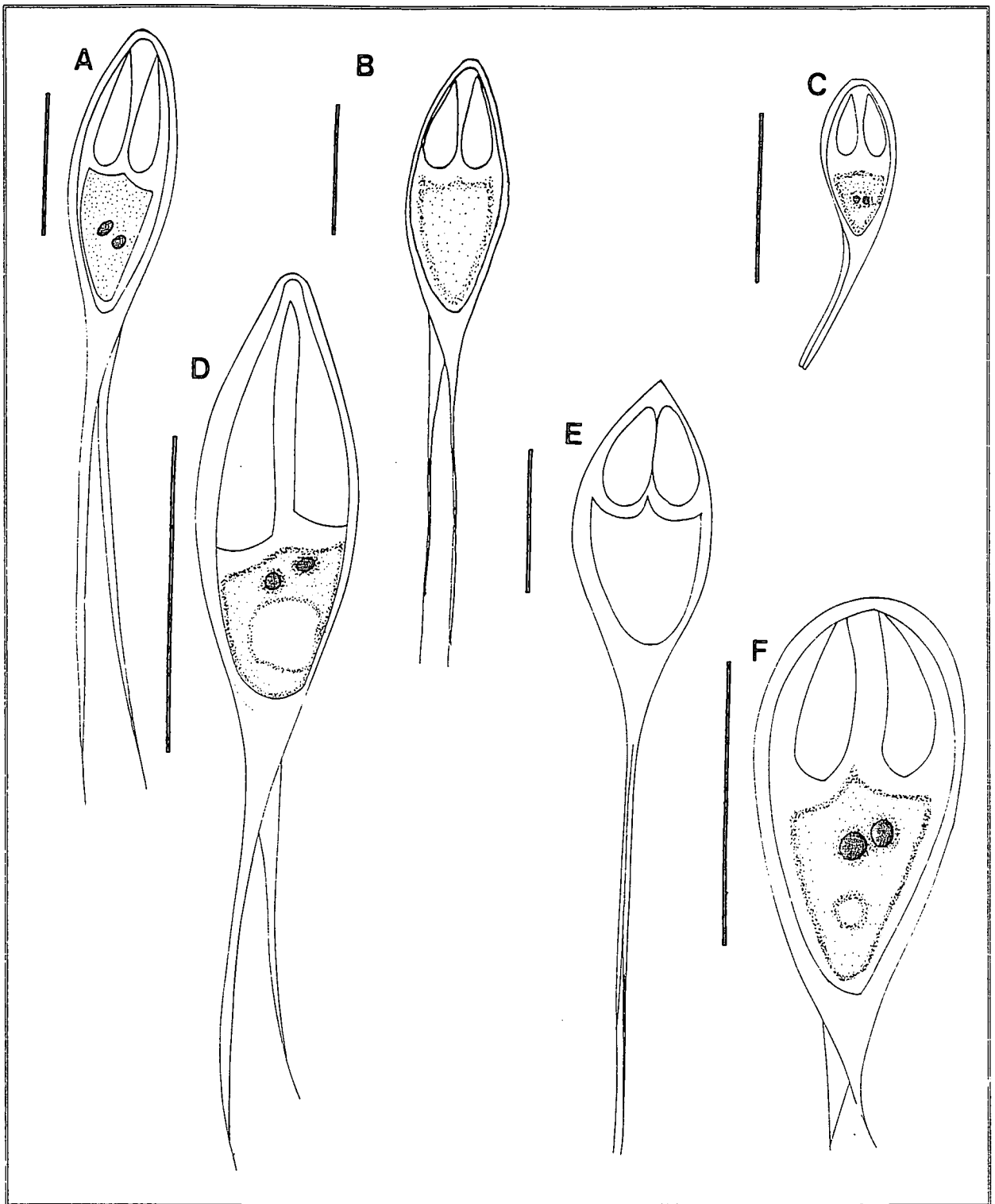


Figure 5.2: Line drawings of, **A-***Henneguya bopeleti* Fomena & Bouix, 1987, **B-***H. branchialis* Ashmawy, Abu-Elwafa, Imam & El-Otifi, 1989, **C-***H. camerounensis* Fomena & Bouix, 1987, **D-***H. chrysichthys* Obiekezie & Enyenihi 1988, **E-***H. clariae* Abolarin, 1971 and **F-***H. ctenopomae* Fomena & Bouix, 1996 [Redrawn from Abolarin (1971a), Fomena & Bouix (1987), Obiekezie & Enyenihi (1988), Ashmawy, Abu-Elwafa, Imam & El-Otifi (1989) and Fomena & Bouix (1996a)]. Scale Bar: 10µm.

Table 5.1 continued: Compendium summarising the African species from the genus *Henneguya* Thélohan, 1892 infecting freshwater fish.

<i>HENNEGUYA LATEROCAPSULATA</i> LANDSBERG, 1987
<p>Type host: <i>Clarias lazera</i> Locality: Israel Location: Dermis between the pectoral and pelvic fins Figure: 5.3 B</p>
REMARKS
<p>The polysporous plasmodia are found in the dermis, situated between the pectoral and pelvic fins and are pale yellow and round to irregular in shape. The structure of the plasmodia is smooth and flattened and found just below the epidermis. Mature spores are fusiform in valvular view with a the widest point of the spore near the posterior end of the anterior most polar capsule. The anterior end of the spore tapers sharply to form a blunt, rounded point with the posterior end also tapering, but being more rounded. The spore body is smooth and composed of two symmetrical valves each tapering beyond the end of the spore cavity to form a broad caudal base. The caudal appendages are separate, thick and divergent, tending to curve half way along the length. The polar capsules are equal in size and pyriform to flask-shaped, tapering to an extended, bluntly pointed neck region with one polar capsule always displaced laterally.</p>
MEASUREMENTS
<p>Total length: 29-36.2µm Spore body length: 13.8-16µm Spore width: 3.7-5.3µm Polar capsules: 4.1-5.3µm (L)×2.2-3µm (W)</p>
<p>Reference: Landsberg (1987)</p>

<i>HENNEGUYA MALAPTERURI</i> FOMENA & BOUIX, 1996
<p>Type host: <i>Malapterurus electricus</i> Country: Cameroon Location: Gills Figure: 5.3 C</p>
REMARKS
<p>In valvular view, the anterior of the spore is rounded and there is a distinct presence of a bulge at the base of the caudal appendages. Two polar capsules are present with 4-5 coils per filament.</p>
MEASUREMENTS
<p>Total length: Unknown Spore body length: 14-18µm Spore width: 8.5-11µm Polar capsules: 5-7.5µm (L)×3-4µm (W).</p>
<p>Reference: Fomena & Bouix (1996b)</p>

Table 5.1 continued: Compendium summarising the African species from the genus *Henneguya* Thélohan, 1892 infecting freshwater fish.

<i>HENNEGUYA NTEMENSIS</i> FOMENA & BOUIX, 1996
<p>Type host: <i>Breinomyrus brachyistus</i></p> <p>Country: Seng River (Cameroon)</p> <p>Location: Gall-bladder wall, kidneys and spleen</p> <p>Figure: 5.3 D</p>
REMARKS
<p>The vegetative stages of this species were not observed. Only diffuse mature spores were found in the affected organs, isolated or grouped, numbering tens to hundreds. The mature spores are very small and ovoid in shape with the anterior end being wider and sometimes rounded. The shell valves are smooth and thin each tapering posteriorly into a thick and short extension. Both caudal appendages are of equal size and the polar capsules are large, pyriform and of equal size, occupying more than half of the spore cavity.</p>
MEASUREMENTS
<p>Total length: 12.5-20.5µm</p> <p>Spore body length: 9-12µm</p> <p>Spore width: 7-9µm</p> <p>Polar capsules: 5-5µm (L)×3-4µm (W).</p>
<p>Reference: Fomena & Bouix (1996a)</p>
<i>HENNEGUYA NYONGENSIS</i> FOMENA & BOUIX, 1996
<p>Type host: <i>Marcusenius moori</i></p> <p>Country: So'o village (Cameroon)</p> <p>Location: Gills</p> <p>Figure: 5.3 E</p>
REMARKS
<p>The plasmodia are ovoid, whitish in colour and located between the secondary gill lamellae or at the base of the primary gill filaments. Plasmodia varied in size between 45-270µm×32-170µm to 450-610µm×50-105µm. The spore body is ovoid in valvular view with its anterior end slightly pointed. The widest region of the spore is observed towards the posterior ends of the polar capsules and the shell valves are thin, smooth and prolonged by two filiform expansions, separated at the base. Both polar capsules are pyriform in shape and of equal size, each having a 'neck-like' structure at the anterior ends.</p>
MEASUREMENTS
<p>Total length: 30.5-36.5µm</p> <p>Spore body length: 10-14µm</p> <p>Spore width: 4.5-6.5µm</p> <p>Polar capsules: 5.5-7µm (L)×3µm (W)</p>
<p>Reference: Fomena & Bouix (1996a)</p>

Table 5.1 continued: Compendium summarising the African species from the genus *Henneguya* Thélohan, 1892 infecting freshwater fish.

<i>HENNEGUYA ODZAI</i> FOMENA & BOUIX, 1996	
<p>Type host: <i>Marcusenius moori</i> Country: Odza II (Cameroon) Location: Gills Figure: 5.3 F</p>	
REMARKS	
<p>These spores have elongate spore bodies with a rounded anterior end. Two tear drop shaped polar capsules can be seen in the anterior end of the spore.</p>	
MEASUREMENTS	
<p>Total length: 29-36µm Spore body length: 13-16µm Spore width: 3.5-4.5µm Polar capsules: 3-5µm (L)× 1-1.5µm (W)</p>	
<p>Reference: Fomena & Bouix (1996a)</p>	

<i>HENNEGUYA SUPRABRANCHIALIS</i> LANDSBERG, 1987	
<p>Type Host: <i>Clarias lazera</i> Locality: Israel Location: Tips of the suprabranchial respiratory organs Figure: 5.4 A</p>	
REMARKS	
<p>Pale yellow to white plasmodia are located at the tips of the suprabranchial respiratory organs (one millimetre in diameter). The mature spores are elongate to oval in valvular view with the anterior half of the spore narrow and rounded and the posterior half being blunt and rounded. The shell valves are smooth and each tapering markedly, forming the thin caudal base. The caudal process is thin and not normally separated, except at the pointed tips. The spores have a distinct sutural ridge and two equal, pyriform to straight polar capsules. The polar capsules are longer than half of the spore length and the sporoplasm is binucleate.</p>	
MEASUREMENTS	
<p>Total length: Spore body length: 12.2-14.3µm Spore width: 5.6-6.9µm Polar capsules: 7.0-8.1µm (L)×1.8-2.3µm (W).</p>	
<p>Reference: Landsberg (1987)</p>	

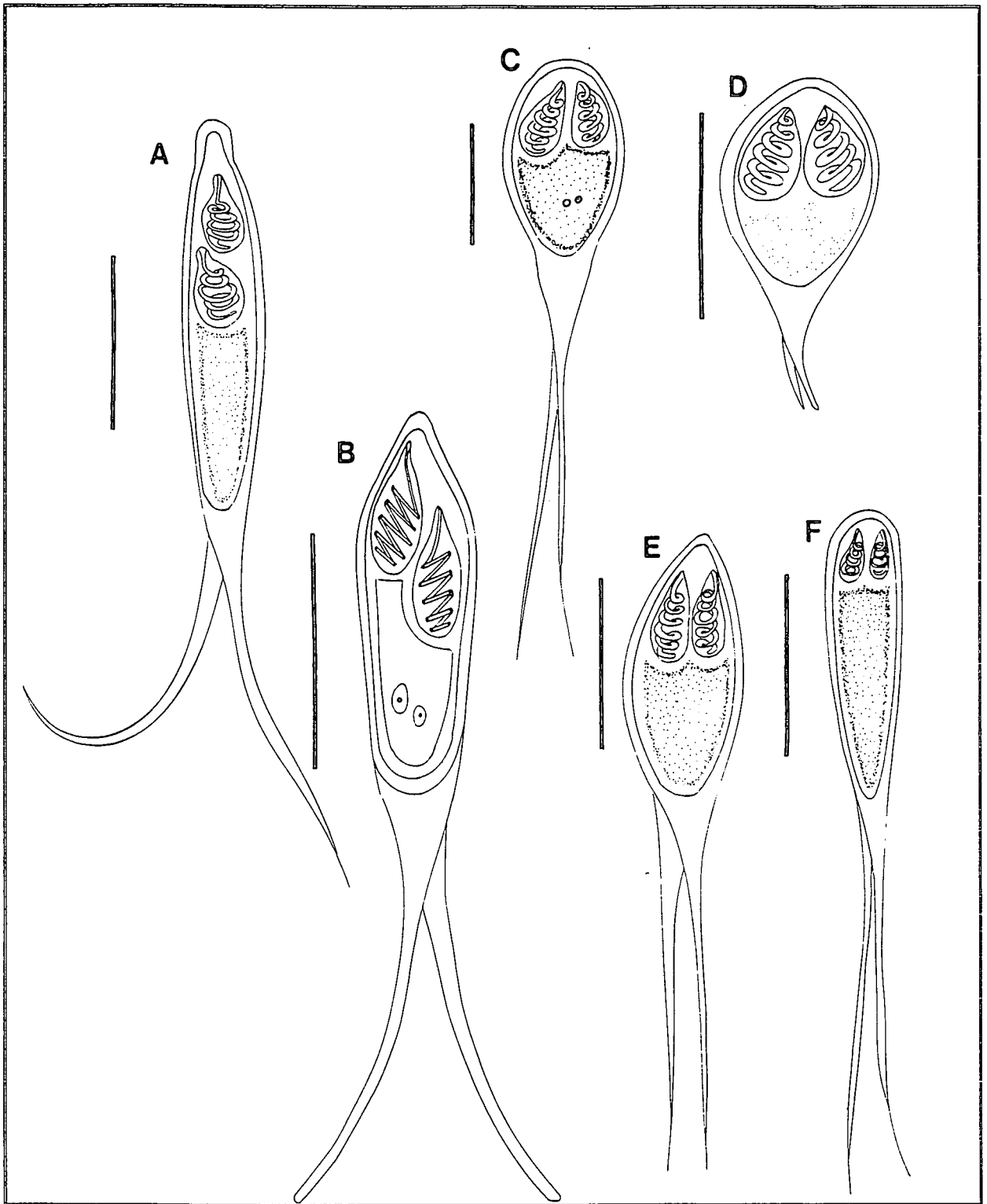


Figure 5.3: Line drawings of A-*Henneguya fusiformis* Kostoingue, Fall, Faye & Toguebaye, 1999, B-*H. laterocapsulata* Landsberg, 1987, C-*H. malapteruri* Fomena & Bouix, 1996, D-*H. ntemensis* Fomena & Bouix, 1996, E-*H. nyongensis* Fomena & Bouix, 1996, F-*H. odzai* Fomena & Bouix, 1996 [Redrawn from Landsberg (1987), Fomena & Bouix (1996a) and Kostoingue, Fall, Faye & Toguebaye (1999)]. Scale bar: 10 μ m.

Table 5.1 continued: Compendium summarising the African species from the genus *Henneguya* Thélohan, 1892 infecting freshwater fish.

<i>HENNEGUYA</i> SP. 1
<p>Host: <i>Ctenopoma maculatum</i></p> <p>Country: Cameroon</p> <p>Location: Gills</p> <p>Figure: 5.4 B</p>
REMARKS
<p>The plasmodia found in the gills of the host vary between 175-310×160-300µm in size. The spore body has an oval appearance in valvular view with the anterior end rounded. Two long filiform caudal appendages are present, clearly separated at the base with two pyriform-shaped polar capsules in the anterior of the spore.</p>
MEASUREMENTS
<p>Total length: 41-48µm</p> <p>Spore body length: 15-19µm</p> <p>Spore width: Unknown</p> <p>Polar capsules: 7-8.9µm (L)×1.6-2.5µm (W).</p>
<p>Reference: Fomena & Bouix (1987)</p>

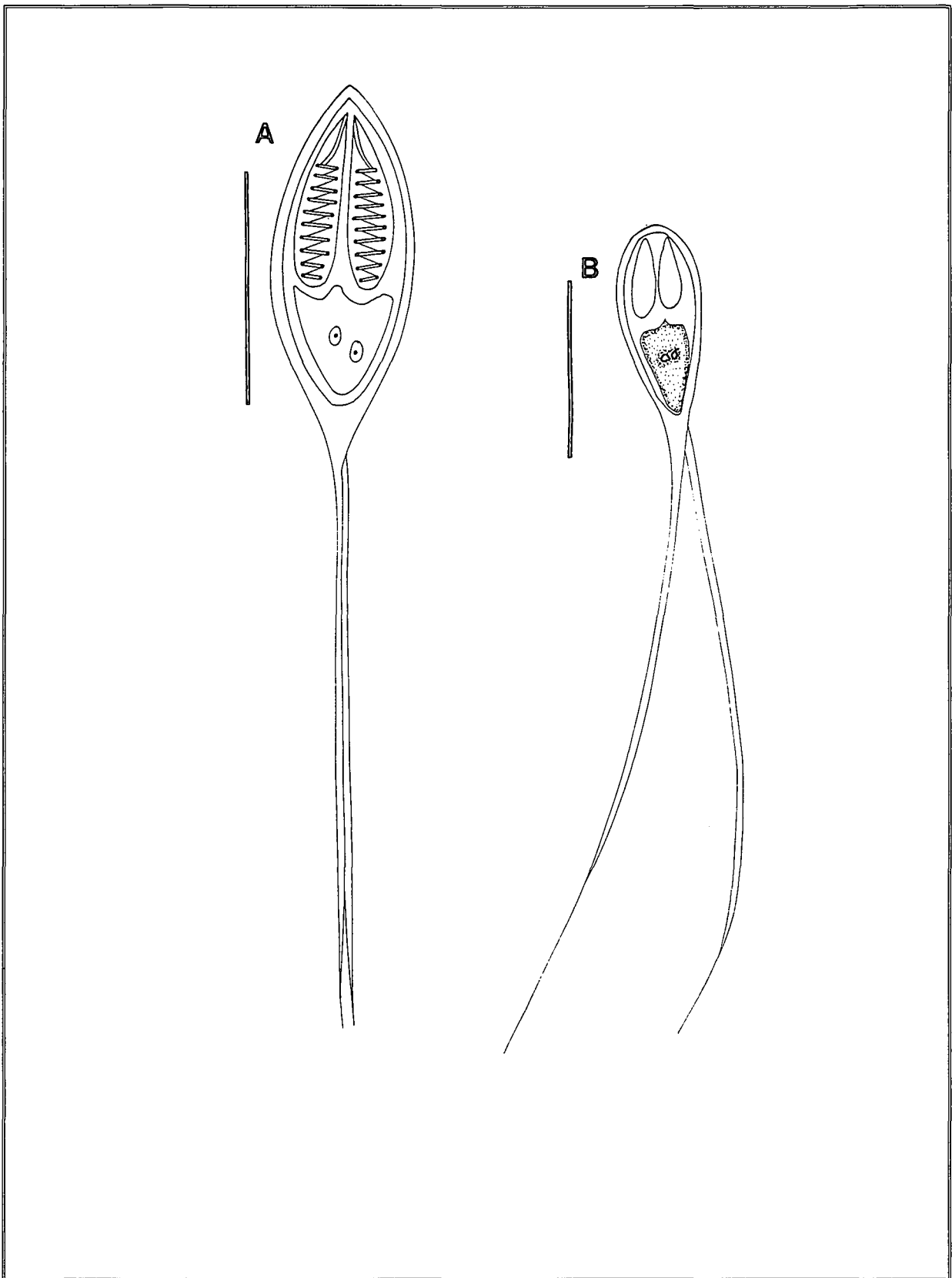


Figure 5.4: Line drawings of, **A-***Henneguya suprabranchialis* Landsberg, 1987, **B-***Henneguya* sp. 1 [Redrawn from Landsberg (1987) and Fomena & Bouix (1987)]. Scale bar: 10 μ m.

HENNEGUYA THELOHAN, 1892 SPECIES INFECTING OKAVANGO FISHES

***HENNEGUYA BRANCHIALIS* ASHMAWY, ABU-ELWAFI, IMAM & EL-OTIFI, 1989**

(Figs. 5.5 A, B, 5.6A, 5.7 A, E, F & 5.8 A)

Host I: *Clarias gariepinus* (Burchell, 1822),

Localities: Lloyds Lagoon, Duba Lagoon, Okavango River and Delta (Botswana)

Location: Within the cartilage of the suprabranchial organ

Prevalence: 11.1% (1/9)

Description:

Vegetative stages: Six sporogonic plasmodia were found within the cartilage at the tips of the suprabranchial respiratory organ. The polysporous plasmodia were round and yellowish in colour and measured 2-4mm in diameter.

The spore: The spore body is elongate to fusiform in valvular view with its anterior and posterior ends tapering to blunt points, measuring 16.2-17.2(17.2±0.5, 10)µm (Figs. 5.5A, 5.6A, 5.8A). The spore body is prolonged by two filiform and thin extensions that are separated with the total length of the spores measuring 38.4-43(40.4±1.85, 10)µm (Figs. 5.5A, 5.6A, 5.7A, 5.8A). Two occasionally, unequal, elongated pyriform shaped polar capsules are situated at the anterior end of the spore and lie parallel to each other measuring 7.5(7.5±0, 10)µm (L)×1.85(1.85±0, 10)µm (W) (Figs. 5.5A, 5.6A, 5.7E, 5.8A). The widest region of the spore is towards the posterior ends of the polar capsules measuring 5-6.25(6±0.50, 10)µm in width. The polar capsules contain polar filaments with nine coils (Fig. 5.7E) and fill almost two thirds of the spore cavity. Two smooth shell valves are visible (Fig. 5.7F) and the two filiform and long expansions are clearly separated at the base (Figs. 5.5A, 5.6A, 5.7A, 5.8A). A narrow sutural ridge is visible surrounding the spore body and it appears as if the spores contained a single binucleate sporoplasm with an iodophilous vacuole.

Host II: *Clarias theodora* Weber, 1897

Localities: Duba Lagoon, Okavango River and Delta, Botswana

Location: Secondary gill lamellae

Prevalence: 100% (1/1)

Description:

Vegetative stages: Sporogonic plasmodia were found within the secondary gill lamellae. The polysporous plasmodia were very small, rounded and whitish in colour. Unfortunately insufficient material made it impossible to provide measurements of the plasmodia.

The spore: In valvular view, the spore body is elongate to fusiform in shape with the anterior and posterior ends rounded to a blunt point, measuring 12-15(13.7 ± 1.06 , 10) μm (Fig. 5.5B). The spore body, extended by two relatively thin filiform expansions, was found to have a total length of 35-40(37.2 ± 2.20 , 10) μm . Two pyriform shaped polar capsules are situated at the anterior end of the spore and measure 5-7(6.1 ± 0.69 , 10) μm (L) \times 1-2(2 ± 0.53 , 10) μm (W) (Fig. 5.5B). The polar capsules appear to be almost parallel to one another and equal in length, taking up two thirds of the spore body length, with the widest region of the spore being at the posterior ends of the polar capsules measuring 4-6(5.2 ± 0.63 , 10) μm in width. Two smooth shell valves are visible and a narrow sutural ridge extends around the spore body. It appears as if the spores contain a single binucleate sporoplasm with an iodophilous vacuole present.

Remarks: Although the spores from *C. gariepinus* have slightly larger dimensions, than those found in the gills of *C. theodora*, both these species conform to the description of *H. branchialis*, since the spore dimensions of both fall within the range of this described species. *Henneguya branchialis* was originally described from the gills of *C. lazera*, which has been synonymised with our local catfish that occurs in southern Africa, namely *Clarias gariepinus* (Skelton 1993). *Clarias theodora* is a new host record.

Other *Henneguya* species infecting *Clarias* hosts in Africa include *H. clariae* Abolarin, 1971, *H. fusiformis* Kostoingue, Fall, Faye & Toguebaye, 1999 and *H. laterocapsulata* Landsberg, 1987. *Henneguya clariae* (Fig. 5.2E), is distinct from *H.*

branchialis in having caudal appendages that appear to be fused. According to Abolarin (1971a), a distinct sutural ridge is absent in *H. clariae*. Furthermore, the total spore length is also relatively longer than that of *H. branchialis*.

Henneguya fusiformis (Fig. 5.3A) and *H. laterocapsulata* (Fig. 5.3B) are distinct from *H. branchialis* due to the unique position of the polar capsules in this species. The spore body shape of *H. fusiformis* is fusiform in frontal view and has two polar capsules of which one is located behind the other (Kostoingue *et al.* 1999). Furthermore, the caudal appendages of *H. fusiformis* are thick and tend to curve away from each other, which differs from the thin straight appendages of *H. branchialis*. Similarly, *H. laterocapsulata* is distinct from *H. branchialis* in having a fusiform spore body that contains one polar capsule that discharges laterally. The caudal appendages of *H. laterocapsulata* are much thicker and curved, originating at a thick caudal base (Landsberg 1987), once again distinct from the thin fusiform appendages of *H. branchialis*.

Morphologically *H. branchialis* is similar to *Henneguya bopeleti* Fomena & Bouix, 1987 (Fig. 5.2A) found in the gills of *Chrysichtys nigrodigitatus*. The latter species does, however, have a longer total body length. Furthermore, the polar capsules of *H. bopeleti* extend to just less than half of the spore body (Fomena & Bouix 1987), while those of *H. branchialis* extend to almost three-quarters of the spore body length. At first observation, *H. branchialis* is also morphologically similar to *Henneguya nyongensis* Fomena & bouix, 1996 (Fig. 5.3E), found in the gills of *Marcusenius moori*. The polar capsules of *H. nyongensis* are, however, shorter and wider and occur in a spore body that is also shorter in length than that of *H. branchialis*. *Henneguya nyongensis* also only has four to five coils in each polar filament (Fomena & Bouix 1996a), compared to approximately eight to nine coils per polar capsule in *H. branchialis*.

HENNEGUYA SP. A**(Figs. 5.5C, 5.6B, 5.7B, 5.8B)****Host:** *Clarias gariepinus* (Burchell, 1822)**Localities:** Lloyds Lagoon, Duba Lagoon, Okavango River and Delta (Botswana)**Location:** Within the secondary gill lamellae**Prevalence:** 22.2% (2/9)**Description:**

Vegetative stages: One to four large, oval to oblong, mature sporogonic plasmodia were found extending into the primary gill filaments. The polysporous plasmodia were yellow to whitish in colour and contained hundreds of spores. They measured 2-5mm in length.

The spore: The mature spore body is elongated to oval in valvular view and has a bluntly pointed, narrow anterior end, measuring 12.3-15(13.7±0.8, 10)µm (Figs. 5.5C, 5.6B, 5.8B). The posterior end is narrowly rounded. The spore body, prolonged by two very filiform, narrow and long extensions, has a total length of 47-50.3(50.3±4.5, 10)µm (Figs. 5.5C, 5.6B, 5.7B, 5.8B). The caudal appendages are normally separated from each other and two pyriform to straight polar capsules of occasionally unequal size are visible in the anterior part of the spore measuring 5-7(6±0.62, 10)µm (Figs. 5.5C, 5.6B). The polar capsules are nearly parallel to each other filling just less than half of the spore body cavity 5-6(5.6±0.63, 10)µm (L)×1.25-1.85(1.55±0.3, 10)µm (W). The widest part of the spore is found towards the posterior of the polar capsules, measuring 5µm across. It appears as if each of the polar capsules contain eight coils in the polar filament. Two smooth shell valves are visible that extend into the two filiform projections (Fig. 5.7B). A narrow sutural ridge is visible and it appears as if the spores contain a single binucleate sporoplasm situated in the posterior part of the spore body.

Remarks: *Henneguya* species infecting similar hosts throughout Africa include *H. branchialis*, *H. clariae*, *H. fusiformis* and *H. laterocapsulata*. All of these myxosporeans were described from *Clarias lazera* in the northern part of the African continent.

Henneguya sp. A differs from *H. branchialis* (Fig. 5.2B) in having a shorter total spore length. The spore bodies are similar in length and thus the ratio of spore body length to total spore length is larger in *Henneguya* sp. A. Furthermore, the polar capsules of *H. branchialis* occupy more than half of the spore body (Ashmawy *et al.* 1989), compared to the polar capsules of *Henneguya* sp. A, that take up less than half of the spore body.

Henneguya sp. A differs from *H. clariae* (Fig. 5.2E) in that the plasmodia of the former are more ovoid to oblong in shape compared to the rounded plasmodia of the latter. Secondly, the caudal appendages of *H. clariae* are fused (Abolarin 1971a) and the total length of the spores is much longer than that of *Henneguya* sp. A. Finally the shape of the spore body of *H. clariae* also differs in having an almost sharply pointed anterior end with two unequally sized polar capsules.

Henneguya fusiformis (Fig. 5.3A) differs significantly from *Henneguya* sp. A in having a fusiform spore body that contains two polar capsules with one situated behind the other (Kostoingue *et al.* 1999). Furthermore, the caudal appendages of *H. fusiformis* are much thicker and tend to curve outwards compared to the thin filiform appendages of *Henneguya* sp. A.

Henneguya sp. A is distinct from *H. laterocapsulata* (Fig. 5.3B) 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. *Henneguya laterocapsulata* also has an anterior spore body which tapers significantly towards a blunt point, compared with the more gradually tapering anterior of *Henneguya* sp. A. The caudal appendages *H. laterocapsulata* extend from a thick caudal base (Landsberg 1987), which is absent in *Henneguya* sp. A and are also thick and divergent, curving outwards half way along its length. This is distinctly different to the thin filiform caudal appendages of *Henneguya* sp. A.

Morphologically *Henneguya* sp. A resembles *H. nyongensis*, *H. bopeleti* and *Henneguya* sp. 1. A number of differences may be noted between these species and *Henneguya* sp. A. *Henneguya nyongensis* (Fig. 5.3E) found in the gills of *Marcusenius moori* in Chad has a wider spore body than that of *Henneguya* sp. A and also differs from the latter in having distinctly shorter caudal appendages. *Henneguya*

sp. A is further distinct from *H. nyongensis* in not having the characteristic 'neck-like' appearance at the anterior ends of the polar capsules as described by Fomena & Bouix (1996a). The spores of *Henneguya* sp. A are much longer in total length than that of *H. nyongensis* and the polar capsules of *Henneguya* sp. A appear longer than those of *H. nyongensis* and consequently take up a larger proportion of the spore body cavity.

Parasitising *Chrysichtys nigrodigitatus* in Cameroon, *H. bopeleti* (Fig. 5.2A) strongly resembles *Henneguya* sp. A. The spore body length of *Henneguya* sp. A is, however, shorter, and the total spore length is longer than that of *H. bopeleti*. The proportions or ratio of spore body length to total spore length is thus smaller in *Henneguya* sp. A.

The spores of *Henneguya* sp. A also resemble *Henneguya* sp. 1 (Fig. 5.4B) recorded from *Ctenopoma maculatum* in Cameroon by Fomena and Bouix (1987), in having similar long caudal appendages. The overall spore dimensions of *Henneguya* sp. A also comply with that of *Henneguya* sp. 1, with only the shape of the spore bodies differing. The anterior end of the spore body of *Henneguya* sp. 1 is slightly broader and more rounded compared to the more narrowly elongated and bluntly pointed shape of the spore body of *Henneguya* sp. A. The length of the spore body of *Henneguya* sp. A is shorter than that of *Henneguya* sp. 1 and thus has a smaller ratio of spore body length to total length.

HENNEGUYA SP. B

(Figs. 5.5D, 5.6C)

Host: *Tilapia rendalli rendalli* (Boulenger, 1896)**Localities:** Lloyds Lagoon, Mohembo Floodplains, Okavango River and Delta,
(Botswana)**Location:** Gills**Prevalence:** 12.5% (1/8)**Description:***Vegetative stages:* No vegetative stages were seen, only spores.

The spore: In valvular view, the round spore body gently tapers to a bluntly rounded posterior end measuring 9.1-10.8(10±0.7, 10)µm in length (Figs. 5.5D, 5.6C). The spore body is extended by two very short caudal appendages and has an average total spore length of 11.5-13.9(13±1.1, 10)µm. Two almost spherical and identical polar capsules are situated at the rounded anterior end of the spore and measures an average of 2.5µm (L) × 2.5µm (W). The widest region of the spore is observed towards the posterior end and measures an average of 7µm in width. Two smooth shell valves are visible and a narrow sutural ridge passes around the entire spore body. The two short expansions are separated at the base and the polar capsules contain filaments with approximately six coils (Fig. 5.5D, 5.6C). It appears as if the spores contain a single large binucleate sporoplasm.

Remarks: No *Henneguya* species have been found parasitising *Tilapia* species in Africa and due to the nature of the very short caudal appendages associated with *Henneguya* sp. B the range of morphologically similar species in Africa is narrowed to two. These include *H. ctenopomae* Fomena & Bouix 1996 and *H. ntemensis* Fomena & Bouix, 1996.

Henneguya sp. B differs from *H. ctenopomae* (Fig. 5.2F) found in the gills of *Ctenopoma nanum* by Fomena & Bouix (1996b) in that the latter myxosporean species has a more elongate to oval body shape, with the anterior end of the spore tapering more sharply to a bluntly rounded point. Furthermore, the polar capsules of *H. ctenopomae* are narrowly elongated compared to the almost spherical polar

capsules of *Henneguya* sp. B. The total length of *H. ctenopomae* is also much longer than that of *Henneguya* sp. B.

The closest resemblance can be struck with *Henneguya ntemensis* (Fig. 5.3D), described from the kidneys of *Breinomyrus brachyistus* by Fomena and Bouix (1996), which also has a very rounded spore body and two very short caudal appendages that are separated. *Henneguya* sp. B is distinct from this species in having much smaller polar capsules that are more spherical and take up relatively little space in the spore body. The polar capsules of *H. ntemensis* are pyriform shaped and are relatively large taking up much of the spore body cavity.

Henneguya sp. B. is distinct from *H. branchialis* and *Henneguya* sp. A in that the caudal appendages are extremely shorter than any of these above mentioned species.

HENNEGUYA SP. C**(Figs. 5.5E, 5.6D, F, 5.7C, 5.8C)****Host:** *Marcusenius macrolepidotis* (Peters, 1852)**Localities:** Lloyds Lagoon, Duba Lagoon, Okavango River and Delta (Botswana)**Location:** Within the secondary gill lamellae**Incidence:** 80% (20/25)**Description:**

Vegetative stages: Many small sporogonic plasmodia were found within the secondary gill lamellae. The polysporous plasmodia were small, oval and whitish in colour, measuring 0.5mm in diameter.

The spore: The mature spores have an ovoid body that is very elongated and measures to 11.3-13.7(13±1.3, 10)µm (Figs. 5.5E, 5.6D, 5.7C, 5.8C). The anterior end of the spore is rounded and towards the posterior end it tapers to a blunt point. Two filiform expansions are visible at the posterior end of the spore body (Figs. 5.5E, 5.6D, 5.7C, 5.8C). Two small teardrop shaped polar capsules of equal size are visible at the anterior end of the spore body measuring 2.5-3.2(2.7±0.7, 10)µm (L)×1µm (W) (Figs. 5.5E, 5.6D, 5.8C). The widest region of the spore is observed towards the posterior ends of the polar capsules measuring 3.75-5(4.3±0.9, 10)µm in width. Two shell valves are visible that are smooth and the prolonged extensions are clearly separated at the base (Fig. 5.7C). The number of coils of the polar filament within the polar capsules is difficult to observe and it appears as if the spores contained a single binucleate sporoplasm.

Remarks: Species from the genus *Henneguya* infecting similar hosts include *H. nyongensis* Fomena & Bouix, 1996 and *H. odzai* Fomena & Bouix, 1996. This species is however distinct from many species like *H. bopeleti*, *H. camerounensis* Fomena & Bouix, 1987, *H. chrysichtyi* Obiekezie & Enyenihi, 1988, *H. clariae*, and *H. nyongensis* in having a rounded anterior spore body, rather than a bluntly pointed one. Species that resemble *Henneguya* sp. C are thus narrowed to *H. malapteruri* Fomena & Bouix, 1996 and *H. odzai* on the basis of having rounded anterior spore bodies.

Henneguya sp. C is most similar to *H. odzai* (Fig. 5.3F), which was described from the gills of *Marcusenius moori* by Fomena & Bouix (1996a). The spore body of *H. odzai* is, however, more elongated than the spore body of *Henneguya* sp. C. A comparison with *H. malapteruri* (Fig. 5.3C) reveals that the spore body of *Henneguya* sp. C is not as round to ovoid in shape as in the case of the former species. The relative sizes of the polar capsules of *Henneguya* sp. C are much smaller than those of *H. malapteruri*. Furthermore, *Henneguya* sp. C does not possess a bulge at the base of the caudal appendages as described for *H. malapteruri* by Fomena & Bouix (1996b).

***HENNEGUYA* SP. D**

(Figs. 5.5F, 5.6E, 5.7D, G, H, 5.8D)

Host: *Schilbe intermedius* Rüppell, 1832

Localities: Lloyds Lagoon, Guma Lagoon, Thoage Lagoon, Duba Lagoon, Okavango River and Delta, (Botswana)

Location: Secondary gill lamellae

Prevalence: 64.5% (51/79)

Description:

Vegetative stages: Only sporogonic plasmodia were found within the secondary gill lamellae. The polysporous plasmodia were ovoid and whitish in colour. They measured 33x9–28µm in size.

The spore: In valvular view, the spore body is ovoid in shape with its anterior end slightly pointed and measuring 12.5-17.5(14.4±1.6, 10)µm (Figs. 5.5F, 5.6E, 5.8D). Two filiform expansions can be observed towards the posterior end of the spore body with the total length of the spores measuring 33-37.5(34.1±2.5, 10)µm (Figs. 5.5F, 5.6E, 5.7D, 5.8D). Two elongated pyriform polar capsules are present in the anterior end of the spore body measuring 4-6.25(5.2±0.7, 10)µm (L)×1-1.25(1.1±0.1, 10)µm (W) (Figs. 5.5F, 5.6E, 5.7G, 5.8D). The widest region of the spore is observed towards the posterior ends of the polar capsules measuring 5-6.25(5.3±0.5, 10)µm. Two shell valves are visible. The shell valves are smooth and extended by two filiform and long expansions clearly separated from the base (Figs. 5.7D, G, H). A narrow sutural ridge is

visible and the polar filaments within the polar capsules contain approximately eight coils. It appears as if the spores contain a single binucleate sporoplasm.

Remarks: *Henneguya* sp. D may be compared with *H. chrysichtyi*, *H. clariae*, *H. bopeleti* and *H. nyongensis* due to similarities in the morphology of the spore bodies. No *Henneguya* species have been recorded from *Schilbe* species in Africa.

Henneguya sp. D differs from *H. bopeleti* (Fig. 5.2A) in having a more elongated to oval spore body shape and also having a shorter total spore length. The caudal appendages of *Henneguya* sp. D are shorter than those of *H. bopeleti* as described by Fomena and Bouix (1987) and the spore body of *Henneguya* sp. D thus takes up more of the total spore length than the spore body of the latter species.

Henneguya sp. D resembles *H. chrysichtyi* (Fig. 5.2D) in having similar spore body length and width. *Henneguya* sp. D, however, differs from *H. chrysichtyi* in having a longer total body length as well as two polar capsules of equal size.

Henneguya sp. D also differs from *H. clariae* (Fig. 5.2E) in having a more elongated spore body and more elongated polar capsules that are equal in length. The spore body of *H. clariae* tapers to a sharper degree than that of *Henneguya* sp. D. The caudal appendages of *Henneguya* sp. D are distinctly separate compared to the occasionally fused caudal appendages of *H. clariae*.

The shape and structure of this species appears to be very similar to *H. nyongensis* (Fig. 5.3E), but differs in the latter by having very distinct 'neck-like' structures at the anterior ends of the polar capsules (Fomena & Bouix 1996a), which are absent in *Henneguya* sp. D.

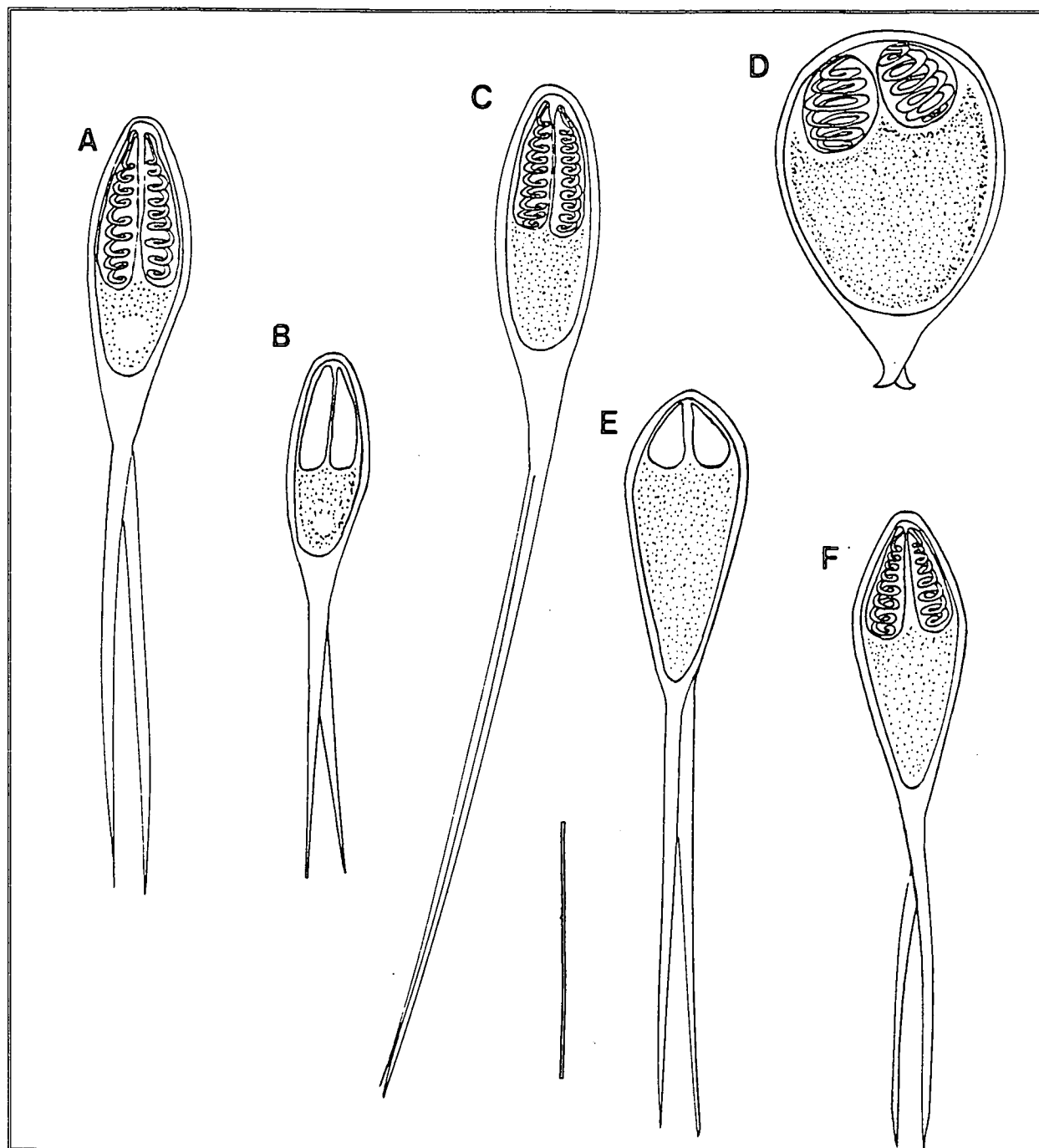


Figure 5.5: Line drawings of *Henneguya* Thélohan, 1892 species collected from the Okavango River and Delta, Botswana. **A-***Henneguya branchialis* Ashmawy, Abu-Elwafa, Imam & El-Otifi, 1989 from *Clarias gariepinus* (Burchell, 1822), **B-***H. branchialis* from *Clarias theodora*e Weber, 1897, **C-***Henneguya* sp. A, from the gills of *C. gariepinus*, **D-***Henneguya* sp. B from the gills of *Tilapia rendalli rendalli* (Boulenger, 1896), **E-***Henneguya* sp. C from the gills of *Marcusenius macrolepidotis* (Peters, 1852), **F-***Henneguya* sp. D from the gills of *Schilbe intermedius* Rüppell, 1832. Scale bar: A,C,D,E,F = 10µm, B = 15µm.

Figure 5.6

Compound light micrographs of *Henneguya* Thélohan, 1892 species collected from fishes in the Okavango River and Delta, Botswana

A: *Henneguya branchialis* Ashmawy, Abu-Elwafa, Imam & El-Otifi, 1989 from the suprabranchial organ of *Clarias gariepinus* (Burchell, 1822)

B: *Henneguya* sp. A from the gills of *C. gariepinus*

C: *Henneguya* sp. B from the gills of *Tilapia rendalli rendalli* (Boulenger, 1896)

D & F: *Henneguya* sp. C from the gills of *Marcusenius macrolepidotis* (Peters, 1852)

E: *Henneguya* sp. D from the gills of *Schilbe intermedius* Rüppell, 1832

Scale bar: 10µm

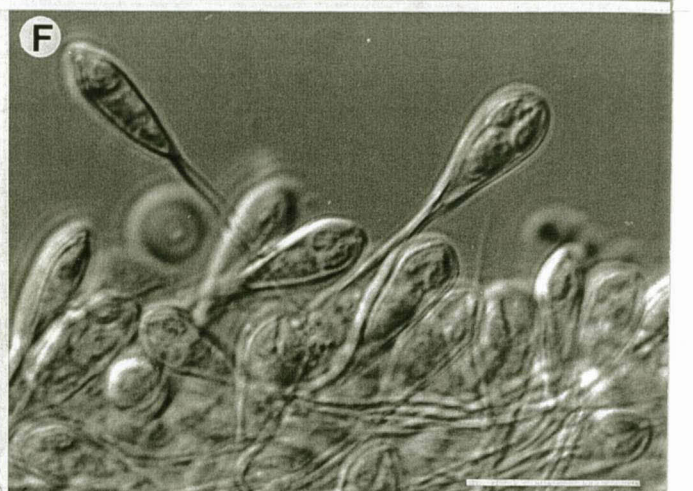
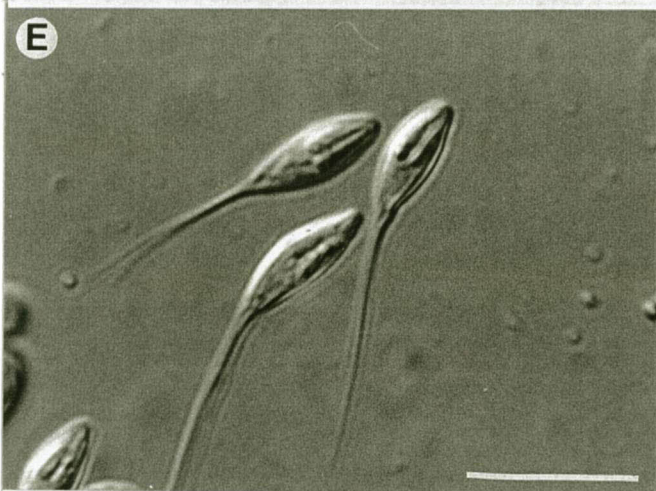
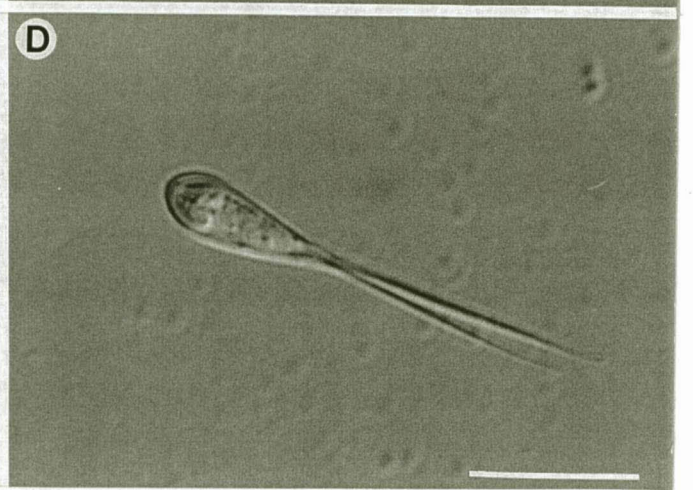
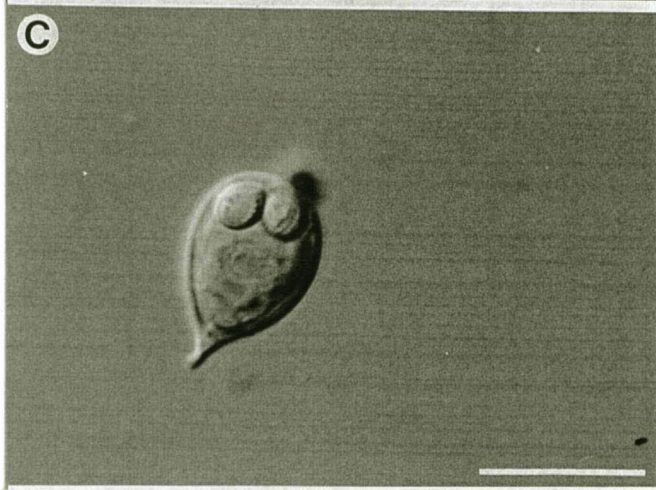
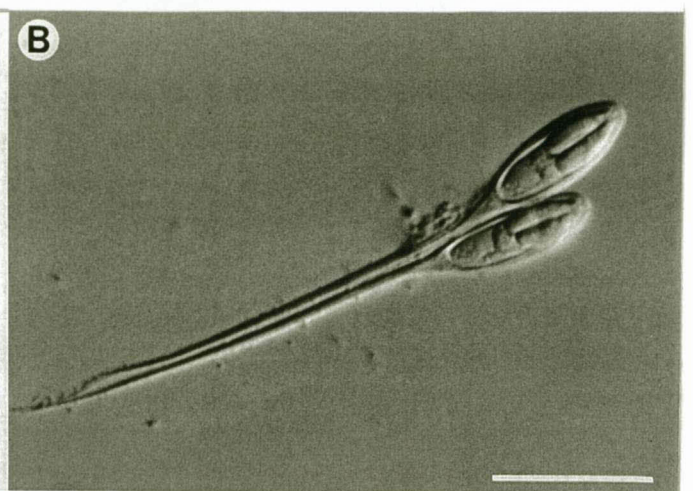
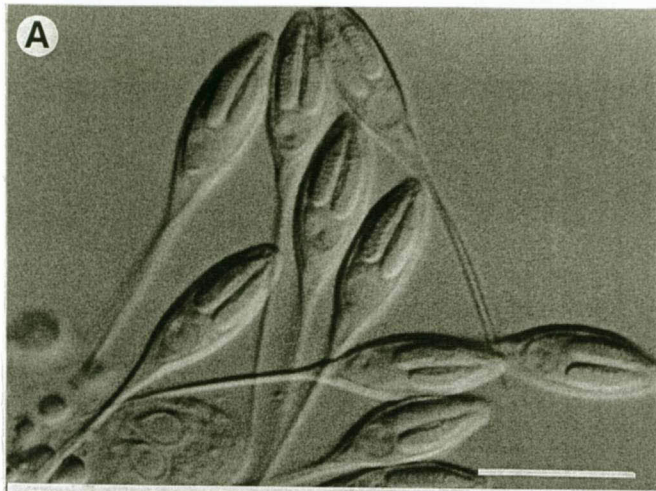


Figure 5.7

Scanning and transmission electron micrographs of *Henneguya* Thélohan, 1892 species collected from fishes in the Okavango River and Delta, Botswana

A: *Henneguya branchialis* Ashmawy, Abu-Elwafa, Imam & El-Otifi, 1989 from the suprabranchial organ of *Clarias gariepinus* (Burchell, 1822)

B: *Henneguya* sp. A from the gills of *C. gariepinus*

C: *Henneguya* sp. C from the gills of *Marcusenius macrolepidotis* (Peters, 1852)

D: *Henneguya* sp. D from the gills of *Schilbe intermedius* Rüppell, 1832

E: Transmission electron micrograph of the spore of *Henneguya* sp. A, illustrating the coils in the polar filament

F: Transmission electron micrograph of the spore of *Henneguya* sp. A, illustrating the two shell valves

G: Transmission electron micrograph of the spore of *Henneguya* sp. D, illustrating the coils in the polar filament

H: Transmission electron micrograph of the spore of *Henneguya* sp. D, illustrating the two shell valves and caudal appendage

Scale bar: 10µm

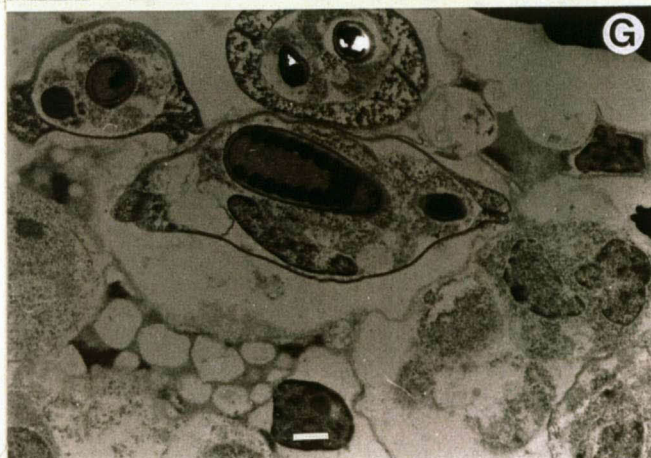
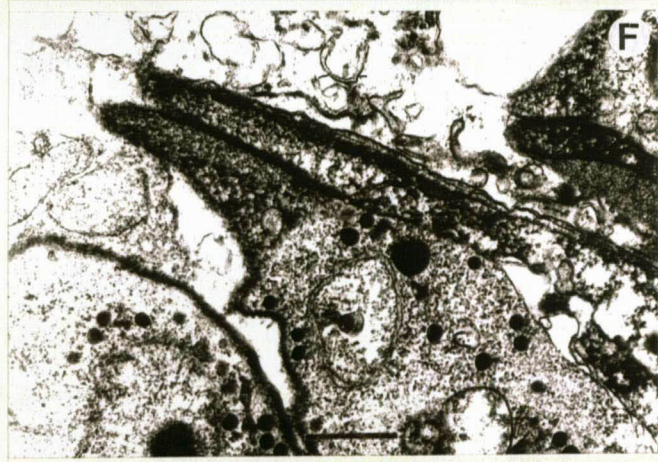
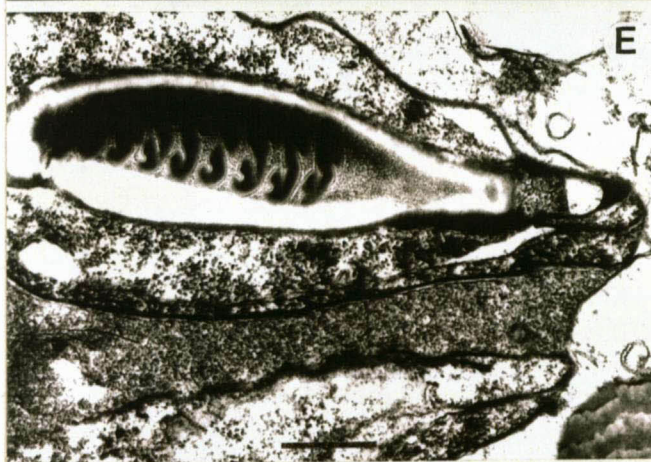
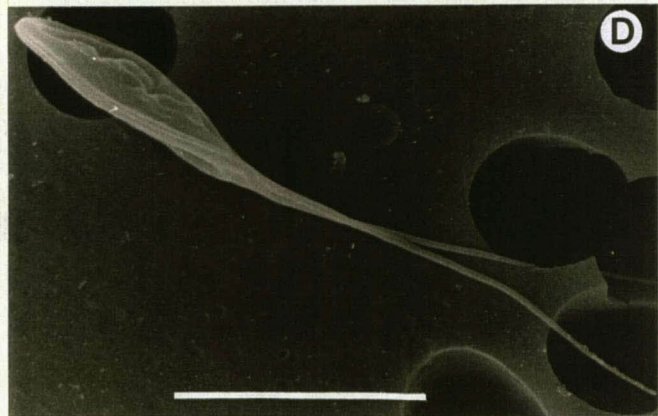
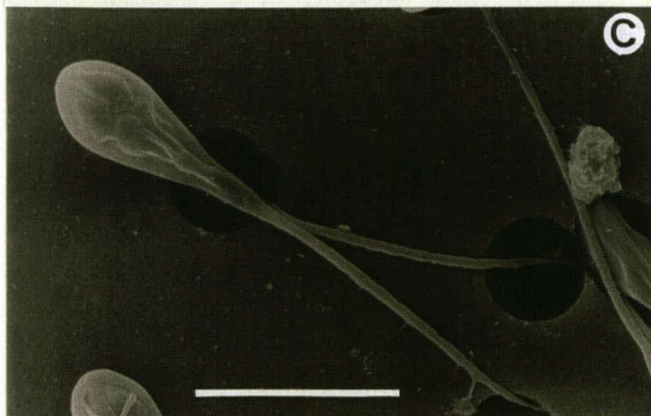
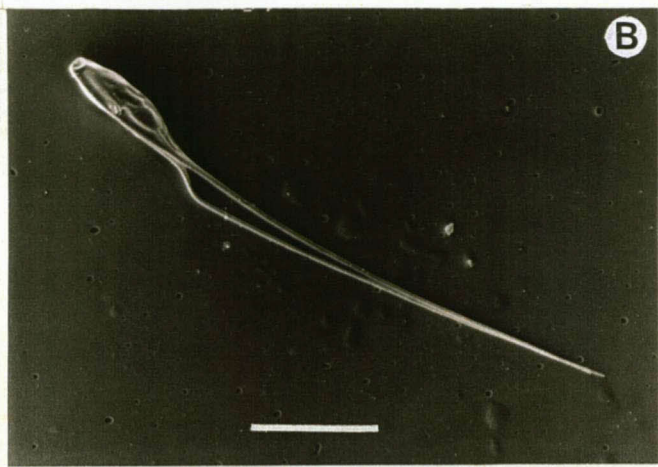
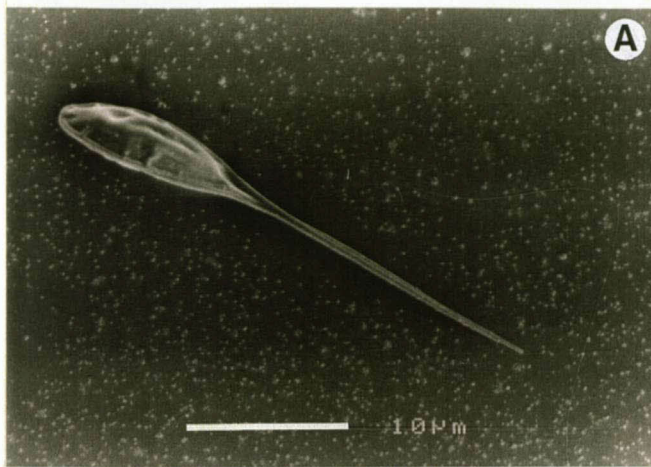


Figure 5.8

Micrographs illustrating silver impregnated *Henneguya* spores collected from fishes
in the Okavango River and Delta, Botswana

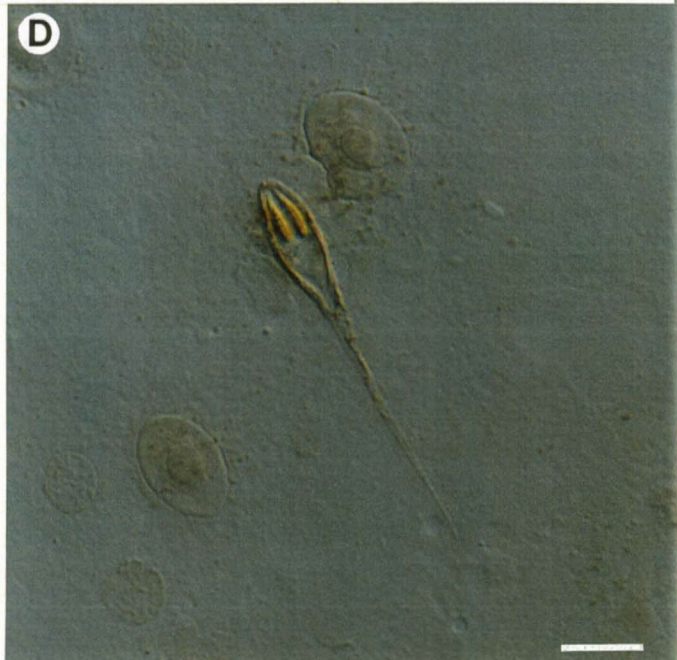
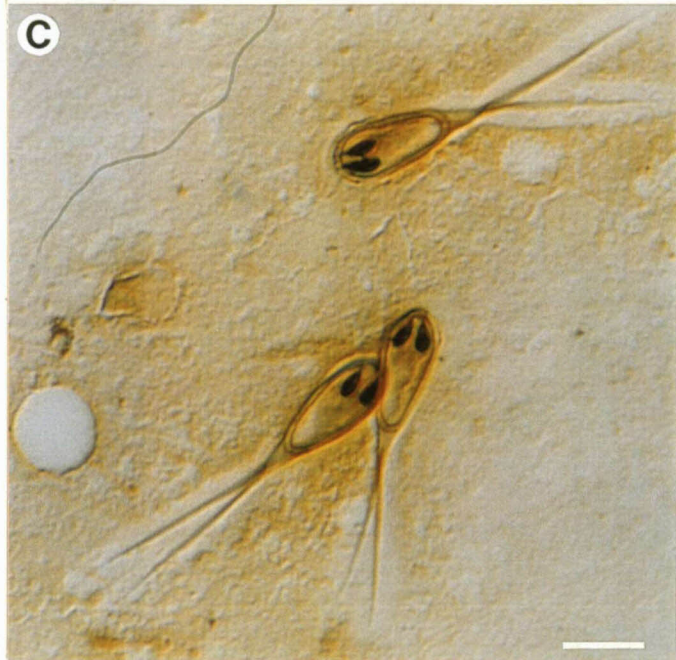
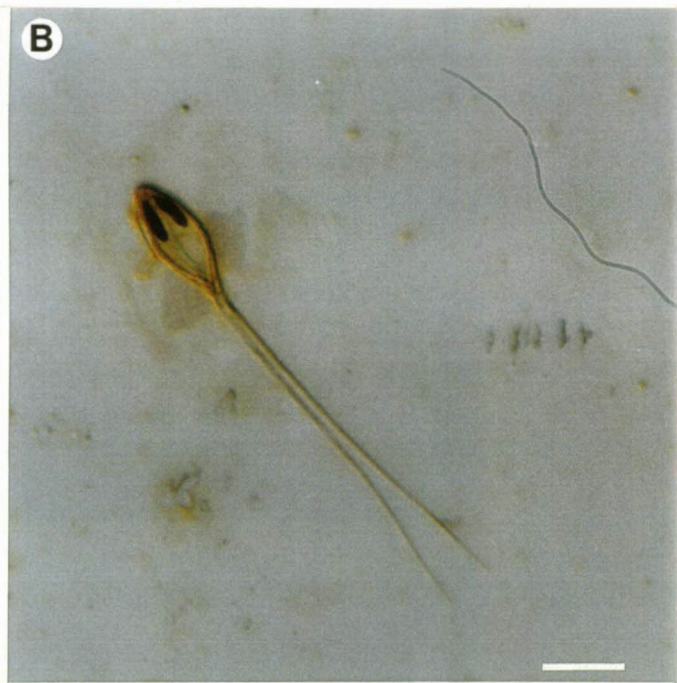
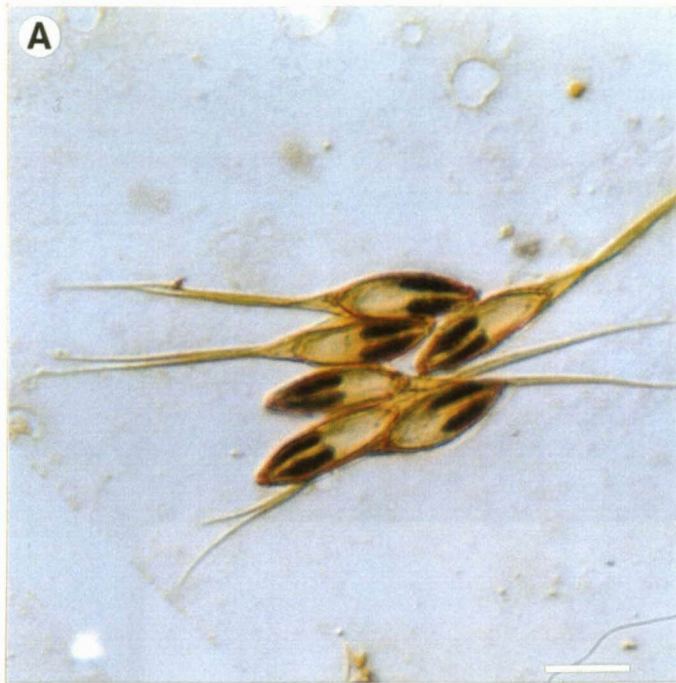
A: *Henneguya branchialis* from the suprabranchial organ of *Clarias gariepinus*
(Burchell, 1822)

B: *Henneguya* sp. A from the gills of *C. gariepinus*

C: *Henneguya* sp. C from the gills of *Marcusenius macrolepidotis* (Peters, 1852)

D: *Henneguya* sp. D from the gills of *Schilbe intermedius* Rüppell, 1832

Scale bar: 10µm



CHAPTER 6

CHAPTER 6



The genus *Myxobolus* Bütschli, 1882

The genus *Myxobolus* (*syn. Myxosoma* Thélohan, 1892; *Lentospora* Plehn, 1905; *Facieplatycauda* Wyatt, 1979 and *Rudicapsula* Kalavati and Narasimhamurti, 1984) forms an enormous group that has well over 450 species described from fishes throughout the world (Lom & Dyková 1992). The spores of this genus are ovoid or rounded in valvular view and biconvex in sutural view with smooth shell valves (Fig. 6.1). Usually two pyriform shaped polar capsules are found in the spore body, with a sutural ridge that may extend to a crescentic ledge. A binucleate sporoplasm is present, often with an iodophilous 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.

In Africa 46 species have been found in freshwater fishes. With the exception of *Myxobolus exiguus* Thélohan, 1895, which was first recorded in Eurasia, most of these species were originally described in Africa. The 46 known *Myxobolus* species found in Africa are summarised below in Table 6.1, including notes on the type hosts and distribution of these species. *Myxobolus* species from Israel have also been included due to the similar fish species occurring there.

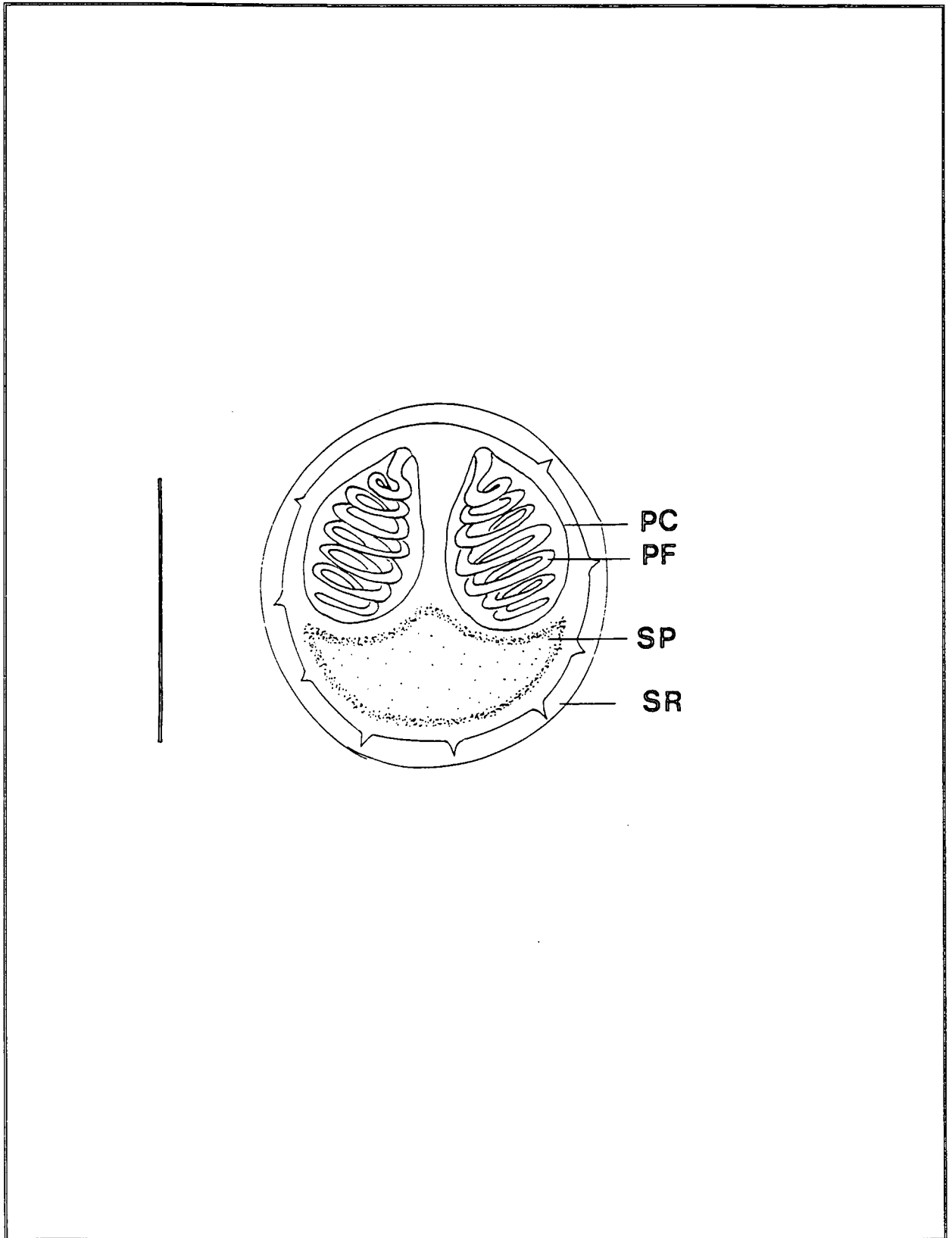


Figure 6.1: Line drawing of a *Myxobolus bizerti* Bahri & Marqués, 1996 spore illustrating specific morphological characteristics of *Myxobolus* Bütschli, 1882 species [Redrawn from Bahri & Marqués (1996)]. PC-Polar capsule, PF-Polar filament, SP-Sporoplasm, SR-Sutural ridge. Scale Bar: 10µm.

Table 6.1: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes

<i>MYXOBOLUS AFRICANUS</i> FOMENA, BOUX & BIRGI, 1985
<p>Type host: <i>Hepsetus odoe</i> Localities: Nyong and Sanaga Basins (Cameroon) Organs: Gills Figure: 6.2 A</p>
REMARKS
<p>The spores are ovoid with a pointed anterior end. An unique characteristic is that one of the two polar capsules discharges laterally.</p>
MEASUREMENTS
<p>Total length: 13.6-17.5 µm Spore width: 5.7-9 µm Polar capsules: 5.5-9.5 µm (L)×1.6-3.5 µm (W)</p>
<p>Reference: Fomena, Bouix & Birgi (1985)</p>
<i>MYXOBOLUS AGOLUS</i> LANDSBERG, 1985
<p>Type host: <i>Oreochromis aureus</i> × <i>O. niloticus</i>, <i>O. niloticus vulcani</i> Localities: Israel Organs: Kidneys and spleen Figure: 6.2B</p>
REMARKS
<p>The spores of this species are ovoid to circular in frontal view, with smooth shell valves that are slightly thicker at the anterior point where the discharging ducts emerge. In side view, the lemon-shaped, thin sutural ridge is indistinct. The two polar capsules are pyriform to flask shaped and are equal in size, reaching the posterior half of the spore. The polar filament has 10-11 coils, which are regularly arranged and spaced forming a column with a more or less straight border. The sporoplasm is binucleate and contains an iodophilous vacuole.</p>
MEASUREMENTS
<p>Total length: 9.8-11.6µm Spore width: 7.5-9.2µm Polar capsules: 6.1-7.4µm (L)×3.1-3.8µm (W)</p>
<p>Reference: Landsberg (1985)</p>

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS AMIETI</i> FOMENA, BOUIX & BIRGL, 1985
<p>Type host: <i>Ctenopoma nanum</i> Localities: Nyong Basin (Cameroon) Organs: Gills, eyes and muscles Figure: 6.2C</p>
REMARKS
<p>The spores are pyriform shaped in valvular view with the posterior end more rounded than the anterior. The polar capsules are pyriform and very elongate, reaching two thirds of the spore length. There are 3 oblique coils in the polar filament.</p>
MEASUREMENTS
<p>Total length: 11.3-15.8µm Spore width: 5.4-8.7µm Polar capsules: 6-10µm (L)×1.4-2.5µm (W)</p>
<p>Reference: Fomena, Bouix & Birgi (1985)</p>

<i>MYXOBOLUS BENINENSIS</i> SAKITI, BLANC, MARQUES & BOUIX, 1991
<p>Type host: <i>Sarotherodon melanotheron</i> Localities: Lake Nokou (Benin) Organs: Gills Figure: 6.2D</p>
REMARKS
<p>The spores are ovoid with a pointed anterior end and the length of the polar capsules take up more than half of the spore length. There are 8-10 coils in the polar filament.</p>
MEASUREMENTS
<p>Total length: 10.5-14µm Spore width: 5.5-9µm Polar capsules: 6-8µm(L)×1.5-3µm (W)</p>
<p>Reference: Sakiti, Blanc, Marqués & Bouix (1991)</p>

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS BILONGI</i> FOMENA, MARQUES, BOUX & NJINÉ, 1994	
<p>Type Host: <i>Labeo</i> sp. Localities: Cameroon Organs: Gills and fins Figure: 6.2E</p>	
REMARKS	
<p>The spores are rounded with the anterior end slightly truncate. Two polar capsules of unequal size are situated in the anterior of the spore and contain 9-10 coils in the polar filament.</p>	
MEASUREMENTS	
<p>Total length: 14-17µm Spore width: 11.5-14.5µm Larger polar capsules: 6.5-8µm (L)×4-6µm (W) Smaller polar capsules width: 4-6.5µm (L)×3-4µm (W)</p>	
<p>Reference: Fomena, Marqués, Bouix & Njiné (1994)</p>	

<i>MYXOBOLUS BRACHYSPORUS</i> (BAKER, 1963)	
<p>Syn. <i>Myxosoma brachyspora</i> Baker, 1963 Type hosts: <i>Tilapia esculenta</i>, <i>T. variabilis</i> Localities: Lake Victoria (Uganda) Organs: Spleen Figure: 6.2F</p>	
REMARKS	
<p>The spores are ellipsoidal in front view with two rounded or ellipsoidal anterior polar capsules that are equal or sub-equal in size.</p>	
MEASUREMENTS	
<p>Total length: 7-7.5µm Spore width: 12-13.5µm Polar capsules: 2.5-3.8µm (L)×2.3-2.5µm (W).</p>	
<p>Reference: Baker (1963)</p>	

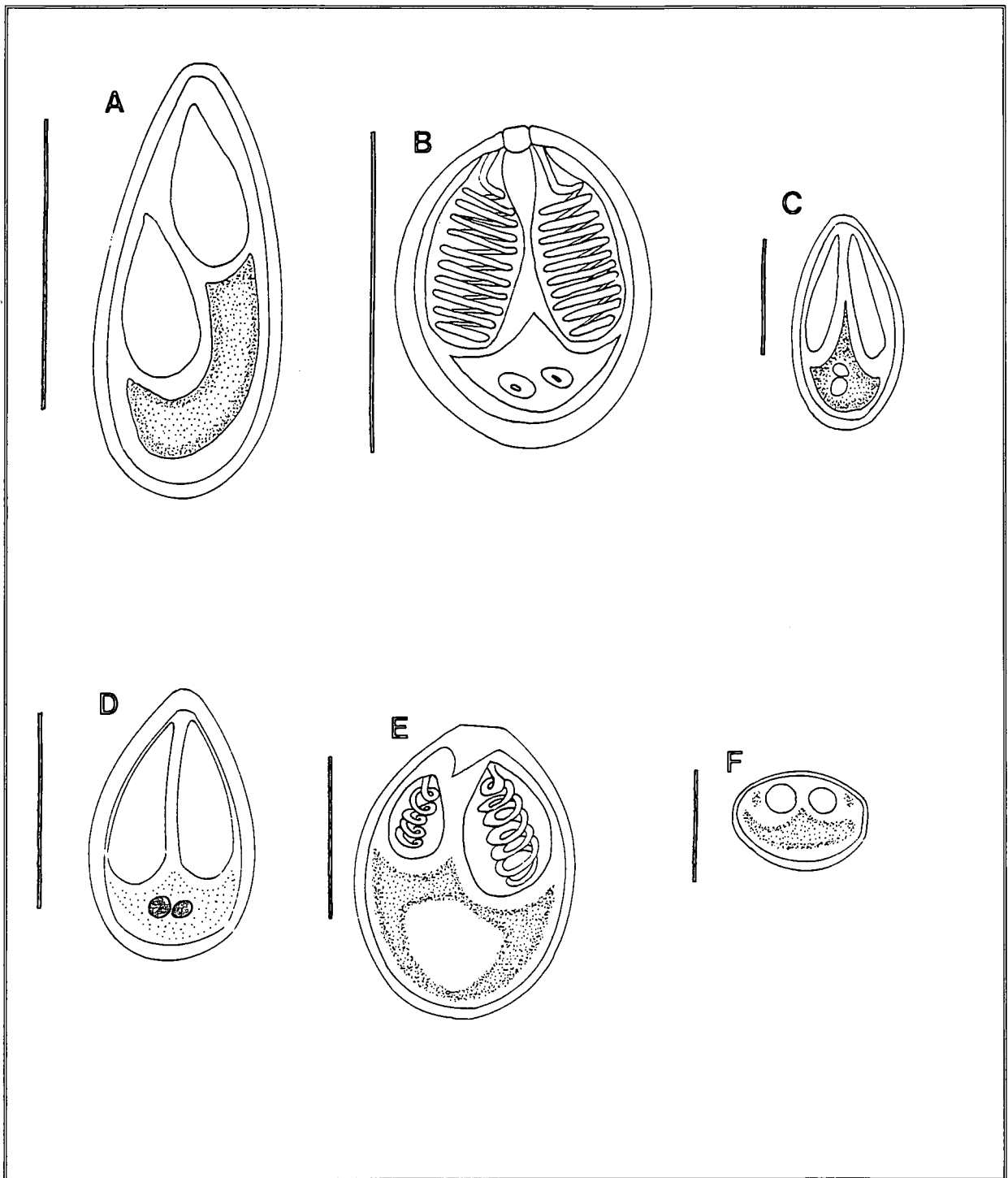


Figure 6.2: Line drawings of **A-***Myxobolus africanus* Fomena, Bouix & Birgi, 1985, **B-***M. agolus* Landsberg, 1985, **C-***M. amieti* Fomena, Bouix & Birgi, 1985, **D-***M. beninensis* Sakiti, Blanc, Marqués & Bouix, 1991, **E-***M. bilongi* Fomena, Marqués, Bouix & Njiné, 1994, **F-***M. brachysporous* (Baker, 1963) [Redrawn from Baker (1963), Fomena, Bouix & Birgi (1985), Landsberg (1985), Sakiti, Blanc, Marqués & Bouix (1991) and Fomena, Marqués, Bouix & Njiné (1994)]. Scale bar: 10µm.

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS BURKINEI</i> KABRÉ, SAKITI, MARQUES & SAWADOGO, 1995
<p>Type host: <i>Labeo coubie</i> Localities: Burkina Faso Organs: Gills and fins Figure: 6.3A</p>
REMARKS
<p>The spores are almost spherical in frontal view and contain two unequally sized polar capsules in the anterior end. The shell valves are smooth and appear thick. There are 5 coils visible in the larger polar capsule and 3 coils in the smaller polar capsule.</p>
MEASUREMENTS
<p>Total length: 11-13µm Spore width: 7-9µm Larger polar capsules: 6-7µm (L)×3-4µm (W) Smaller polar capsules: 4-5µm (L)×5-3µm (W)</p>
<p>Reference: Kabré, Sakiti, Marqués & Sawadago (1995)</p>
<i>MYXOBOLUS CAMEROUNENSIS</i> FOMENA, MARQUES & BOUIX, 1993
<p>Type host: <i>Oreochromis niloticus</i> Localities: Yaounde (Cameroon) Organs: Gills, eyes and muscles Figure: 6.3B</p>
REMARKS
<p>The spores are ovoid with a narrowed anterior extremity and a rounded posterior extremity. The valves are smooth and thin with the two polar capsules containing 6-7 coils in the filaments. An iodophilous vacuole is visible in the sporoplasm.</p>
MEASUREMENTS
<p>Total length: 14-22µm Spore width: 10-16µm Polar capsules: 6-8µm (L)×2.6-4.5µm (W)</p>
<p>Reference: Fomena, Marqués & Bouix (1993)</p>

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS CIARIENSIS</i> KOSTOINGUE, FAYE & TOGUEBAYE, 1998
<p>Type host: <i>Brycinus macrolepidotis</i> Localities: Chad Organs: Gills Figure: 6.3C</p>
REMARKS
<p>This species forms small plasmodia that measure 0.3-0.8mm in length. The spores are ovoid with rounded anterior and posterior ends and have 9 indents along the interior surface of the sutural ridge.</p>
MEASUREMENTS
<p>Total length: 9-11µm Spore width: 5-6µm Polar capsules: 2-3µm (L)×1-2µm (W)</p>
<p>Reference: Kostoingue, Faye & Toguebaye (1998)</p>

<i>MYXOBOLUS CITHARINOPSI</i> KOSTOINGUE, FAYE & TOGUEBAYE, 1998
<p>Type host: <i>Citharinops distichodoides</i> Localities: Mailo (Chad) Organs: Gills Figure: 6.3D</p>
REMARKS
<p>This species forms a number of spherical plasmodia within the gill filaments of the host and measure 0.5-1.5mm in diameter. The spores are ovoid in shape with an anterior end that tapers more sharply than the rounded posterior end. Two pyriform shaped polar capsules are situated in the anterior end and are equal in size.</p>
MEASUREMENTS
<p>Total length: 9-11µm Spore width: 5-7µm Polar capsules: 4-5µm (L)×1-2.5µm (W)</p>
<p>Reference: Kostoingue, Faye & Toguebaye (1998)</p>

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS CLARII</i> MANDOUR, GALAL & ABED, 1993
<p>Syn. <i>Myxobolus</i> sp. Kostoingue & Toguebaye, 1994</p> <p>Type host: <i>Clarias lazera</i></p> <p>Localities: Assuit (Egypt)</p> <p>Organs: Testis</p> <p>Figure: 6.3E</p>
REMARKS
<p>These spores are almost spherical in frontal view and have two ovoid polar capsules situated in the anterior end of the spore.</p>
MEASUREMENTS
<p>Total length: 9-12µm</p> <p>Spore width: 7.5-10µm</p> <p>Polar capsules: 3.5-5µm (L)×2-2.5µm (W)</p>
<p>References: Mandour, Galal & Abed (1993)</p>

<i>MYXOBOLUS COMOEI</i> KABRE, SAKITI, MARQUES & SAWADAGO, 1995
<p>Type host: <i>Clarias anguillaris</i></p> <p>Localities: Comoe & KOMPIENGA dam (Burkina Faso)</p> <p>Organs: Gills</p> <p>Figure: 6.3F</p>
REMARKS
<p>The spores of this species are almost spherical with the anterior end slightly pointed. Two large pyriform shaped polar capsules are found in the anterior end of the spore.</p>
MEASUREMENTS
<p>Total length: 10-12µm</p> <p>Spore width: 8-9µm</p> <p>Polar capsules: 4-5µm (L)×2.5-3µm (W)</p>
<p>References: Kabré, Sakiti, Marqués & Sawadago (1995)</p>

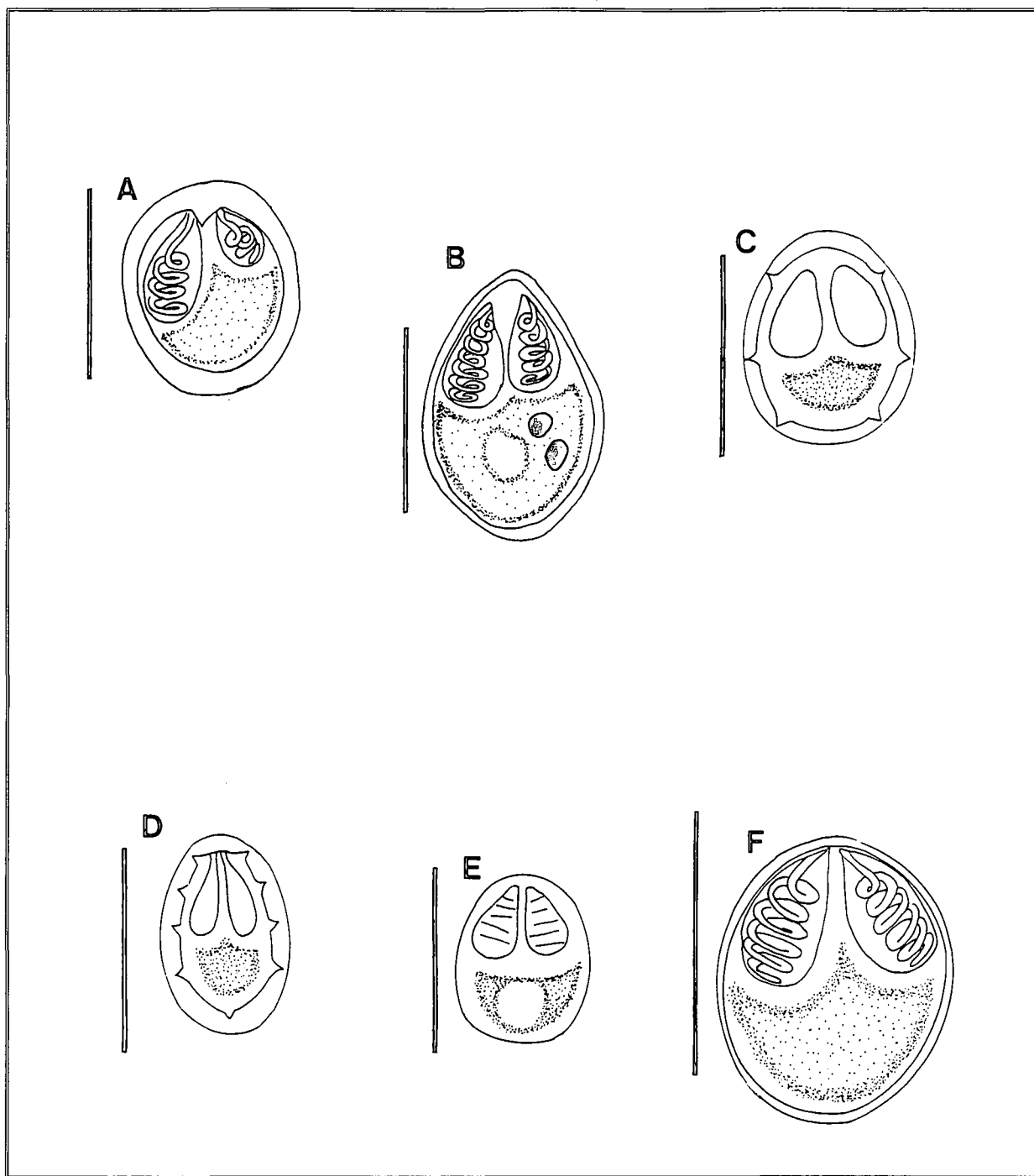


Figure 6.3: Line drawings of **A-***Myxobolus burkinei* Kabré, Sakiti, Marqués & Sawadago, 1995, **B-***M. camerounensis* Fomena, Marqués & Bouix, 1993, **C-***M. chariensis* Kostoïngue, Faye & Toguebaye, 1998, **D-***M. citharinopsi* Kostoïngue, Faye & Toguebaye, 1998, **E-***M. clarii* Mandour, Galal & Abed, 1993, **F-***M. comoei* Kabré, Sakiti, Marqués & Sawadago, 1995 [Redrawn from Kabré, Sakiti, Marqués & Sawadago (1995), Fomena, Marqués & Bouix (1993), Kostoïngue, Faye & Toguebaye (1998), Mandour, Galal & Abed (1993)]. Scale Bar 10µm.

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS DAHOMEYENSIS</i> SIAU, 1971
<p>Type host: <i>Synodontis ansorgi</i> Localities: Porto Novo (Benin) Organs: Ovaries Figure: 6.4A</p>
REMARKS
<p>The spores of this species are ovoid to pyriform in shape and possess an anterior end that tapers to a greater degree than the posterior end. Two polar capsules are situated in the anterior end of the spore and contain 4-5 coils in the polar filament.</p>
MEASUREMENTS
<p>Total length: 12µm Spore width: 6µm Polar capsules: 4-5µm (L)×2-3µm (W)</p>
<p>References: Siau (1971)</p>

<i>MYXOBOLUS DISTICHODI</i> KOSTOÏNGUE & TOGUEBAYE, 1994
<p>Type host: <i>Distichodus engycephalis</i> Localities: Mailo (Chad) Organs: Gills, liver and intestine Figure: 6.4B</p>
REMARKS
<p>The spores of this species are ellipsoidal to elongate in frontal view. Two relatively small polar capsules are situated in the anterior end of the spore cavity and take up only about one third of the spore.</p>
MEASUREMENTS
<p>Total length: 10-11µm Spore width: 5-6µm Polar capsules: 4-5µm (L)×1-2µm (W)</p>
<p>References: Kostoïngue & Toguebaye (1994)</p>

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS DOSSOUTSAKITI</i> , BLANC, MARQUES & BOUIX, 1991
<p>Hosts: <i>Tillapia zillii</i>, <i>Hemichromis fasciatus</i> and <i>T. mosambica</i> × <i>Oreochromis niloticus</i></p> <p>Localities: Lake Nokou (Benin)</p> <p>Organs: Gills</p> <p>Figure: 6.4C</p>
REMARKS
<p>These spores are almost spherical in frontal view and possess two polar capsules of unequal size in the anterior end. There is a small intercapsular process visible and the sporoplasm is binucleate. The larger polar capsule contains 7-9 coils in the polar filament and the smaller one has 5-6 coils.</p>
MEASUREMENTS
<p>Total length: 8.5-11µm</p> <p>Spore width: 8-10.5µm</p> <p>Larger polar capsules: 4.5-6.5µm (L)×2.5-5µm (W)</p> <p>Smaller polar capsules: 3-5.5µm (L)×2-3.5µm (W)</p>
<p>References: Sakiti, Blanc, Marqués & Bouix (1991)</p>

<i>MYXOBOLUS EQUATORIALIS</i> LANDSBERG, 1985
<p>Type host: <i>Oreochromis aureus</i> × <i>O. niloticus</i></p> <p>Localities: Israel</p> <p>Organs: Spleen</p> <p>Figure: 6.4D</p>
REMARKS
<p>The spores are pyriform in frontal view with the anterior end more slender than the posterior end. The shell valves are smooth and slightly thicker at the anterior point where the discharging ducts emerge. In side view the spore are lenticular to flattened with an indistinct sutural ridge. The polar capsules are ovoid to pyriform, of unequal size and situated equatorially. The anterior end of each capsule appears to have an extremely attenuated neck region with the discharging ducts running inwards from the anterior end of the spore.</p>
MEASUREMENTS
<p>Total length: 13.1-14.9µm</p> <p>Spore width: 7-8.6µm</p> <p>Larger polar capsules: 4-4.9µm (L)×3.1-4.2µm (W)</p> <p>Smaller polar capsules: 3.1-4µm (L)×2.5-3.2µm (W)</p>
<p>References: Landsberg (1985)</p>

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS FOTOI</i> FOMENA, MARQUÉS & BOUIX, 1993
<p>Type host: <i>Oreochromis niloticus</i> Localities: Younde (Cameroon) Organs: Gills Figure: 6.4 E</p>
REMARKS
<p>Polysporic, spherical plasmodia of variable sizes occur in the fatty tissue overlying the extremity of the gill arches and measure 215-432mm ×190-410mm. The spores are globoid seen from the front, with no intercapsular process. The polar filaments display 5 or 6 coils in the sub-oval polar capsules of equal size.</p>
MEASUREMENTS
<p>Total length: 13.4-16µm Spore width: 10-13.8µm Larger polar capsules: 3.8-5µm (L)×3.2-4.3µm (W)</p>
<p>References: Fomena, Marqués & Bouix (1993)</p>

<i>MYXOBOLUS GALILAEUS</i> LANDSBERG, 1985
<p>Type host: <i>Sarotherodon galilaeus</i> Localities: Lake Tiberias (Israel) Organs: Kidneys and spleen Figure: 6.4F</p>
REMARKS
<p>The spores of this species are ovoid in frontal view with a flattened anterior end and contain 3-12 notches in the sutural edge. In side view the spores are lenticular in shape with the sutural ridge moderate to distinct. The polar capsules are of equal size and are ovoid with the anterior ends convergent. There are 4-5 regularly arranged coils in the polar filament, which are slightly oblique to the longitudinal axis of the spore. The sporoplasm is binucleate and contains an iodophilous vacuole.</p>
MEASUREMENTS
<p>Total length: 10.3-13.1µm Spore width: 7.9-10µm Larger polar capsules: 3.1-4µm (L)×2.3-3.1µm (W)</p>
<p>References: Landsberg (1985)</p>

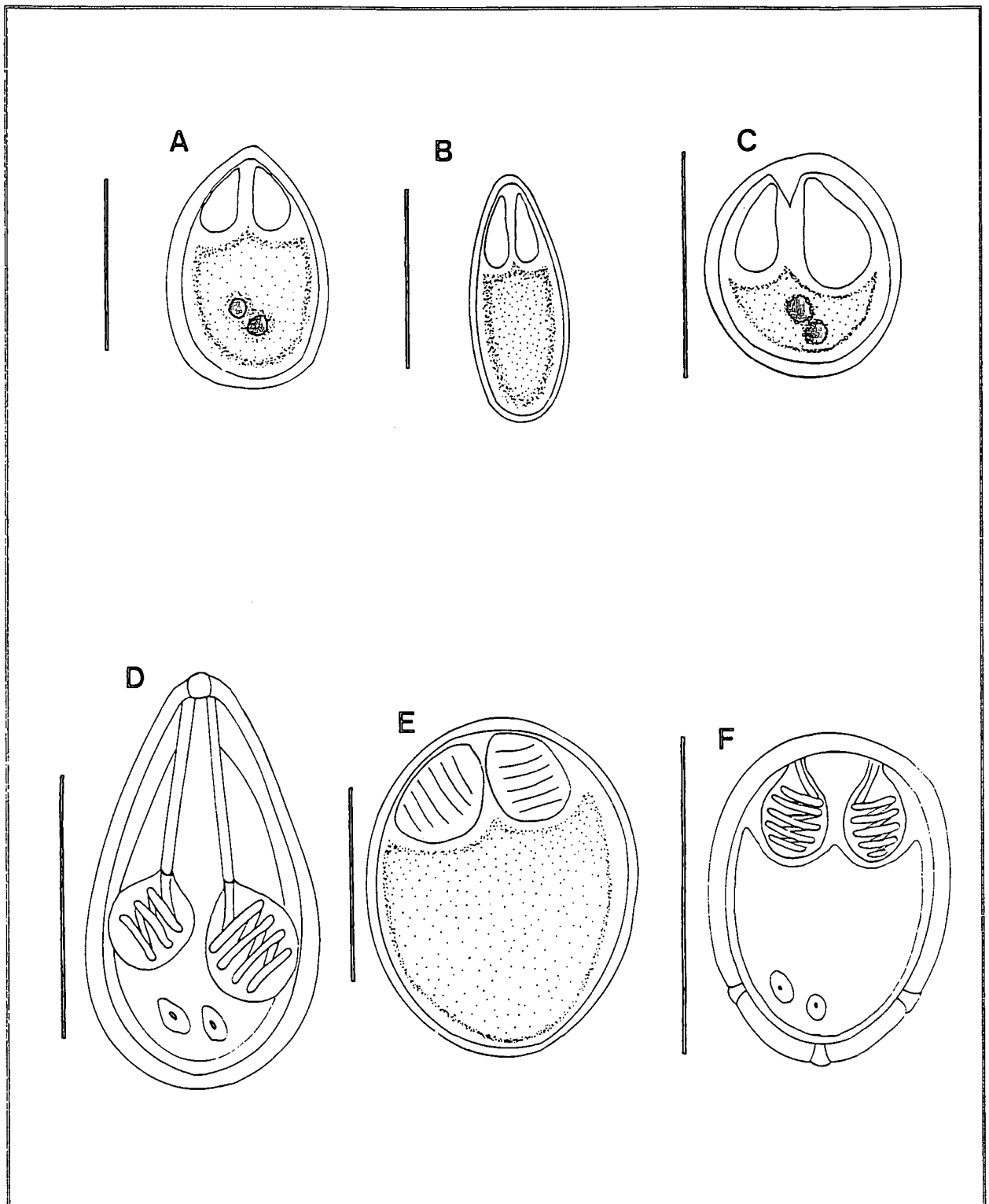


Figure 6.4: Line drawings of A-*Myxobolus dahomeynsis* Siau, 1971, B-*M. distichodi* Kostoingue & Toguebaye, 1994, C-*M. doussoui* Sakiti, Blanc, Marqués & Bouix, 1991, D-*M. equatorialis* Landsberg, 1987, E-*M. fotoi* Fomena, Marqués and Bouix, 1993, F-*M. galilaeus* Landsberg, 1985 [Redrawn from Siau (1971), Kostoingue & Toguebaye (1994), Sakiti, Blanc, Marqués & Bouix (1991) and Fomena, Marqués and Bouix (1993)]. Scale bar: 10 μ m.

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS HETEROSPORUS</i> (BAKER, 1963)
<p>Syn. <i>Myxosoma heterospora</i></p> <p>Hosts: <i>Tilapia esculenta</i>, <i>T. variabilis</i>, <i>Oreochromis niloticus</i></p> <p>Localities: Lake George (Uganda)</p> <p>Organs: Liver, kidney, spleen</p> <p>Figure: 6.5A</p>
REMARKS
<p>The spores of this species are so variable in shape that the author at first thought they belonged to different species. All the spores contain two anterior polar capsules, which are usually slightly unequal in size, with two generative nuclei visible in the sporoplasm. The spores are divided into three main types. Type (I) spores are ovoid, ellipsoidal or rounded in front view, with a blunt anterior end that is as broad as the posterior end. These spores contain short ovoid polar capsules that take up only one third of the length of the spores. Type (II) spores are ovoid or pyriform in front view, with a pointed anterior end and two medium length pyriform polar capsules filling about half the spore length. Type (III) spores are ovoid or ellipsoidal in front view, with a pointed anterior end and two long ovoid or pyriform polar capsules that are sometimes curved and take up more than half the spore length.</p>
MEASUREMENTS
<p>Total length: Type (I): 8.5-17µm, Type (II): 9-15µm, Type (III): 10-14.5µm</p> <p>Spore width: Type (I): 6.5-11µm, Type (II): 6.5-10.5µm, Type (III): 6.3-8.0µm</p> <p>Polar capsules: Type (I): 2-5.5µm (L)×1.5-3.5µm (W), Type (II): 3-7µm (L)×1.5-3µm (W), Type (III): 5.5-9.5µm×1.8-3µm (W).</p>
<p>Reference: Baker (1963)</p>
<i>MYXOBOLUS HOMEOSPORUS</i> BAKER, 1963
<p>Type Host: <i>Tilapia esculenta</i>, <i>T. variabilis</i></p> <p>Localities: Lake Victoria (Uganda)</p> <p>Organs: Muscles</p> <p>Figure: 6.5B</p>
REMARKS
<p>This species has plasmodia associated with diffuse yellowish pigment among the muscle fibres, which lies immediately below the dermis. The plasmodia are elevated and measure 1-2mm in diameter. The spores are ovoid in frontal view with the anterior end slightly narrower the posterior. Two fairly large ovoid polar capsules are present in the anterior end of the spore.</p>
MEASUREMENTS
<p>Total length: 7-7.5µm</p> <p>Spore width: 12-13.5µm</p> <p>Larger polar capsules: 2.5-3.8µm (L)×2.3-2.5µm (W)</p>
<p>References: Baker (1963)</p>

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS HYDROCYNIS</i> KOSTOÏNGUE & TOGUEBAYE, 1994
<p>Type Host: <i>Hydrocynis forskali</i> Localities: Mailo (Chad) Organs: Gills Figure: 6.5C</p>
REMARKS
The spores of this species are ellipsoidal and contain two elongated polar capsules.
MEASUREMENTS
<p>Total length: 13-14µm Spore width: 8-10µm Larger polar capsules: 4-5µm (L)×2-3µm (W)</p>
References: Kostoïngue & Toguebaye (1994)

<i>MYXOBOLUS ISRAELENSIS</i> LANDSBERG, 1985
<p>Hosts: <i>Oreochromis niloticus</i> × <i>O. aureus</i>, <i>Sarotherodon galilaeus</i>, <i>O. niloticus vulcani</i> Localities: Lake Tiberias (Israel) Organs: Kidneys and spleen Figure: 6.5D</p>
REMARKS
In front view the spores are ovoid to pyriform with the anterior end narrower than the posterior end. The shell valves are smooth and slightly thicker at the anterior point between the space where the discharging ducts emerge. In side view the spores are lenticular with an indistinct sutural ridge and a thin sutural line. The polar capsules are flask-shaped, of equal size and converge in the anterior end of the spore. The polar filaments are arranged loosely with 7-8 coils located at an oblique angle to the longitudinal axis of the polar capsule.
MEASUREMENTS
<p>Total length: 11.5-14µm Spore width: 7.5-10µm Larger polar capsules: 7-8.5µm (L)×3-4µm (W)</p>
References: Landsberg (1985)

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS KAINJAE</i> OBIKEZIE & OKAEME, 1990
<p>Syn. <i>M. ovariae</i> nom. nud.</p> <p>Hosts: <i>Haplochromis angustifrons</i>, <i>H. elegans</i></p> <p>Localities: Lake Lake George (Uganda) and New Busa (Nigeria)</p> <p>Organs: Ovaries</p> <p>Figure: 6.5E</p>
REMARKS
<p>Paperna (1973) created <i>Myxobolus ovariae</i> for a parasite from the gonads of <i>Haplochromis angustifrons</i> and <i>H. elegans</i>, in Lake George (Uganda) without any description. Obiekezie & Okaeme (1990) provided a full description and consequently renamed it. The spores of this species are almost spherical in frontal view and contain 8 notches in the sutural edge. Two small pyriform shaped polar capsules are present in the anterior end of the spore and each contains 3 oblique coils in the polar filaments.</p>
MEASUREMENTS
<p>Total length: 8-10µm</p> <p>Spore width: 6.5µm</p> <p>Polar capsules: 2-2.5µm (L)×1-1.5µm (W)</p>
<p>References: Obiekezie & Okaeme (1990)</p>

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS KRIEBIENSIS</i> FOMENA & BOUX, 1994
<p>Type host: <i>Brycinus longipinnus</i></p> <p>Localities: Lobe and Sanaga Basin (Cameroon)</p> <p>Organs: Skin, eyes and kidneys</p> <p>Figure: 6.5F</p>
REMARKS
<p>The plasmodia of this species are spherical or ellipsoidal and whitish in colour and measure 0.3 to 1 mm in diameter. These plasmodia are found irregularly scattered across the body, from the operculum to the tail. Some diffuse spores were found in the kidneys. The spores are relatively large in size, ovoid and elongated, with the anterior end narrower than the rounder, larger posterior end. Shell valves are smooth and two pyriform polar capsules are situated in the anterior half of the spore. In each polar capsule the polar filament coils in tight whorls that are perpendicularly placed from the great axis. The number of coils varies between 19 and 28. The polar capsules fill almost the whole spore cavity with a reduced sporoplasm filling the rest of the spore.</p>
MEASUREMENTS
<p>Total length: 20.2-23 µm</p> <p>Spore width: 9-10 µm</p> <p>Larger polar capsules: 14.5-17.6 µm (L)×3-4 µm (W)</p> <p>Smaller polar capsules: 13.5-16.9 µm (L)×3-4 µm (W)</p>
<p>References: Fomena & Bouix (1994)</p>
<i>MYXOBOLUS MAILAOENSIS</i> KOSTOÏNGUE, FAYE & TOGUEBAYE, 1998
<p>Host: <i>Synodontis gambiensis</i></p> <p>Localities: Mailo (Chad)</p> <p>Organs: Kidneys</p> <p>Figure: 6.6A</p>
REMARKS
<p>These spores are found scattered within the kidney and are ovoid to elongate, containing two large polar capsules that fill almost the entire spore cavity.</p>
MEASUREMENTS
<p>Total length: 13-15 µm</p> <p>Spore width: 8-9 µm</p> <p>Polar capsules: 6-7 µm (L)×2-3 µm (W)</p>
<p>References: Kostoïngue, Faye & Toguebaye (1998)</p>

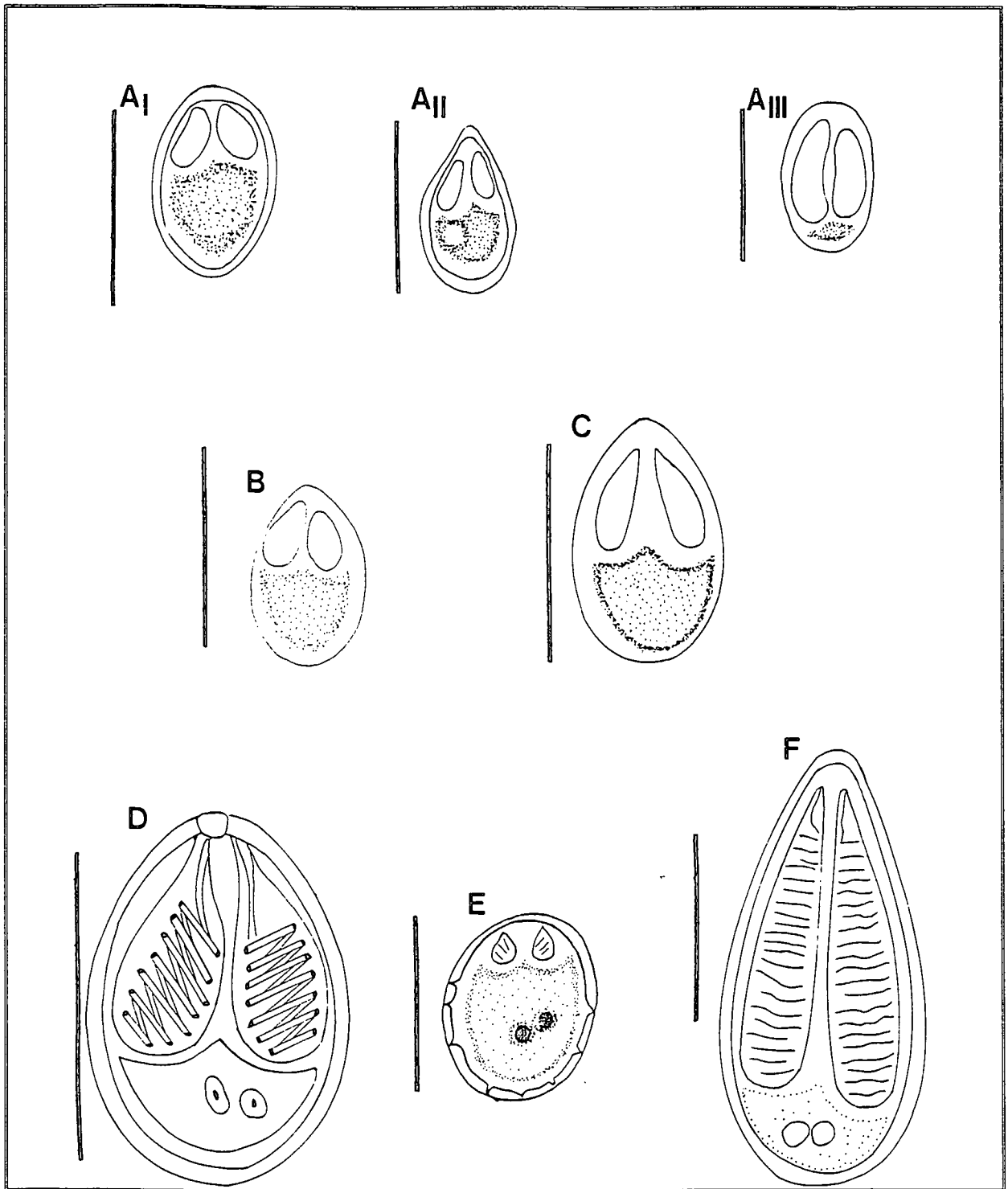


Figure 6.5: Line drawing of A-*Myxobolus heterosporus* (Baker, 1963) AI-Type I, AII-Type II, AIII-Type III, B-*M. homeosporus* Baker, 1963, C-*M. hydrocyni* Kostoingue & Toguebaye, 1994, D-*M. israelensis* Landsberg, 1985, E-*M. kainjiae* Obiekezie & Okaeme, 1990, F-*M. kriebiensis* Fomena & Bouix, 1994 [Redrawn from Baker (1963), Landsberg (1985), Obiekezie & Okaeme (1990), Fomena & Bouix (1994), Kostoingue & Toguebaye (1994)]
Scale Bar 10 μ m.

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS MARAENSIS</i> KOSTOINGUE, FAYE & TOGUEBAYE, 1998
<p>Syn. <i>Myxobolus</i> sp. Kostoingue & Toguebaye, 1994</p> <p>Type host: <i>Citharinus citharinus</i></p> <p>Localities: Chari (Chad)</p> <p>Organs: Gills</p> <p>Figure: 6.6B</p>
REMARKS
<p>The plasmodia found are ovoid to elongate and measure 0.5-1.7mm in length. The spores of this species are ovoid with the anterior end slightly pointed and nine notches are visible on the sutural ridge. Two polar capsules of unequal size are found in the anterior end of the spore.</p>
MEASUREMENTS
<p>Total length: 13-15µm</p> <p>Spore width: 8-9µm</p> <p>Larger polar capsules: 4-5µm (L)×2-3µm (W)</p> <p>Smaller polar capsules: 3-3.5µm (L)×2-3µm (W)</p>
<p>References: Kostoingue, Faye & Toguebaye (1998)</p>
<i>MYXOBOLUS NDJAMENAENSIS</i> KOSTOINGUE, FAYE & TOGUEBAYE, 1998
<p>Host: <i>Citharinus citharinus</i></p> <p>Localities: Chari (Chad)</p> <p>Organs: Kidneys</p> <p>Figure: 6.6C</p>
REMARKS
<p>Large spherical plasmodia measuring 3.3-7mm in diameter are found in the kidneys of the host. The spores are ovoid in frontal view with the posterior and anterior ends both rounded. Two small ovoid polar capsules are situated in the anterior of the spore and fill approximately two thirds of the spore cavity.</p>
MEASUREMENTS
<p>Total length: 13-14µm</p> <p>Spore width: 10-11µm</p> <p>Polar capsules: 5-6µm (L)×4-5µm (W)</p>
<p>Reference: Kostoingue, Faye & Toguebaye (1998)</p>

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS NILEI</i> (FAISAL & SHALABY, 1987)
<p>Syn. <i>Myxosoma tilapiae</i></p> <p>Type host: <i>Oreochromis niloticus</i></p> <p>Localities: Egypt</p> <p>Organs: Gills, skin, eyes, kidneys and pancreas</p> <p>Figure: 6.6D</p>
REMARKS
<p><i>Myxosoma tilapiae</i>, a parasite of <i>O. niloticus</i> was renamed by Fomena and Bouix (1997) due to the fact that the genus <i>Myxosoma</i> Thélohan, 1892 is now considered a junior synonym of <i>Myxobolus</i>. On transfer to <i>Myxobolus</i>, <i>M. tilapiae</i> would have become a secondary homonym and thus required renaming since it was pre-occupied by <i>Myxobolus tilapiae</i> (Abolarin, 1974). The spores of this species are ovoid to spherical in shape with two flask shaped polar capsules converging in the anterior end of the spore. The polar filaments within are loosely arranged with 5-6 coils located at an oblique angle to the longitudinal axis of the polar capsule.</p>
MEASUREMENTS
<p>Total length: 11.5-12.5µm</p> <p>Spore width: 7.5-8.5µm</p> <p>Polar capsules: 7-8µm (L)×3-3.5µm (W)</p>
<p>Reference: Faisal & Shalaby (1987)</p>

<i>MYXOBOLUS NILOTICUS</i> FAHMY, MANDOUR & EL-NAFFAR, 1971
<p>Type host: <i>Labeo niloticus</i></p> <p>Localities: Egypt</p> <p>Organs: Fins</p> <p>Figure: No figure in original description</p>
REMARKS
<p>The spores of this species are oval in shape and contain two unequally sized ovoid polar capsules in the anterior end. Each individual spore is surrounded by a thick refractile wall</p>
MEASUREMENTS
<p>Total length: 10-12µm</p> <p>Spore width: 6.5-8µm</p> <p>Larger polar capsules: 5-7µm (L)×2.5-3.5µm (W)</p> <p>Smaller polar capsules: 2.5-4.5 µm(L)×1.5-2µm (W)</p>
<p>Reference: Fahmy, Mandour & El-Naffar (1971)</p>

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS NJINEI</i> FOMENA, BOUX & BIRGI, 1985
<p>Hosts: <i>Barbus compactacanthus</i>, <i>B. guirali</i>, <i>B. batesii</i>, <i>B. martorelli</i> Localities: Nyong and Sanaga Basins (Cameroon) Organs: Gills Figure: 6.6E</p>
REMARKS
<p>The spores of this species are almost spherical in shape and have an anterior end that is truncate with two relatively large polar capsules also situated at this end.</p>
MEASUREMENTS
<p>Total length: 14-20µm Spore width: 11.5-18.5µm Polar capsules: 6.5-9µm (L)×3.5-5.5µm (W)</p>
<p>Reference: Fomena, Bouix & Birgi (1985)</p>

<i>MYXOBOLUS NKOLYAENSIS</i> FOMENA & BOUX, 1994
<p>Type host: <i>Barbus jae</i> Localities: Nyong Basin (Cameroon) Organs: Gills Figure: 6.7A</p>
REMARKS
<p>The spores of this species are of variable size and are almost spherical in frontal view and lenticular in side view. Both polar capsules are subspherical, volumous and of equal sizes. Some tetralogical forms presenting 3 polar capsules have been observed. The sutural line is straight and prominent and a reduced sporoplasm fills the rest of the spore.</p>
MEASUREMENTS
<p>Total length: 8-11µm Spore width: 7.2-11.5µm Polar capsules: 3.5-5.5µm (L)×2.2-3.5µm (W)</p>
<p>Reference: Fomena & Bouix (1994)</p>

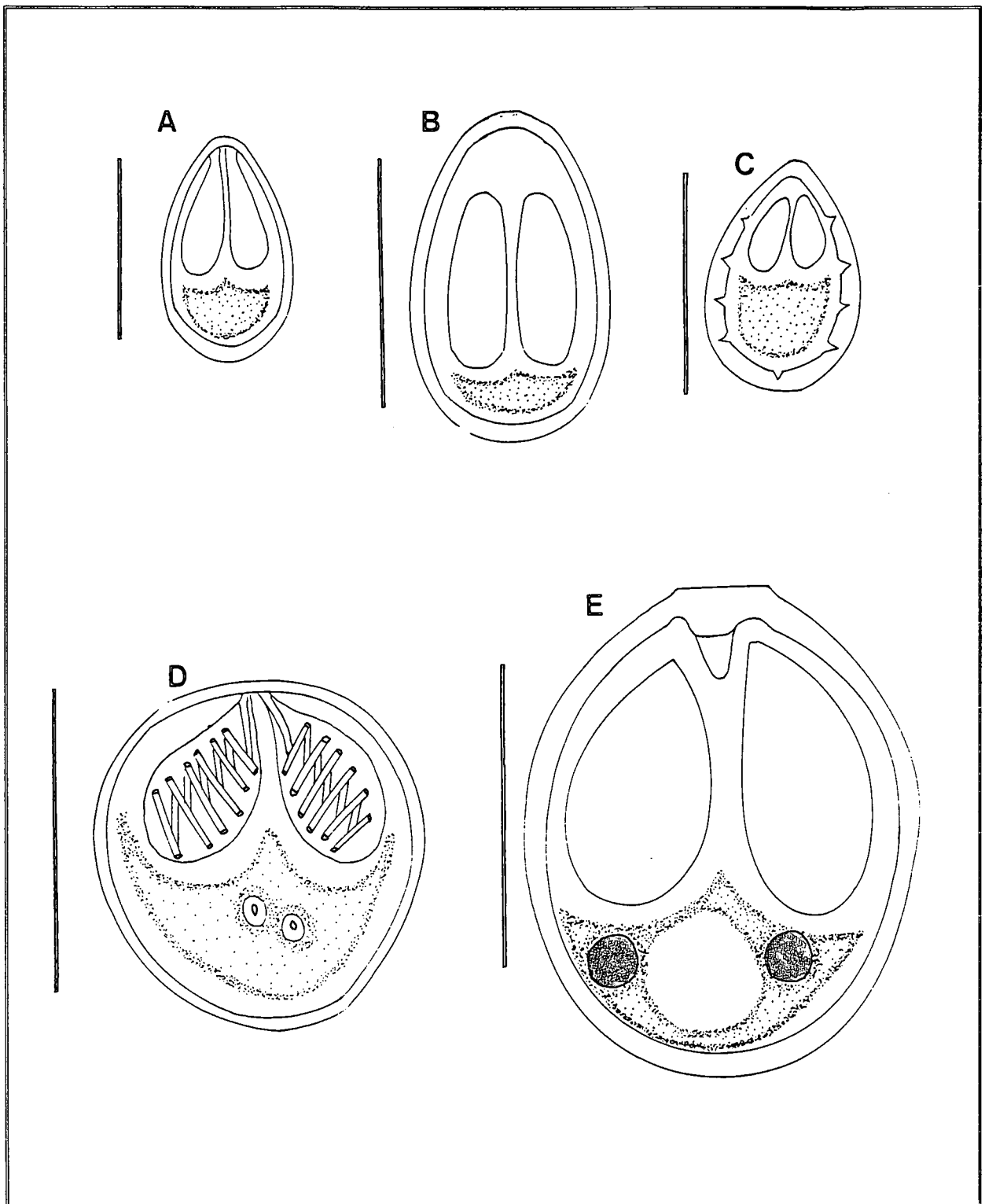


Figure 6.6: Line drawings of A-*Myxobolus mailaoensis* Kostoingue, Faye, & Toguebaye, 1998, B-*M. maroensis* Kostoingue, Faye & Toguebaye, 1998, C-*M. ndjamaensis* Kostoingue, Faye & Toguebaye, 1998, D-*M. nilei* (Faisal & Shalaby, 1987), E-*M. njinei* Fomena, Bouix & Birgi, 1985 [Redrawn from Fomena, Bouix & Birgi (1985), Faisal & Shalaby (1987), Kostoingue, Faye & Toguebaye (1998)] Scale Bar: 10 μ m.

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS NOKOUEENSIS</i> SAKITI, BLANC, MARQUES & BOUIX, 1991
<p>Type host: <i>Sarotherodon melanotheron</i></p> <p>Localities: Lake Nokou (Benin)</p> <p>Organs: Gills</p> <p>Figure: 6.7B</p>
REMARKS
<p>These spores are ovoid in shape with an anterior end that is narrower than the posterior end. Two polar capsules equal in size are found in the anterior half of the spore and there are 5-6 coils present in the polar filament. An intercapsular process is also present.</p>
MEASUREMENTS
<p>Total length: 8-11.5µm</p> <p>Spore width: 5-7µm</p> <p>Polar capsules: 2.5-4µm (L)×1.5-2.5µm (W)</p>
<p>Reference: Sakiti, Blanc, Marqués & Bouix (1991)</p>

<i>MYXOBOLUS NYONGANA</i> (FOMENA, BOUIX & BIRGI, 1985)
<p>Syn. <i>Myxobolus barbi</i> Fomena, Bouix & Birgi, 1985</p> <p>Hosts: <i>Barbus aspilus</i>, <i>B. jae</i>, <i>B. camptacanthus</i>, <i>B. guirali</i>, <i>B. martorelli</i></p> <p>Localities: Nyong Basin (Cameroon)</p> <p>Organs: Fins</p> <p>Figure: 6.7C</p>
REMARKS
<p><i>Myxobolus barbi</i> Fomena, Bouix & Birgi, 1985 is renamed by Fomena & Bouix (1997) <i>M. nyongana</i> after the Nyong Basin, where the hosts were captured. Tripathi (1953) already attributed the name <i>M. barbi</i> to a different species parasitising <i>Barbus ticto</i>. The plasmodia of this species are ovoid to spherical and are found in the secondary gill lamellae. Spores are ovoid in frontal view with the anterior end tapering to a blunt point and the posterior end rounded. Two pyriform shaped polar capsules are situated in the anterior of the spore and there are 6-9 coils in the polar filament.</p>
MEASUREMENTS
<p>Total length: 7.3-13µm</p> <p>Spore width: 5-7µm</p> <p>Polar capsules: 5-7µm (L)×1.4-2.5µm (W)</p>
<p>Reference: Fomena, Bouix & Birgi (1985)</p>

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS OLOI</i> FOMENA & BOUX, 1994
<p>Hosts: <i>Barbus aspilus</i>, <i>B. camptacanthus</i>, <i>B. guirali</i>, <i>B. martorelli</i> Localities: Nyong River (Cameroon) Organs: Gills, kidneys and heart Figure: 6.7D</p>
REMARKS
<p>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. The anterior ends of the spores are slightly fusiform. Two asymmetric polar capsules are found in the anterior end of the spore and 4-5 coils are visible in the larger capsule and 3 in the smaller one.</p>
MEASUREMENTS
<p>Total length: 6.3-11.5µm Spore width: 5.1-9.4µm Larger polar capsules: 4-7µm (L)×1.8-4µm (W) Smaller polar capsules: 2.2-5µm (L)×1.5-2.5µm (W)</p>
<p>Reference: Fomena & Bouix (1994)</p>

<i>MYXOBOLUS POLYCENTROPSI</i> FOMENA, BOUX & BIRGI, 1985
<p>Syn. <i>Myxobolus microcapsularis</i> Sakiti, Blanc, Marqués & Bouix, 1991 Type Host: <i>Polycentropsis abbreviata</i> Localities: Sanaga Basin (Cameroon) Organs: Gills Figure: 6.7E</p>
REMARKS
<p><i>Myxobolus microcapsularis</i> Sakiti, Blanc, Marqués & Bouix, 1991, a parasite of <i>Tilapia zillii</i> was synonymised with <i>M. polycentropsi</i> since the morphometric characteristics of the two species are alike and the host fish is not a criterion for recognising species. In frontal view the spores are ellipsoidal to elongate, with the posterior end slightly wider than the anterior end. Two small polar capsules are situated in the anterior end of the spore.</p>
MEASUREMENTS
<p>Total length: 11.8-14.4µm Spore width: 5.6-10µm Polar capsules: 3.5-4.6µm (L)×1.5-2.3µm (W)</p>
<p>References: Fomena, Bouix & Birgi (1985)</p>

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS SARIGI</i> LANDSBERG, 1985
<p>Hosts: <i>Oreochromis niloticus</i> × <i>O. aureus</i>, <i>Sarotherodon galilaeus</i>, <i>O. niloticus</i></p> <p>Localities: Lake Tiberias (Israel)</p> <p>Organs: Kidneys and spleen</p> <p>Figure: 6.7F</p>
REMARKS
<p>The spores are ovoid in frontal view with a flattened anterior end that is as wide as the posterior end. Two smooth shell valves are present and in side view the spores are lenticular in shape with an indistinct sutural line. The two ovoid to pyriform polar capsules are of equal size with the anterior ends narrower and more pointed than the posterior ends. The capsules are non-convergent and contain 4-5 loosely arranged coils in the polar filament.</p>
MEASUREMENTS
<p>Total length: 9.9-13.1µm</p> <p>Spore width: 7.9-9.6 µm</p> <p>Polar capsules: 4.1-5.2µm (L)×2.9-4.0µm (W)</p>
<p>Reference: Landsberg (1985)</p>

<i>MYXOBOLUS SAROTHERODONI</i> SAKITI, BLANC, MARQUES & BOUIX, 1991
<p>Type Host: <i>Sarotherodon melanotheron</i></p> <p>Localities: Lake Nokou (Benin)</p> <p>Organs: Gills</p> <p>Figure: 6.8A</p>
REMARKS
<p>These spores are ovoid in frontal view with the anterior end tapering to a blunt point and the posterior end rounded. Two small pyriform shaped polar capsules are situated in the anterior end of the spore and fill approximately one fourth of the spore cavity.</p>
MEASUREMENTS
<p>Total length: 9-13µm</p> <p>Spore width: 7.5-10µm</p> <p>Polar capsules: 2-4µm (L)×2-3µm (W)</p>
<p>Reference: Sakiti, Blanc, Marqués & Bouix (1991)</p>

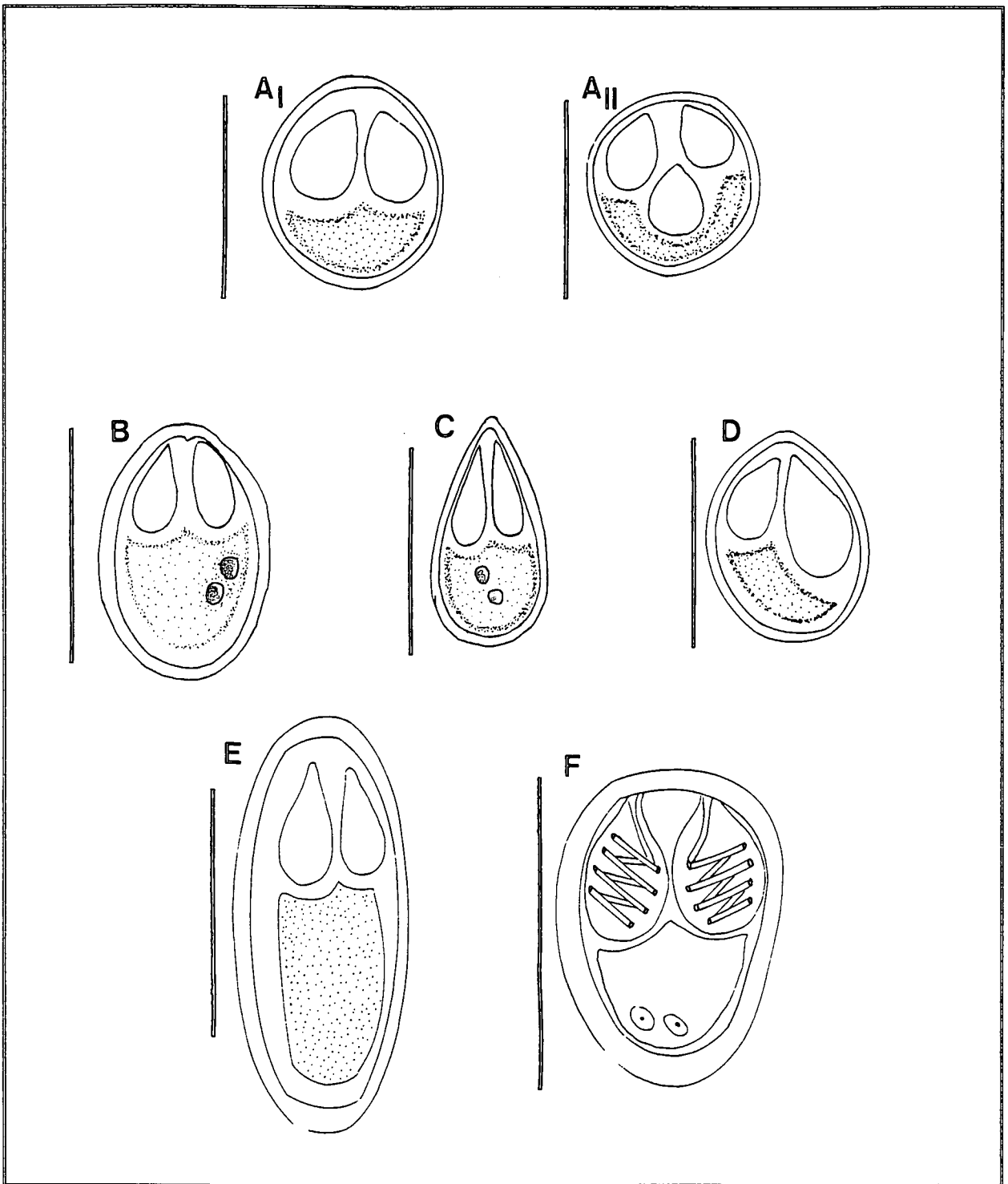


Figure 6.7: Line drawings of, A1 & AII-*Myxobolus nkolyaensis* Fomena & Bouix 1994, B-*M. nokoueensis* Sakiti, Blanc, Marqués & Bouix, 1991, C-*M. nyongana* (Fomena, Bouix & Birgi, 1985), D-*M. oloi* Fomena & Bouix, 1994, E-*M. polycentropsi* Fomena, Bouix & Birgi, 1985, F-*M. sarigi* Landsberg, 1985 [Redrawn from Fomena, Bouix & Birgi (1985), Landsberg (1985), Sakiti, Blanc, Marqués & Bouix (1991), Fomena & Bouix (1994)]
Scale bar: 10µm.

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS STENOSUS</i> PAPERNA, 1973
<p>Type Host: <i>Synodontis schall</i> Localities: Uganda Organs: Gills Figure: 6.8B</p>
REMARKS
<p>These spores are ovoid in frontal view with an anterior end that is broader and more rounded than the narrower posterior end. Two pyriform polar capsules that do not converge are situated in the anterior end of the spore.</p>
MEASUREMENTS
<p>Total length: 11-12.5µm Spore width: 7.5-8.5µm Polar capsules: 5-5.5µm (L)×3-3.5µm (W)</p>
<p>Reference: Paperna (1973)</p>

<i>MYXOBOLUS SYNODONTI</i> FOMENA, BOUX & BIRGI, 1985
<p>Type host: <i>Synodontis batesii</i> Localities: Nyong Basin (Cameroon) Organs: Stomach wall Figure: 6.8C</p>
REMARKS
<p>In frontal view the spores are ellipsoid with the anterior end rounded. Two pyriform shaped polar capsules are situated in the anterior end of the spores.</p>
MEASUREMENTS
<p>Total length: 12-15µm Spore width: 5.8-6.9µm Polar capsules: 5.6-7µm (L)×1.7-2.5µm (W)</p>
<p>Reference: Fomena, Bouix & Birgi (1985)</p>

Table 6.1 continued: Compendium summarising the *Myxobolus* Bütschli, 1882 species infecting African freshwater fishes.

<i>MYXOBOLUS TILAPIAE</i> ABOLARIN, 1974
<p>Hosts: <i>Tilapia zilli</i>, <i>Oreochromis niloticus</i>, <i>Sarotherodon galilaeus</i></p> <p>Localities: Nigeria</p> <p>Organs: Gills and fins</p> <p>Figure: 6.8D</p>
REMARKS
<p>The plasmodia, varying between 0.5-2mm in length and appear as white pustules. The spores are variable in shape, but are mostly rectangular with blunt corners. Some may be oblong showing a pointed anterior end, while others are symmetrically oval. The polar capsules are restricted to the first quarter of the spore cavity and are mostly equal in size.</p>
MEASUREMENTS
<p>Total length: 12-20µm</p> <p>Spore width: 7.5-11µm</p> <p>Polar capsules: 2-3.5µm (L)×2-2.5µm (W)</p>
<p>Reference: Abolarin (1974)</p>

<i>MYXOBOLUS ZILLEI</i> SAKITI, BLANC, MARQUES & BOUIX, 1991
<p>Syn. <i>Myxobolus latesi</i> Kostoingue & Toguebaye, 1994</p> <p>Type host: <i>Tilapia zillei</i></p> <p>Localities: Lake Nokou (Benin)</p> <p>Organs: Gills</p> <p>Figure: 6.8E</p>
REMARKS
<p><i>Myxobolus latesi</i> Kostoingue & Toguebaye, 1994, a parasite of <i>Lates niloticus</i>, is synonymised by Fomena & Bouix (1997) with <i>M. zillii</i> because the criterion used to distinguish the two is an insignificant difference observed in polar capsule length. The spores of this species have a pointed anterior end and rounded posterior end. Two pyriform shaped polar capsules that do not converge are situated in the anterior end of the spore. An intercapsular process is present between the two polar capsules.</p>
MEASUREMENTS
<p>Total length: 8-11µm</p> <p>Spore width: 6-8µm</p> <p>Polar capsules: 4-6µm (L)×2-3µm (W)</p>
<p>Reference: Sakiti, Blanc, Marqués & Bouix (1991)</p>

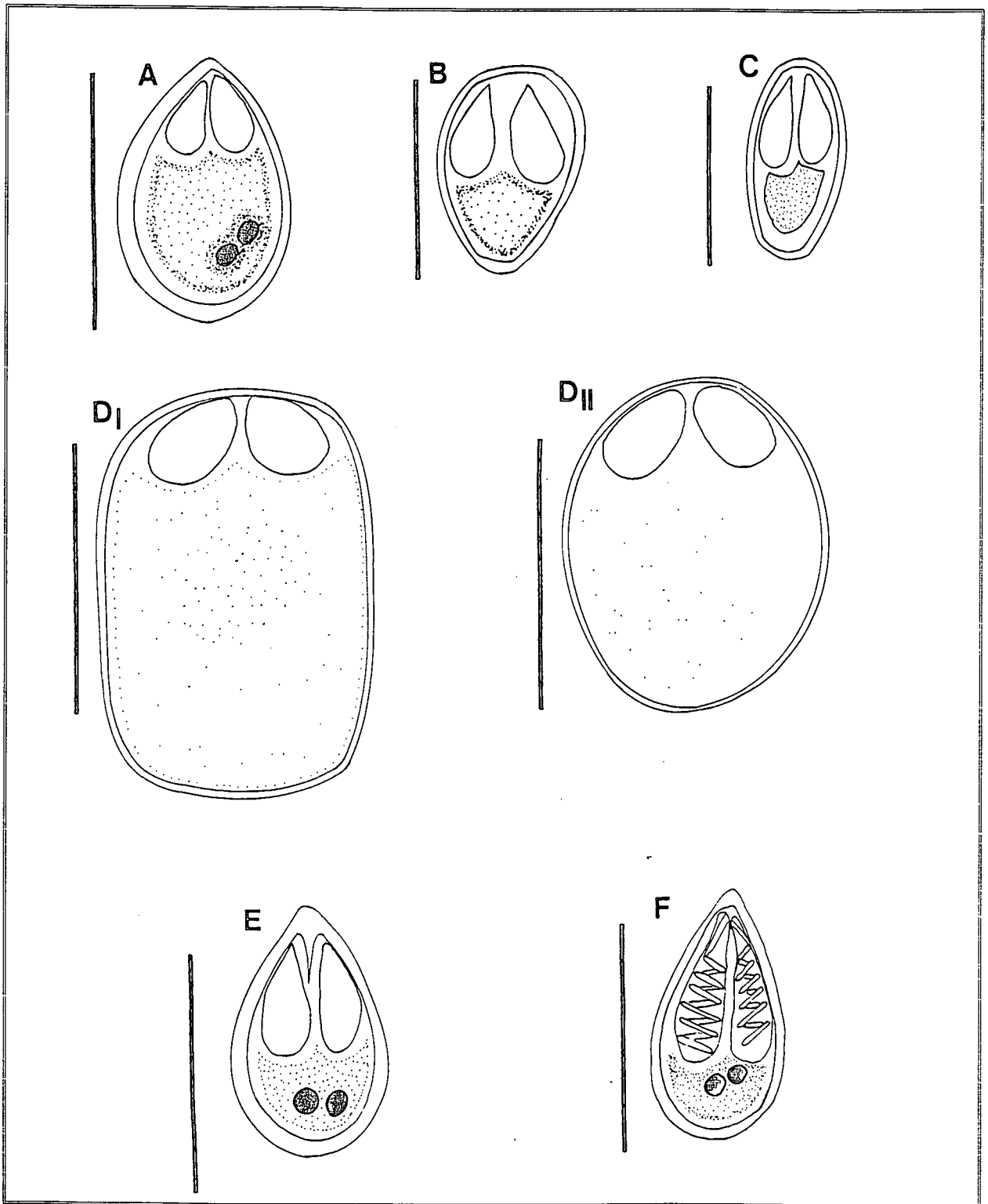


Figure 6.8: Line drawings of A- *M. sarotherodoni* Sakiti, Blanc, Marques & Bouix, 1991, B-*M. stenosis* Paperna, 1973, C-*M. synodonti* Fomena, Bouix & Birgi, 1985, D I & D II-*M. tilapiae* Abolarin, 1974, E-*M. zilleri* Sakiti, Blanc, Marques & Bouix, 1991, F-*Myxobolus* sp. (Obiekezie & Okaeme 1990) [Redrawn from Paperna (1973), Abolarin (1974), Fomena, Bouix & Birgi (1985), Obiekezie & Okaeme (1990), Sakiti, Blanc, Marques & Bouix (1991)] Scale Bar: 10 μ m.

MYXOBOLUS BÜTSCHLI, 1882 SPECIES INFECTING OKAVANGO FISHES***MYXOBOLUS AFRICANUS* FOMENA, BOUIX & BIRGI, 1985**

(Figs. 6.9A, 6.11A, 6.13A)

Host: *Hepsetus odoe* (Bloch, 1794)**Locality:** Lloyds Lagoon, Mokoro lagoon, Thoage Lagoon, Okavango River and Delta, (Botswana)**Location:** Gills**Incidence:** 25% (7/28)**Description:**

Vegetative stages: Only sporogonic plasmodia were found within the secondary gill lamella. The polysporous plasmodia were spherical in shape and whitish in colour. They measured approximately 1mm in diameter.

The spore: In valvular view, the spore body was found to be ovoid in shape with its anterior end pointed and measuring 15-17(16.7 ± 0.67 , 11) μm (Figs. 6.9A, 6.13A). The widest region of the spore was observed towards the posterior end of the polar capsules measuring 4-6(5.4 ± 0.45 , 11) μm in width. Two shell valves are visible with a well visible sutural ridge. The shell valves appear to be smooth (Fig. 6.11A). Two polar capsules of equal size were found situated in the anterior part of the spore, one of the polar capsules discharges laterally (Fig. 6.13A). Polar capsules measured 3-5(4.0 ± 0.15 , 11) μm (L) \times 1.5-2(2 ± 0.15 , 11) μm (W). Approximately six coils of the polar filament were visible within the polar capsules. It appears as if the spores contained a single sporoplasm.

Remarks: The distinct morphology and spore dimensions of these spores match those of *Myxobolus africanus* Fomena, Bouix & Birgi 1985. Fomena, Bouix and Birgi (1985) originally described this myxosporean species in Cameroon, also from the African pike, *Hepsetus odoe* and since it has been found on the same host in Botswana, as well as in the same organ confirms its identification as *M. africanus*.

MYXOBOLUS CAMEROUNENSIS FOMENA, MARQUÉS & BOUIX, 1993**(Figs. 6.9B, C, 6.10A, 6.11B)****Host I:** *Oreochromis andersonii* (Castelnau, 1861)**Locality:** Xaro Mainstream, Okavango River and Delta (Botswana)**Location:** The gill arch and buccal cavity**Prevalence:** 86% (6/7)**Description:**

Vegetative stages: Sporogonic plasmodia were found within the epithelium of the buccal cavity as well as in the gill arch of the host. The polysporous plasmodia were spherical to elongate in shape and whitish in colour, measuring 1-3mm in length.

The spore: In valvular view, the spore body is slightly elongate to ovoid in shape with its anterior end bluntly pointed and the posterior end rounded, measuring 16.2-17.5(16.7±0.5, 10)µm (Figs. 6.9B, 6.10A). The widest region of the spore is observed behind the posterior ends of the polar capsules measuring 11.2-12.5(11.6±0.60, 10)µm in width. Two smooth shell valves are (Fig. 6.11B) visible with a narrow sutural ridge passing along the edges of the spore. Two rounded pyriform shaped polar capsules of equal size are situated in the anterior part of the spore measuring 6.8-7.5(7.3±0.32, 10)µm (L)×3-3.8(3.6±0.42, 10)µm (W). Five to six coils are visible in the polar filament and it appears as if the spores contain a single sporoplasm with two nuclei visible.

Host II: *Tilapia ruweti* (Poll & Thys van den Audenaerde, 1965)

Locality: Etsatsta Mainstream, Okavango River and Delta (Botswana)

Location: Within the gill arch

Prevalence: 100% (1/1)

Description:

Vegetative stages: Only sporogonic plasmodia were found within the gill arch. The polysporous plasmodia were oblong in shape and whitish in colour measuring 1-2mm in length.

The spore: In valvular view, the spore body is ovoid in shape with the anterior end slightly pointed and the posterior end rounded, measuring 15-18(17.0 ± 0.97 , 9) μm (Fig. 6.9C). The widest region of the spore is observed towards the posterior ends of the polar capsules measuring 10-11.2(11.7 ± 0.68 , 9) μm in width. Two smooth shell valves are visible with a sutural ridge passing along the edge of the spore. Two pyriform shaped polar capsules, equal in size, are situated in the anterior part of the spore, measuring 6.8-7.5(7.4 ± 0.22 , 9) μm (L) \times 3.7-3.8(3.8 ± 0.05 , 9) μm (W). The polar filament within the polar capsules has approximately five to six coils. It appears as if the spores contained a single large binucleate sporoplasium.

Remarks: The morphological descriptions of the spores from both these hosts are practically identical and it is suffice to say that the two are the same species, occurring in different hosts. Morphologically the spores conform to the description of *M. camerounensis* described by Fomena *et al.* (1993) from the gills of *Oreochromis niloticus* in Cameroon. These are both new host records for this species as well as a new geographical record. *Myxobolus* species described from *Tilapia* and *Oreochromis* fish hosts in Africa include *M. agolus* Landsberg, 1985, *M. brachysporous* (Baker, 1963), *M. doussoui* Sakiti, Blanc, Marqués & Bouix, 1991, *M. equatorialis* Landsberg, 1985, *M. fotoi* Fomena, Marqués & Bouix, 1985, *M. heterosporus* (Baker, 1963), *M. homeosporus* Baker, 1963, *M. israelensis* Landsberg, 1985, *M. nilei* (Faisal & Shalaby, 1987), *M. tilapiae* Abolarin, 1974, *M. sarigi* Landsberg, 1985 and *M. zillei* Sakiti, Blanc, Marqués & Bouix, 1991. Comparisons of *M. camerounensis* with these species reveal the following differences:

The latter is distinct from *M. agolus* (Fig.6.2B), parasitising kidneys and spleen of, amongst others, *Oreochromis niloticus vulcani*, because the *M. camerounensis* has ovoid to spherical spores and has polar capsules that reach the posterior half of the spore, taking up more than half of the spore cavity. The polar filaments in *M. agolus* have 10 to 11 coils (Landsberg 1985), compared to the five to six of *M. camerounensis*.

Myxobolus brachysporous (Fig. 6.2F) found in the spleen of *T. esculenta* and *T. variabilis* by Baker (1963), differs in having a spore that has a width that is wider than the length of the spore and not being regularly ellipsoidal. The polar capsules of the former are also more pear-shaped to spherical, with the polar filaments displaying approximately five to seven coils. Compared to *M. doussoui* (Fig. 6.4C), occurring in, amongst others, the gills of *Tilapia zillii* and *Hemichromis fasciatus*, *M. camerounensis* is distinct in having a more elongated to ovoid body, compared to the almost spherical shape of the former species. Furthermore, the polar capsules of *M. doussoui* are unequal in size (Sakiti *et al.* 1991) and take up a large area within the spore cavity leaving only a small space for the sporoplasm.

Myxobolus camerounensis differs from *M. equatorialis* (Fig.6.4D) which was described from the spleen of an *Oreochromis aureus* × *O. niloticus* hybrid, because *M. equatorialis* has a more distinct pyriform shaped body, with an anterior end that is more slender tapering to a point. Furthermore *M. equatorialis* has very unique polar capsules, being pyriform, of unequal size and situated in almost the centre of the spore cavity with an extremely attenuated neck region (Landsberg 1987). Compared to *M. fotoj* (Fig. 6.4E), described from the gills of *O. niloticus* by Fomena *et al.* (1993), *M. camerounensis* is distinct since the former species has almost spherical spores that show no differences in anterior and posterior appearance, both ends being rounded. The polar capsules are also different, being smaller and sub-oval compared with the pyriform shape of *M. camerounensis*.

The spore body of *M. camerounensis* differs from *M. heterosporous* type (I) and (II) (found in *T. esculenta*, *T. variabilis* and *Oreochromis niloticus*), described by Baker (1963), in having an anterior end that tapers slightly more than the posterior end (Fig. 6.5A). Compared to *M. heterosporous* type (III), *M. camerounensis* differs in having

an oval to elongate spore body that does not taper sharply to a blunt point. Furthermore the polar capsules of *M. heterosporous* are very slender and elongate, compared with the pyriform shaped polar capsules of *M. camerounensis*.

Myxobolus homeosporous (Fig. 6.5B), from the muscles of *T. esculenta* and *T. variabilis*, is morphologically similar to *M. camerounensis*, but differs in having ovoid spores that are not slightly elongated. The polar capsules of *M. homeosporous* are also slightly smaller and thus although the spore dimensions are similar, the polar capsules of *M. camerounensis* take up more space in the spore cavity. *Myxobolus camerounensis* differs significantly in shape from *M. tilapiae* (Fig. 6.8D), found in the gills and fins of *T. zillii*, *O. niloticus* and *Sarotherodon galilaeus* by Abolarin (1974), which has distinctly rectangular to oval shaped spores that have similar posterior and anterior ends. Furthermore, the polar capsules of *M. tilapiae* are almost spherical in shape, compared to the more pyriform shaped polar capsules of *M. camerounensis*.

Myxobolus israelensis (Fig. 6.5D), from the gills of, amongst others, *O. niloticus vulcani*, has a more elongate to ovoid spore body than *M. camerounensis*. The polar capsules of *M. israelensis* also takes up more than half of the total spore body (Landsberg 1985) and has seven to eight coils in each polar filament. *Myxobolus camerounensis* also differs from *M. nilei*, found in various organs of *O. niloticus*, by Faisal and Shalaby (1987), because the latter myxosporean species has an almost spherical spore shape, with two polar capsules that fill almost half of the spore cavity.

Myxobolus camerounensis differs significantly from *M. sarigi* (Fig. 6.7F), found in the kidneys and spleen of amongst others, *Sarotherodon galilaeus* and *Oreochromis niloticus*, because according to Landsberg (1985), the spores of *M. sarigi* are ovoid, with a flattened anterior end that is as wide as the posterior end. *Myxobolus sarigi* spores also possess two polar capsules that do not converge in the anterior of the spore.

Myxobolus zillei (Fig. 6.8E), also found in the gills of *T. zillii*, is much smaller than *M. camerounensis* with the anterior end of the former species tapering more sharply to a blunt point. The presence of a very distinct intercapsular process between two

very slender and elongate polar capsules (Sakiti *et al.* 1991) distinguishes this species from *M. camerounensis*.

MYXOBOLUS HYDROCYNII KOSTOÏNGUE & TOGUEBAYE, 1994

(Figs. 6.9D, 6.10B, 6.11C, 6.13B, C)

Host: *Hydrocymus vittatus* Castelnau, 1861

Locality: Xaro Mainstream, Etsatsta Mainstream, Okavango River and Delta
(Botswana)

Location: Gill operculum and gill arch

Prevalence: 33% (3/9)

Description:

Vegetative stages: Sporogonic plasmodia were found within the epithelial cells of the gill operculum as well as within the gill arch cartilage. The polysporous plasmodia were spherical in shape and whitish in colour. They measured approximately 1mm in diameter.

The spore: The spore body is ovoid in valvular view, with its anterior and posterior ends round, measuring 8.7-10.1(9.9±0.38, 10)µm (Figs. 6.9D, 6.10B, 6.13B). The widest region of the spore is observed towards the posterior ends of the polar capsules and measures 6.2-7.5(7.2±0.39, 10)µm in width. Two shell valves are visible with a sutural ridge passing around the edge of the spore. The shell valves appear to be smooth (Fig. 6.11C) and two slender polar capsules of equal size are found situated in the anterior part of the spore, measuring 3.7-5(4.5±0.63, 10)µm (L)×1-1.2(1.2±0.13, 10)µm (W). The number of coils in the polar filament (Fig. 6.13C) within the polar capsules is difficult to observe with the aid of a light microscope and it appears as if the spores contain a single sporoplasm.

Remarks: The morphology, spore dimensions and host genus of this species conforms to that of *Myxobolus hydrocyni*. This is a new host and geographical record for this species and when compared with *M. amieti* Fomena, Bouix & Birgi, 1985, *M. exiguus* Thélohan, 1895, *M. noukoueensis* Blanc Marqués & Bouix, 1991, *M.*

nyongana (Fomena, Bouix & Birgi, 1985) and *M. zillei* the following morphological differences can be found.

Myxobolus hydrocyni is similar in overall shape to *M. amieti* (Fig.6.2C), which was found in various organs of *Ctenopoma nanum* by Fomena *et al.* (1985), with both species having two polar capsules that do not lie parallel to each other, but only converge in the anterior half of the spore. Furthermore, the spores of this species are more spherical than the slender, more elongate spores of *M. amieti*. Finally the polar capsules of *M. amieti* extend through more than half of the spore cavity which differs from those of *M. hydrocyni* that reach only the centre of the spore.

Found in the gills of *Abramis brama*, *Mugil capito* and *M. chelo* by Thélohan (1895), *Myxobolus exiguus* Thélohan, 1895 differs from *M. hydrocyni* since the sutural ridge of the former species has six indented markings, which differs from the smooth sutural ridge surface of the latter myxosporean species. The anterior spore body of *M. exiguus* also tapers to a greater degree than the anterior end of *M. hydrocyni*. Having a similar spore body shape to *M. noukoueensis* (Fig. 6.7B), a parasite of *Sarotherodon melanotheron*, *M. hydrocyni* is distinct in having polar capsules that extend to the centre of the spore and are not short or pyriform shaped. Compared with *M. nyongana* (Fig. 6.7C) found in various *Barbus* species, *M. hydrocyni* differs since the former has a much sharper tapering anterior end. *Myxobolus zillei* (Fig. 6.8E) has an anterior spore body that tapers to a blunt point that is distinct from the more rounded anterior of *M. hydrocyni*. According to Sakiti *et al.* (1991), there is also a distinct intercapsular process in *M. zillei*, which is absent in *M. hydrocyni*. The polar capsules of *M. zillei* are more pyriform and volumous in shape, taking up a larger portion in the spore cavity.

MYXOBOLUS NYONGANA FOMENA, BOUIX & BIRGI 1994

(Figs. 6.9E, 6.10C, 6.11D, 6.13D)

Host: *Barbus poechii* Steindachner, 1911**Locality:** Etsatsta Mainstream, Okavango River (Botswana)**Location:** Secondary gill lamellae**Incidence:** 100% (1/1)**Description:**

Vegetative stages: Only sporogonic plasmodia were found within the secondary gill lamellae. The polysporous plasmodia were small and rounded in shape, whitish in colour, measuring 1mm in diameter.

The spore: In valvular view, the spore body is teardrop to ovoid in shape with its anterior end tapering to a blunt point, measuring 11-11.2(11.2±0.26, 12)µm (Figs. 6.9E, 6.10C). The widest region of the spore is observed towards the centre of the sporoplasm, measuring 6.1-7(6.5±0.31, 12)µm in width. Two smooth shell valves are visible (Fig. 6.11D) as well as a narrow sutural ridge, which appears to be slightly broader at the posterior end of the spore. Two polar capsules of occasionally unequal size are situated in the anterior part of the spore, measuring 3-5.5(4.4±0.79, 12)µm (L)×1.25-2.5(1.6±0.44, 12)µm (W) (Figs. 6.10C, 6.13D). The polar filament coils approximately seven times within the polar capsules and it appears as if the spores contain a single binucleate sporoplasm.

Remarks: The overall morphology of these spores conforms to the description of *M. nyongana* and this description can also be noted as a new host and geographical record. Species from the genus *Myxobolus* found in hosts from the genus *Barbus* in Africa include *M. nijinei* Fomena, Bouix & Birgi, 1985, *M. nkolyaensis* Fomena & Bouix, 1994 and *M. oloi* Fomena & Bouix, 1994.

Myxobolus nyongana differs from *M. nijinei* (Fig. 6.6F) since the latter has a spherical to ovoid spore with rounded posterior and anterior ends. The spores are also much larger than the spores of *M. nyongana*. Compared with *M. nkolyaensis* (Fig. 6.7A), *M. nyongana* is distinct because the former has an almost spherical spore with sub-

spherical polar capsules. Furthermore *M. nkolyaensis* has a reduced sporoplasm and occasionally has a third polar capsule in the spore cavity (Fomena & Bouix 1997). *Myxobolus oloi* (Fig. 6.7D) differs from *M. nyongana* in having an oval spore body with asymmetric polar capsules containing four to five coils in the polar filaments and furthermore these spores are smaller in overall dimension to that of *M. nyongana*.

MYXOBOLUS SP. A**(Figs. 6.9F, 6.10D, 6.11E, 6.12A, B, 6.13E, F)****Host:** *Clarias gariepinus* (Burchell, 1822)**Locality:** Lloyds Lagoon, Duba Lagoon, Okavango River (Botswana)**Location:** Ovaries**Prevalence:** 22.2% (2/9)**Description:**

Vegetative stages: Only sporogonic plasmodia were found within the ovaries. The polysporous plasmodia were spherical and whitish in colour and measured 2-3mm in diameter.

The spore: In valvular view, the spore body is ovoid to spherical in shape with its anterior end bluntly rounded, measuring 13.7-15 (13.9 ± 0.4 , 10) μm (Figs. 6.9F, 6.10D, 6.13E, F). The widest region of the spore is observed towards the posterior ends of the polar capsules and measures 10-11.2 (10.8 ± 0.5 , 10) μm in width. Two smooth shell valves are visible (Fig. 6.11E) with two pyriform polar capsules of equal size converging in the anterior part of the spore, measuring 6-6.2 (6.2 ± 0.12 , 10) μm (L) \times 3-3.7 (3.5 ± 0.13 , 10) μm (W) (Figs. 6.10D, 6.13E, F). Five to six coils of the polar filament (Figs. 6.12A, B) are observed in the polar capsules and it appears as if the spores contain a single binucleate sporoplasm with a large iodophilous vacuole.

Remarks: *Myxobolus* species described from *Clarias* hosts in Africa are *M. clarii* Mandour, Galal & Abed, 1993 and *M. comoei* Kabré, Sakiti, Marqués & Sawadago, 1995. This species described above is very similar to *M. clarii* (6.3E), the only difference being that the anterior end of *Myxobolus* sp. A has a small blunt point, which appears to be absent in the former species. *Myxobolus* sp. A strongly resembles *M. comoei* (Fig. 6.3F) having the same almost spherical spore body. It does, however, differ because the latter species has two polar capsules that take up about half the space in the spore cavity while the polar capsules of *Myxobolus* sp. A only take up about one third of the spore cavity. The anterior end of *Myxobolus* sp. A has a small blunt point which is absent in *M. comoei*.

Morphological comparisons can also be made with *M. bilongi* Fomena, Marqués, Bouix & Njiné, 1994 (Fig. 6.2E), *M. camerounensis* (Fig. 6.3B), *M. fotoi* (Fig. 6.4E) and *M. njinei* (Fig. 6.6E). Firstly, *Myxobolus* sp. A is distinct from *M. bilongi*, found in the gills of a *Labeo* sp. by Fomena *et al.* (1994), since the latter myxosporean possesses two polar capsules of unequal sizes. When compared with *M. camerounensis*, a difference can be seen in the anterior spore bodies. The anterior end of *M. camerounensis* is much narrower than its posterior end, whereas, the anterior and posterior ends of *Myxobolus* sp. A are more or less similar in size.

Myxobolus fotoi differs from *Myxobolus* sp. A in having an almost completely spherical spore and also having polar capsules that are sub-spherical and take up approximately one fourth of the spore cavity. *Myxobolus njinei*, a parasite of various *Barbus* species, has a much more oval spore shape, thus differing from the more spherical spore body of *Myxobolus* sp. A. Furthermore, *M. njinei* has two distinctly unequally sized polar capsules that take up almost two thirds of the spore body (Fomena *et al.* 1994) and are also much larger than the spores of *Myxobolus* sp. A.

MYXOBOLUS SP. B**(Figs. 6.9G, 6.10E, 6.11F, 6.14A)****Host:** *Barbus thamalakanensis* Fowler, 1935**Locality:** Etsatsta Mainstream, Okavango River (Botswana)**Location:** Secondary gill filaments**Incidence:** 100% (1/1)**Description:**

Vegetative stages: The polysporous plasmodia were found within the secondary gill lamellae of the host and were whitish in colour and very small and rounded.

The spore: In valvular view, the spores are extremely elongated, pyriform to teardrop shaped, with the anterior end tapering sharply to a point and the posterior end being rounded, measuring 12.8-15(13 ± 0.94 , 9) μm (Figs. 6.9G, 6.10E, 6.14A). Two smooth shell valves are visible (Fig. 6.11F) and a narrow sutural ridge passes around the entire spore and appears to be slightly broader at the posterior end. Two extremely elongated, pyriform shaped polar capsules of unequal length are situated almost parallel to one another in the anterior half of the spore, measuring 7-8(7.5 ± 0.35 , 9) μm (L) \times 1.25-2.5(2.3 ± 0.43 , 9) μm (W) (Figs. 6.10E, 6.14BA). It seems as if the polar filaments contain seven to eight coils in the polar capsules. The widest part of the spore is observed towards the posterior ends of the polar capsules, measuring 6.2-8(6.8 ± 0.65 , 9) μm in width. A small sporoplasm is situated in the posterior half of the spore.

Remarks: *Myxobolus* sp. B does not conform exactly to any of the known African *Myxobolus* species, but can be compared with *M. njinei*, *M. nkolyaensis*, *M. nyongana* and *M. oloi*, all of which parasitise *Barbus* species.

Myxobolus sp. B is distinct from *M. njinei*, *M. nkolyaensis* and *M. oloi* because all these species have spherical spore bodies. Of all the *Myxobolus* species infecting *Barbus* fish hosts in Africa, the closest resemblance is with *M. nyongana* (Fig. 6.7C) described by Fomena *et al.* (1985). *Myxobolus* sp. B is, however, distinct from this species in having a much more elongated spore body with extremely extended polar capsules that fill approximately two thirds of the spore cavity.

Other morphological comparisons can be made with *M. amieti*, *M. beninensis* Sakiti, Blanc, Marqués & Bouix, 1991 and *M. kriebiensis* and a *Myxobolus* sp. described by Obiekezie and Okaeme (1990). Compared to *M. amieti* (Fig. 6.2C), *Myxobolus* sp. B has a very slender spore body that tapers to a sharper degree, forming a narrow anterior end. Furthermore, the polar capsules of *Myxobolus* sp. B are more elongate and almost parallel to one another.

Myxobolus sp. B differs from *M. beninensis* (Fig. 6.2D), found in the gills of *S. melanotheron* by Sakiti *et al.* (1991), in having a more slender and elongated spore body with a more pointed anterior end. The polar capsules of *M. beninensis* also take up more than half of the spore body, but are slightly more volumous and are equal in size.

Myxobolus sp. B is very similar to *M. kriebiensis* (Fig. 6.5F), which was found in various organs of *Brycinus longipinnus* by Fomena and Bouix (1994), also having very elongated spores. The anterior end of *Myxobolus* sp. B is, however, much narrower and tapers to a sharper degree to form a blunt point. The anterior end of *M. kriebiensis* is also narrow, but does not taper to the same degree. The polar capsules of *M. kriebiensis* are very volumous and fill just about the entire spore cavity and also has between 19 and 28 coils in the polar filament. The spores of *M. kriebiensis* are also much larger than *Myxobolus* sp. B.

Myxobolus sp. B is extremely similar to a *Myxobolus* sp. described by Obiekezie and Okaeme (1990) (Fig. 6.8F) from the kidneys and spleen of various cichlid species. This appears to be the same species, but it is difficult to be sure since the spore sizes differ slightly and it appears that there is a difference in the shell valve thickness.

MYXOBOLUS SP. C

(Figs. 6.9 H, 6.10F, 6.11G, 6.14B)

Host: *Barbus paludinosus* Peters, 1852**Locality:** Etsatsta Mainstream, Okavango River (Botswana)**Location:** Secondary gill lamellae**Incidence:** 71% (5/7)**Description:**

Vegetative stages: Only sporogonic plasmodia were found within the secondary gill lamellae. The polysporous plasmodia were small, rounded and whitish in colour and measured 0.3mm in diameter.

The spore: In valvular view, the spore body is pyriform to ovoid in shape with its anterior end tapering to a blunt point and the posterior end rounded, measuring 11.2-13.7(12 ± 0.87 , 10) μm (Figs. 6.9H, 6.10F, 6.14B). The widest region of the spore is observed towards the posterior ends of the polar capsules measuring 7.5-10(8.6 ± 0.75 , 10) μm in width. Two smooth shell valves are visible (Fig. 6.11G) with a sutural ridge visible along the edge of the spore, becoming broader towards the posterior end. Two polar capsules of equal size are situated in the anterior part of the spore measuring 5-6.8(5.7 ± 0.88 , 10) μm (L) \times 2-2.5(2.4 ± 0.21 , 10) μm (W) (Figs. 6.10F, 6.14B). The polar filaments have six to seven coils within the polar capsules and it appears as if the spores contain a single binucleate sporoplasm situated in the posterior end of the spore.

Remarks: The spores described above do not definitely conform to an already described species and when compared to *M. njinei*, *M. nkolyaensis*, *M. nyongana* and *M. oloi*, all of which parasitise *Barbus* host species in Africa, the following differences can be found between these species and *Myxobolus* sp. C.

Myxobolus sp. C is distinct from *M. njinei* (Fig. 6.6E) described by Fomena *et al.* (1985), in having an anterior end that tapers to a blunt point and polar capsules that are completely spherical in shape. *Myxobolus* sp. C differs from *M. nkolyaensis* (Fig. 6.7A) 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 *Myxobolus* sp. C. *Myxobolus nyongana* (Fig. 6.7C) is similar to *Myxobolus* sp. C in having a spore body that tapers anteriorly to a blunt point with a rounded posterior end. The spores of *Myxobolus* sp. C are not as slender as those of *M. nyongana*. The polar capsules of *Myxobolus* sp. C do not lie parallel to one another, as in the case of *M. nyongana*. *Myxobolus* sp. C is distinct from *M. oloi* (Fig. 6.7D) because according to Fomena and Bouix (1994), the latter species has an almost entirely spherical body with two unequal polar capsules.

Morphologically similar species that infect hosts other than *Barbus* species include *M. amieti*, *M. beninensis*, *M. israelensis*, *M. noukeensis* and a *Myxobolus* sp. 2 described by Fomena and Bouix (1985). Comparisons of *Myxobolus* sp. C with these species reveal the following differences.

Myxobolus sp. C is similar to *M. amieti* (Fig. 6.2C) 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 cavity. Although having a similar spore shape, *Myxobolus* sp. C is distinct from *M. beninensis* (Fig. 6.2D) in that the latter species has two polar capsules that take up two thirds of the spore cavity. The spores of *Myxobolus* sp. C are also slightly wider than those from *M. beninensis*. *Myxobolus* sp. C is very similar to *M. israelensis* (Fig. 6.5D), having similar spore dimensions, but differs because 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 cavity, leaving little place for the sporoplasm (Landsberg 1985).

Myxobolus sp. C appears to conform to the description of *Myxobolus* sp. 2 (Fomena & Bouix 1985). A definite identification cannot be made with certainty since differences in spore sizes were noted.

MYXOBOLUS SP. D

(Figs. 6.9I, 6.10G, 6.11H, 6.14C, D)

Host: *Tilapia rendalli rendalli* (Boulenger, 1896)**Locality:** Lloyds Lagoon, Mohembo Floodplains, Okavango River and Delta (Botswana)**Location:** Buccal cavity**Incidence:** 12.5% (1/8)**Description:**

Vegetative stages: Only sporogonic plasmodia were found within the gills. The polysporous plasmodia were rounded and whitish in colour and measured 0.5mm in diameter.

The spore: In valvular view, the spore body is oblong to oval in shape with its anterior and posterior ends bluntly rounded, measuring 14-15.5(15 ± 0.39 , 10) μm (Fig. 6.9I, 6.10G, 6.14C,D). The widest region of the spore is observed towards the centre of the spore body and measures 12-12.6(12.3 ± 0.27 , 10) μm in width. Two smooth shell valves are visible (Fig. 6.11H) and a narrow sutural ridge can be seen surrounding the spore. Two almost spherical to pyriform shaped polar capsules of equal size are situated in the anterior end of the spore, measuring 3.8-5(4.6 ± 0.55 , 10) μm (L) \times 3-4(3.5 ± 0.44 , 10) μm (W). The polar filaments have five to six coils within the polar capsules (Fig. 6.14C, D) and it appears as if the spores contain a single large sporoplasm.

Remarks: *Myxobolus* sp. D possibly conforms to the description of *M. tilapiae*. It is difficult to be certain about this identification since three different diagrams are presented in the description of which only one resembles *Myxobolus* sp. D. Thus, although no definite identification has been made, *Myxobolus* sp. D can be compared with *M. brachysporous*, *M. doussoui*, *M. heterosporus*, *M. homeosporus*, *M. tilapiae* and *M. zillei*, based on the fact that these species all occur in *Tilapia* hosts in Africa.

Myxobolus sp. D is distinct from *M. brachysporous* (Fig. 6.2F) described by Baker (1963), in that the latter has a spore body that has a spore width longer than its length. *Myxobolus dossoi* (Fig. 6.4C) differs from *Myxobolus* sp. D in having an almost

spherical spore body with two unequal pyriform polar capsules. The spores of *Myxobolus* sp. D are also somewhat larger than those of *M. dossoui*. *Myxobolus* sp. D is similar to *M. heterosporus* type (I) (Fig. 6.5A) having a similar overall spore shape. The polar capsules of *M. heterosporus* are, however, more pyriform shaped, compared with the almost spherical shaped polar capsules of *Myxobolus* sp. D. This species differs from *M. heterosporus* type (II) and (III) because these two spore shapes taper towards the anterior ends.

Myxobolus homeosporus (Fig. 6.5B) is distinct from *Myxobolus* sp. D in having an anterior end that is slightly narrower than the posterior end. The polar capsules of *Myxobolus* sp. D are also more spherical than those of *M. homeosporus*. *Myxobolus* sp. D is distinct from *M. zillei* (Fig. 6.8E) because the latter has a bluntly pointed anterior end (Sakiti *et al.* 1991), which differs significantly from that of the former. The spores of *Myxobolus* sp. D are also larger than the spores of *M. zillei*.

Due to being morphologically similar, comparisons of *Myxobolus* sp. D can be made with *M. polycentropsi* Fomena, Bouix & Birgi, 1985 and *M. synodonti* Fomena, Bouix & Birgi, 1985, parasites of *Polycentropsis abbreviata* and *Synodontis batesii*, respectively. The former myxosporean species is similar to *Myxobolus* sp. D in having anterior and posterior ends that are both bluntly rounded. The polar capsules of *M. polycentropsi* (Fig. 6.7E) are, however, more pyriform in shape (Fomena *et al.* 1985), compared to the almost spherical ones in *Myxobolus* sp. D.

Finally, *Myxobolus synodonti* (Fig. 6.8C) is distinct from *Myxobolus* sp. D in having an anterior end that is slightly more tapered than the more rounded posterior end. The polar capsules of *M. synodonti* are much larger and elongated, compared to the almost spherical polar capsules of *Myxobolus* sp. D.

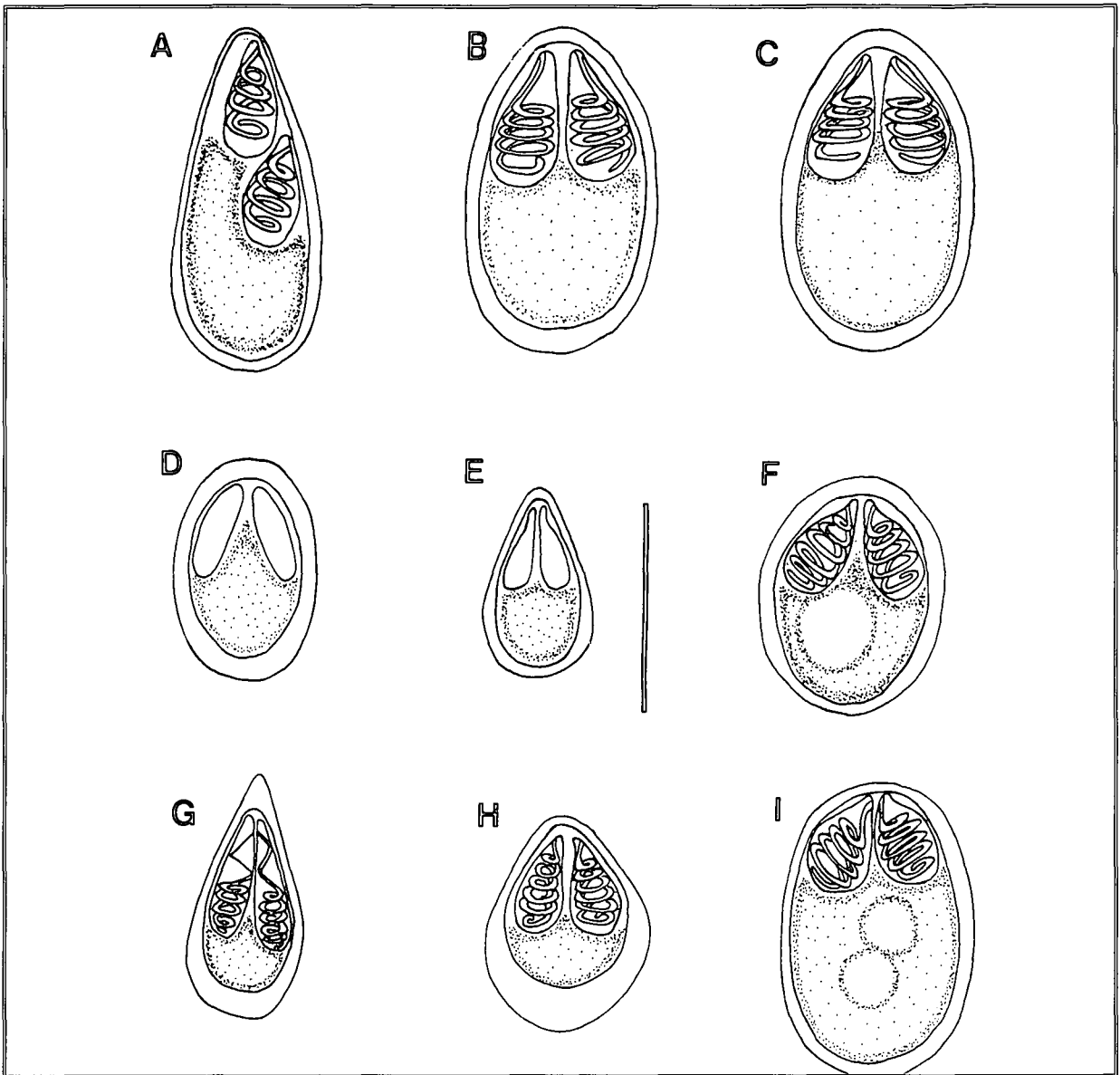


Figure 6.9: Line drawings of *Myxobolus* species collected from the Okavango River and Delta, Botswana. A-*Myxobolus africanus* Fomena, Bouix & Birgi, 1985 from *Hepsetus odoe* (Bloch, 1794) B-*M. camerounensis* Fomena, Marqués & Bouix, 1993 from *Oreochromis andersonii* (Castelnaud, 1861), C- *M. camerounensis* from *Tilapia ruweti* (Poll & Thys van den Audenaerde, 1965) D-*M. hydrocyni* Kostoingue & Toguebaye, 1994 from *Hydrocynis vittatus* Castelnaud, 1861, E-*M. nyongana* (Fomena, Bouix & Birgi, 1985) from *Barbus poechii* Steindachner, 1911, F-*Myxobolus* sp. A from *Clarias gariepinus* (Burchell, 1822), G-*Myxobolus* sp. B from *Barbus thamalakanensis* Fowler, 1935, H-*Myxobolus* sp. C from *Barbus paludinosus* Peters, 1852, I-*Myxobolus* sp. D from *Tilapia rendalli rendalli* (Boulenger, 1896). Scale bar 10 μ m.

Figure 6.10

Compound light micrographs of *Myxobolus* Bütschli, 1882 species collected from fishes in the Okavango River and Delta, Botswana

A: *Myxobolus camerounensis* Fomena, Marqués & Bouix, 1993 from the gill arch of *Oreochromis andersonii* (Castelnaud, 1861)

B: *M. hydrocyni* Kostoingue & Toguebaye, 1994 from the gill arch of *Hydrocynus vittatus* Castelnaud, 1861

C: *M. nyongana* (Fomena, Bouix & Birgi, 1985) from the gills of *Barbus poechii* Steindachner, 1911

D: *Myxobolus* sp. A from the ovaries of *Clarias gariepinus* (Burchell, 1822)

E: *Myxobolus* sp. B from the gills of *Barbus thamalakanensis* Fowler, 1935

F: *Myxobolus* sp. C from the gills of *Barbus paludinosus* Peters, 1852

G: *Myxobolus* sp. D from the gills of *Tilapia rendalli rendalli* (Boulenger, 1896)

Scale bar: 10µm

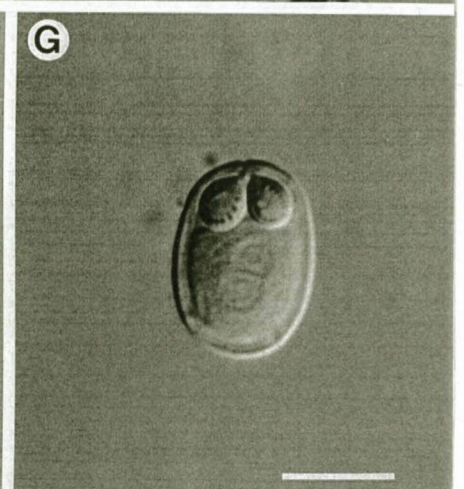
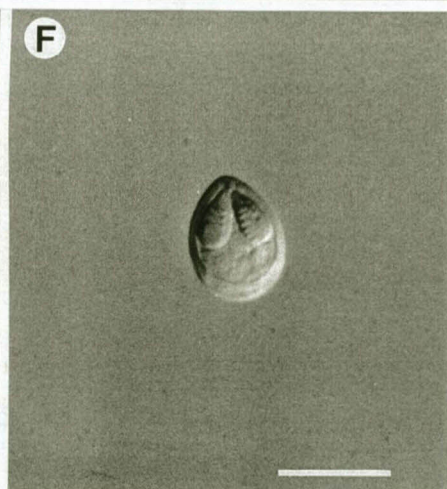
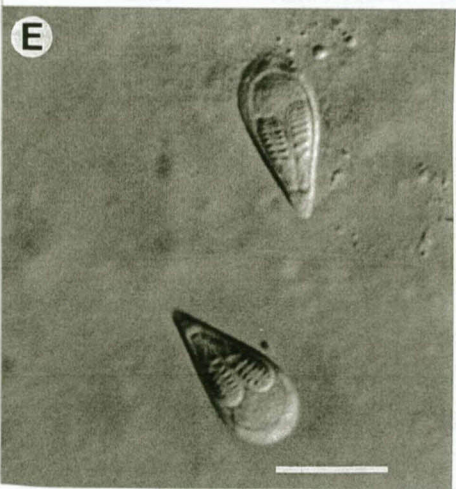
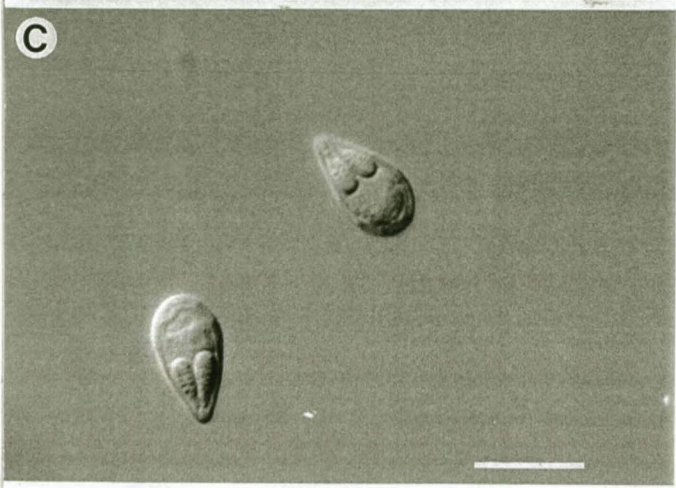
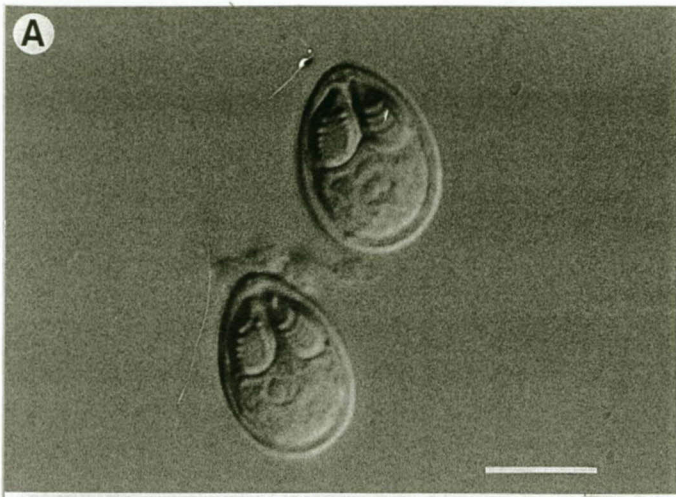


Figure 6.11

Scanning electron micrographs of *Myxobolus* Bütschli, 1882 species collected from fishes in the Okavango River and Delta, Botswana

A: *Myxobolus africanus* Fomena, Bouix & Birgi, 1985 from the gills of *Hepsetus odoe* (Bloch, 1794)

B: *Myxobolus camerounensis* Fomena, Marqués & Bouix, 1993 from the gill arch of *Oreochromis andersonii* (Castelnau, 1861)

C: *M. hydrocyni* Kostoïngue & Toguebaye, 1994 from the gill arch of *Hydrocynus vittatus* Castelnau, 1861

D: *M. nyongana* (Fomena, Bouix & Birgi, 1985) from the gills of *Barbus poechii* Steindachner, 1911

E: *Myxobolus* sp. A from the ovaries of *Clarias gariepinus* (Burchell, 1822)

F: *Myxobolus* sp. B from the gills of *Barbus thamalakanensis* Fowler, 1935

G: *Myxobolus* sp. C from the gills of *Barbus paludinosus* Peters, 1852

H: *Myxobolus* sp. D from the gills of *Tilapia rendalli rendalli* (Boulenger, 1896)

Scale bar: 10µm

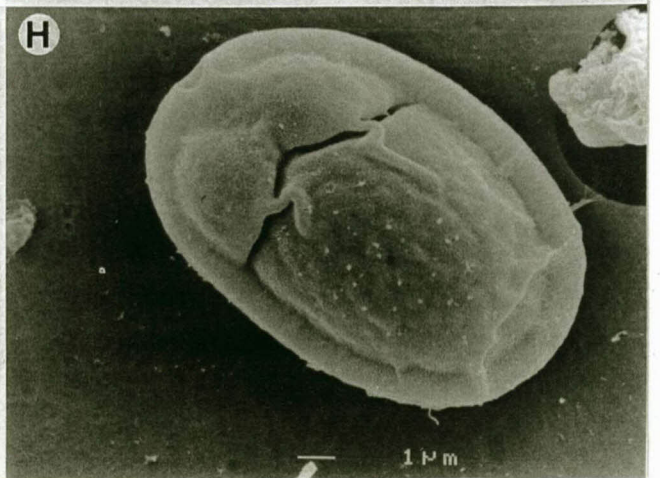
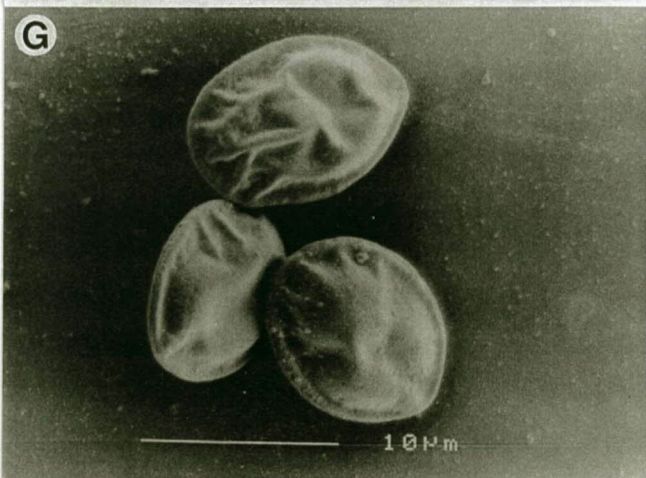
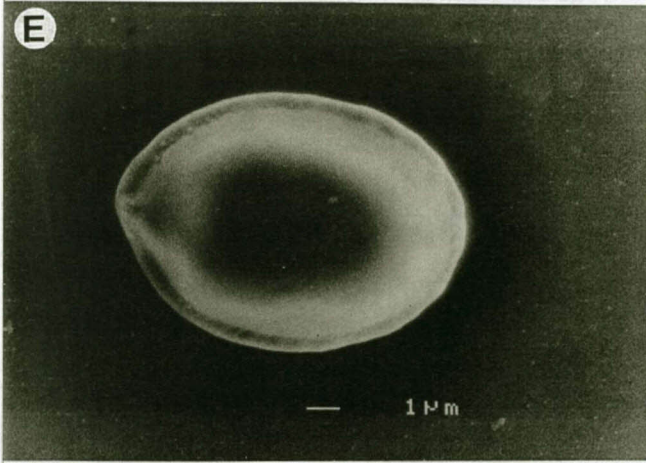
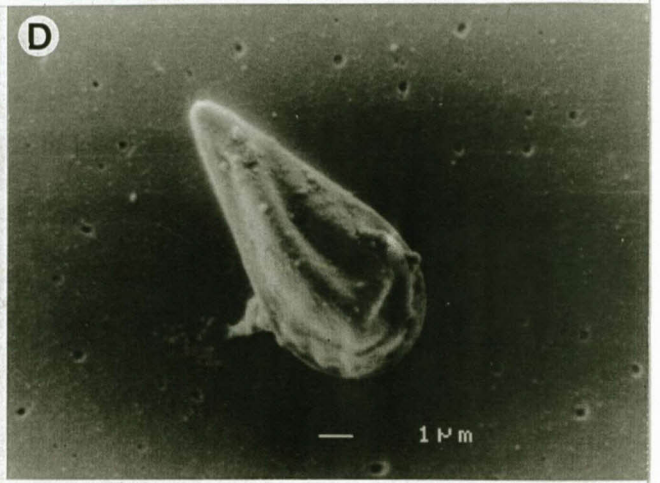
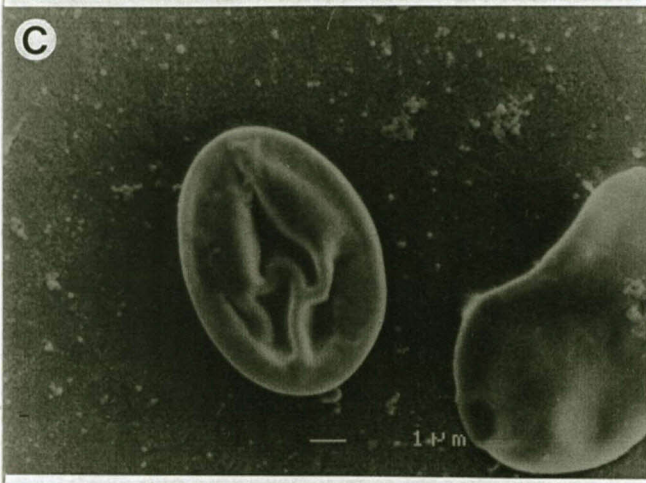
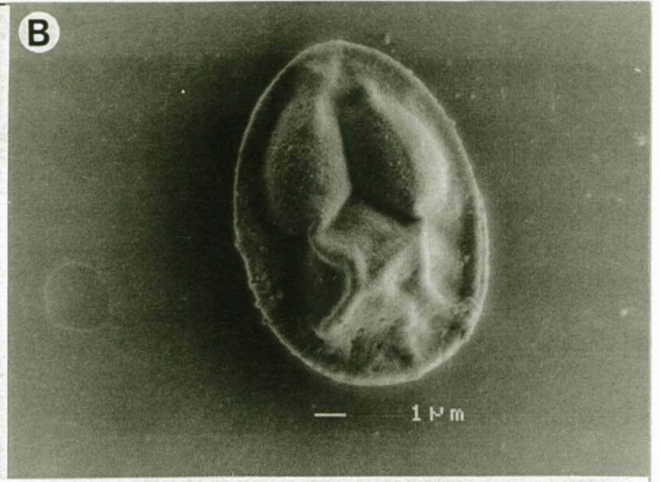
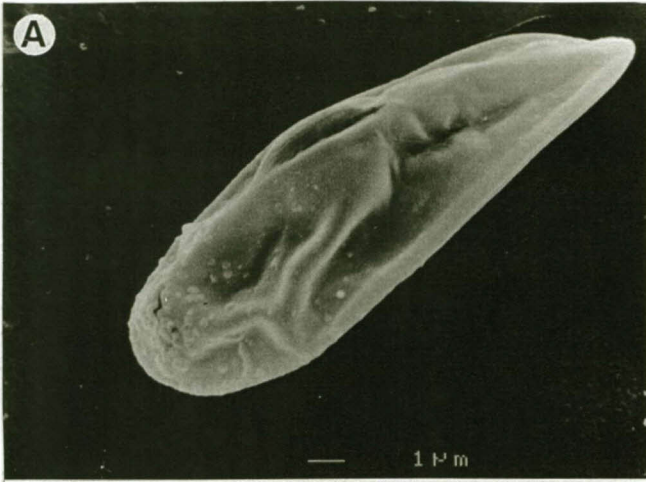


Figure 6.12

Transmission electron micrographs of *Myxobolus* Bütschli, 1882 species collected from fishes in the Okavango River and Delta, Botswana

A: *Myxobolus* sp. A from the ovaries of *Clarias gariepinus* (Burchell, 1822) showing the polar filament in the polar capsules

B: *Myxobolus* sp. A showing the two shell valves and polar filament coils

Scale bar: 10 μ m

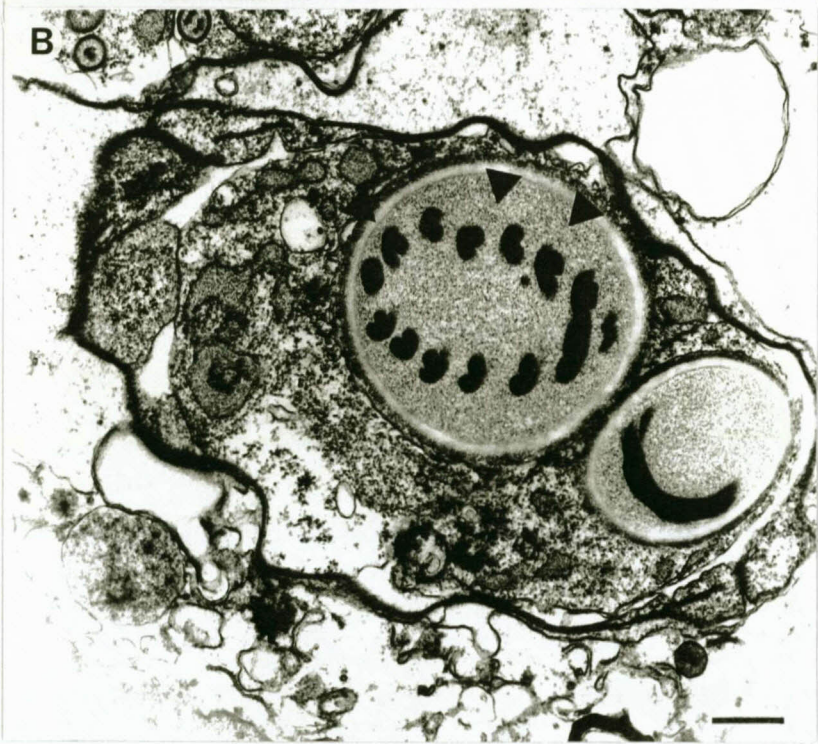
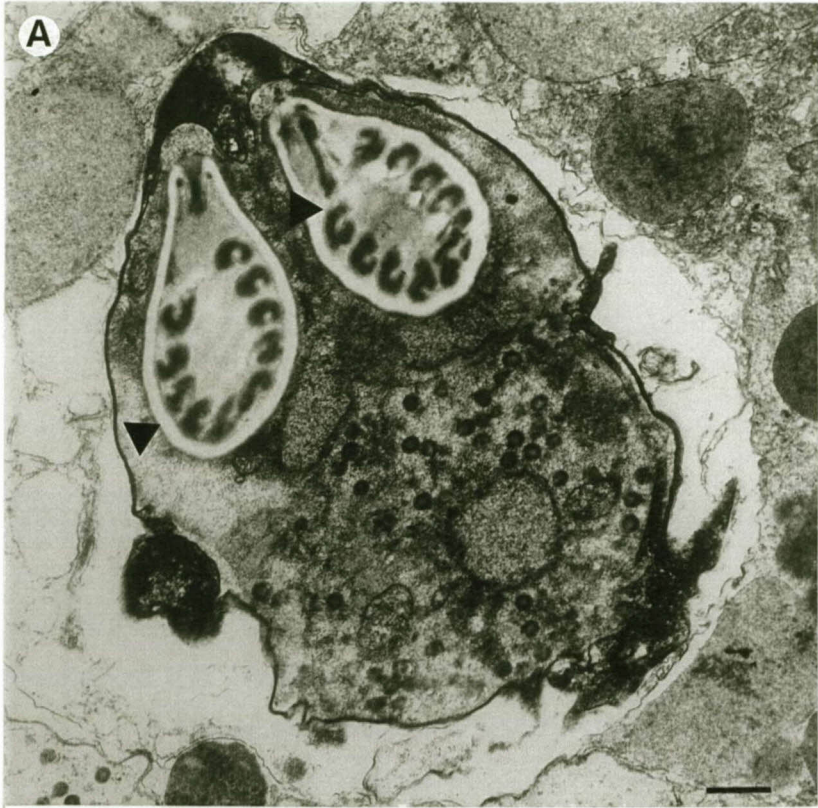


Figure 6.13

Micrographs illustrating silver impregnated *Myxobolus* Bütschli, 1882 spores collected from fishes in the Okavango River and Delta, Botswana

A: *Myxobolus africanus* Fomena, Bouix & Birgi, 1985 from the gills of *Hepsetus odoe* (Bloch, 1794)

B: *M. hydrocyni* Kostoingue & Toguebaye, 1994 from the gill arch of *Hydrocynus vittatus* Castelnau, 1861

C: *M. hydrocyni* showing extruded polar filament

D: *M. nyongana* (Fomena, Bouix & Birgi, 1985) from the gills of *Barbus poechii* Steindachner, 1911

E *Myxobolus* sp. A from the ovaries of *Clarias gariepinus* (Burchell, 1822)

F: *Myxobolus* sp. A showing extruded polar filament

Scale bar: 10µm

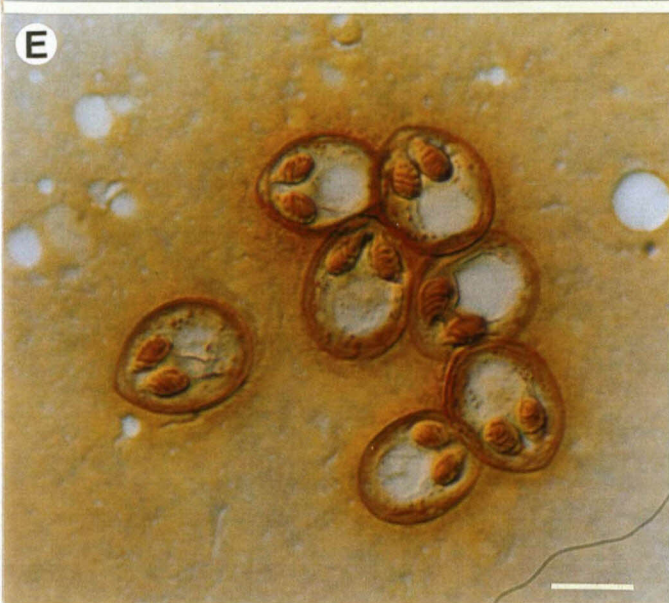
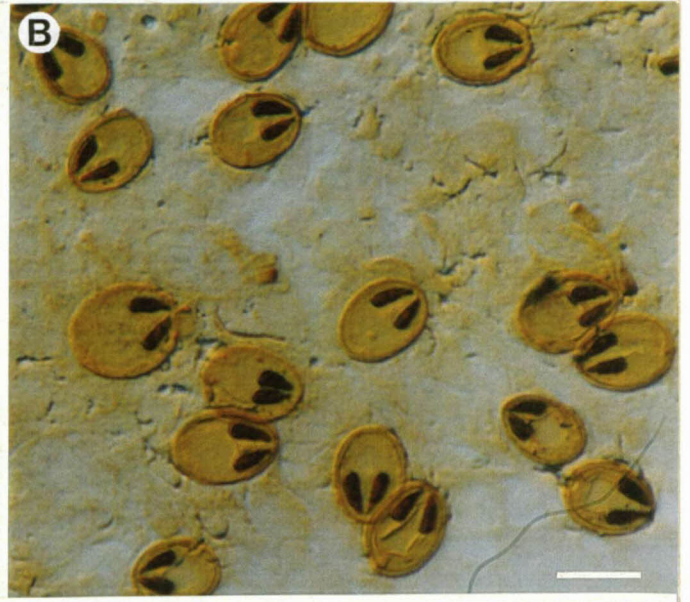
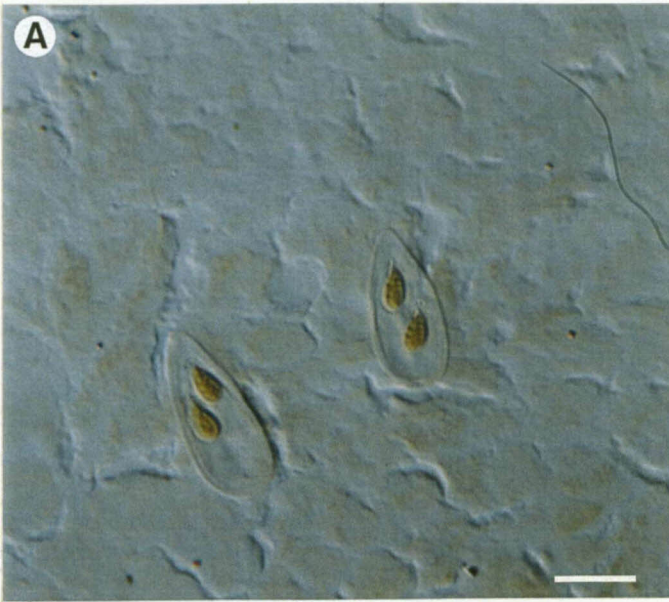


Figure 6.14

Micrographs illustrating silver impregnated *Myxobolus* Bütschli, 1882 spores collected from fishes in the Okavango River and Delta, Botswana

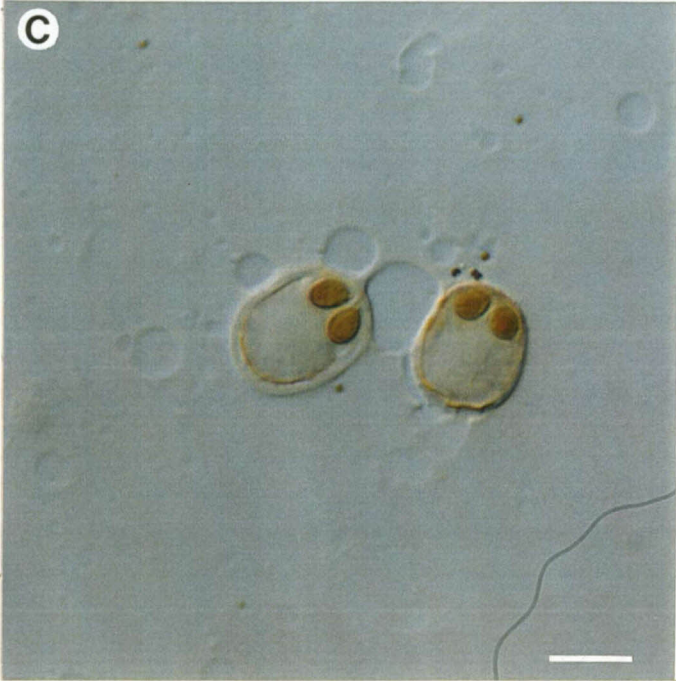
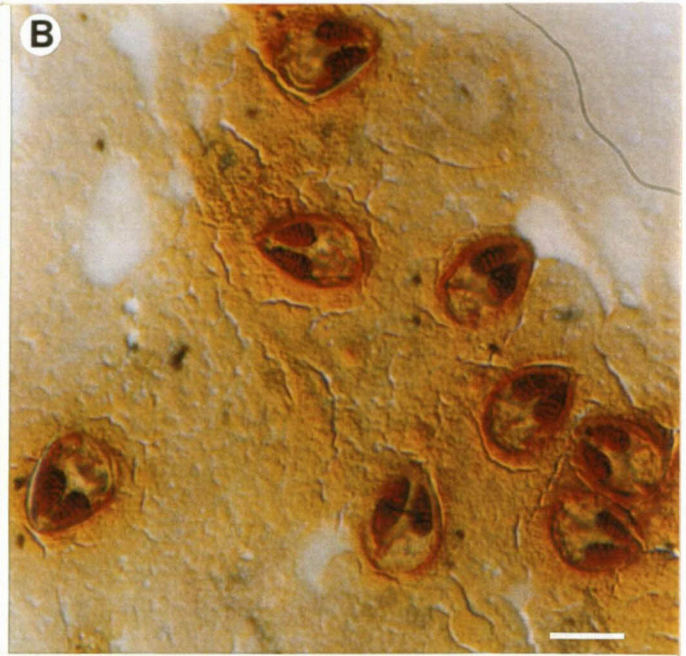
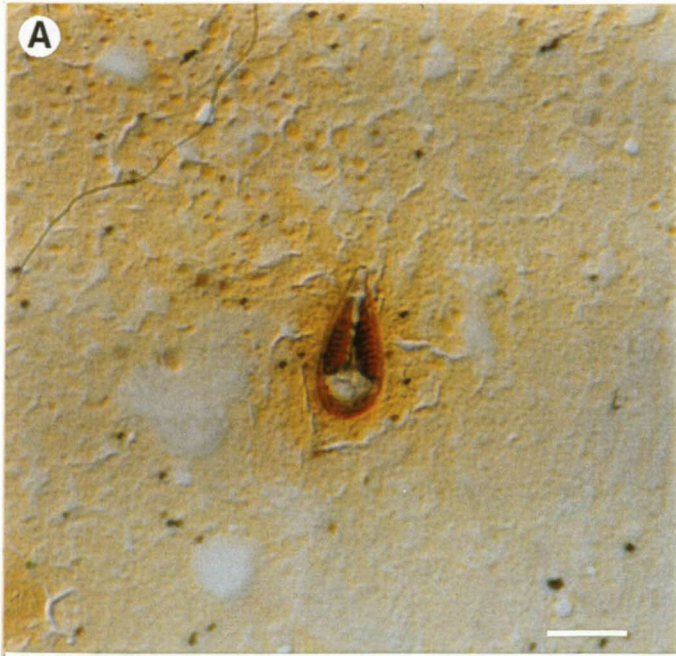
A: *Myxobolus* sp. B from the gills of *Barbus thamalakanensis* Steindachner, 1911

B: *Myxobolus* sp. C from the gills of *Barbus paludinosus* Peters, 1852

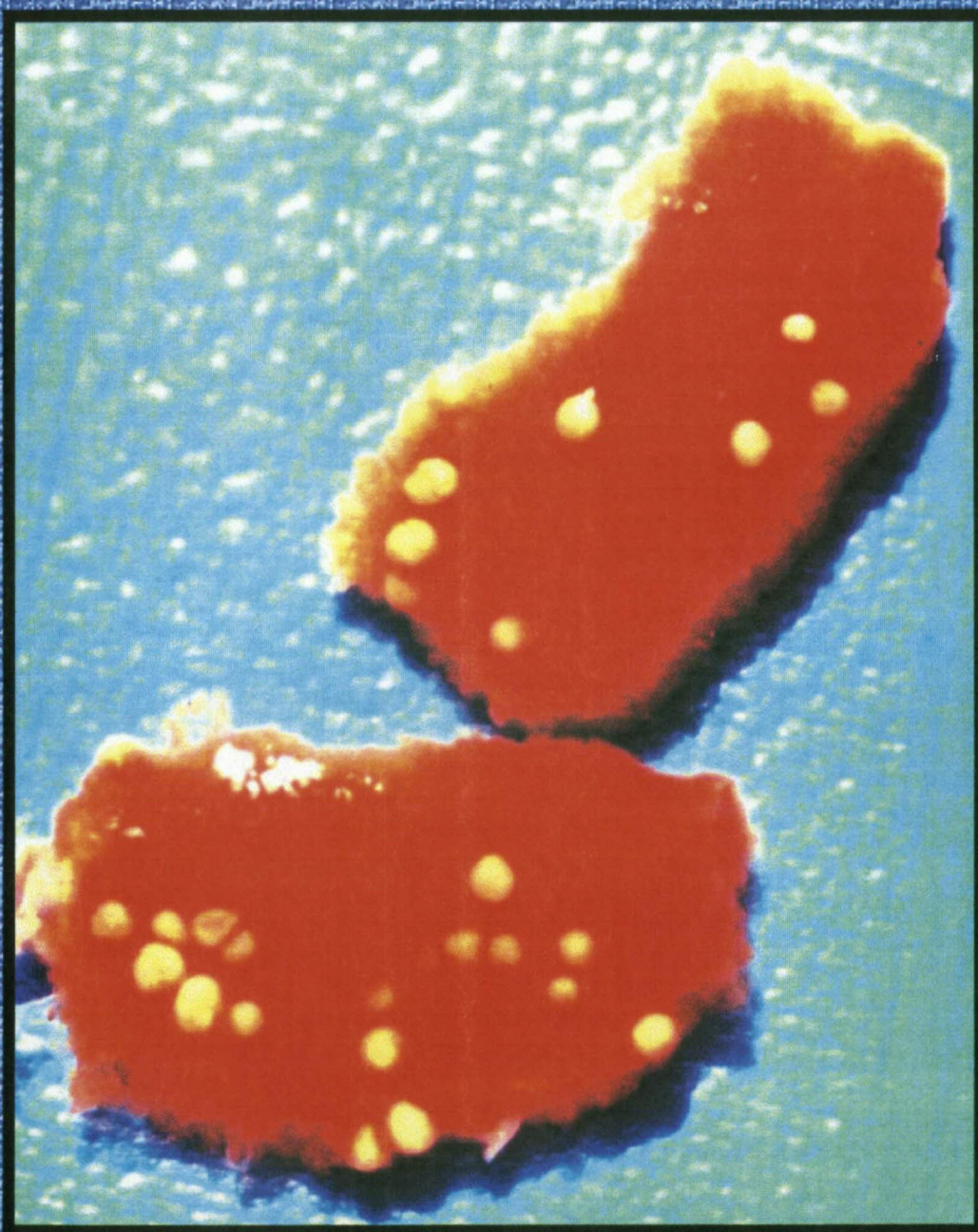
C: *Myxobolus* sp. D from the gills of *Tilapia rendalli rendalli* (Boulenger, 1896)

D: *Myxobolus* sp. D showing an extruded polar filament

Scale bar: 10µm



CHAPTER 7



Myxosporean/host relationships

The information collected from the Okavango River in Botswana during June and July 1998 and 1999 is summarised in Table 7.1. A total of 275 fish representing 31 species from nine families were examined over two years of fieldwork. Collections were concentrated in the riverine panhandle during 1998 with collections taking place in localities that were in close proximity to one another. Sampling during 1999 was concentrated in the upper permanent swamp region.

As described in Chapter 5 and 6, a total of five myxosporean species from the genus *Henneguya* were found parasitising five different fish hosts, while a total of eight myxosporeans from the genus *Myxobolus* were found parasitising nine different host fish species. The overall prevalence of myxosporean infections in all the fish species examined was 25% (4/16) in 1998 and 45% (10/22) for 1999 (Fig. 7.1). During 1999 the genus *Myxobolus* was predominant (Fig. 7.2).

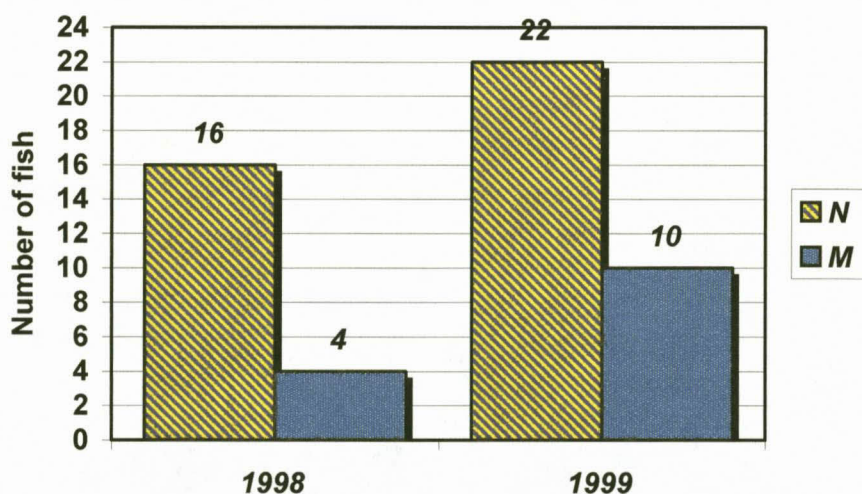


Figure 7.1: Histogram showing the total number of Okavango fish species infected with myxosporeans in 1998 and 1999 (N = Total number of fish species examined, M = Total number of fish species infected with myxosporeans).

Table 7.1: Summary of results and infections of myxosporeans collected in June/July 1998 and 1999 from the Okavango River System in Botswana.

N- Total number of fish examined

S- Mean size and size range of fish hosts (mm)

Inf- Number of hosts infected

P- Prevalence expressed as a percentage (%)

O- Organs of fish hosts infected

M- Myxosporean species infecting host

L- Localities where hosts were collected

Fish host	Year	N	S	Inf	P	O	M	L
MORMYRIDAE								
<i>Marcusenius macrolepidotis</i> (Peters, 1852)	1998, 1999	25	191(150-227)	20	80	Gills	<i>Henneguya</i> sp. C	Lloyds & Duba Lagoons
CYPRINIDAE								
<i>Barbus afrovernayi</i> Nichols & Boulton, 1927	1999	4	25, 35, 35, 30	0				Mohembo Floodplains, Duba Lagoon
<i>Barbus haasianus</i> David, 1936	1999	2	27, 25	0				Mohembo Floodplains
<i>Barbus multilineatus</i> Worthington, 1933	1999	12	27(25-30)	0				Mohembo Floodplains, Etsatsta Mainstream, Duba Lagoon
<i>Barbus paludinosus</i> Peters, 1852	1999	7	36(26-45)	5	71	Gills	<i>Myxobolus</i> sp. C	Etsatsta Mainstream, Duba Lagoon
<i>Barbus poechii</i> Steindachner, 1911	1999	1	36	1	100	Gills	<i>Myxobolus nyongana</i> (Fomena, Bouix & Birgi, 1985)	Etsatsta Mainstream
<i>Barbus thamalakanensis</i> Fowler, 1953	1999	1	30	1	100	Gills	<i>Myxobolus</i> sp. B	Etsatsta Mainstream
<i>Labeo lunatus</i> Jubb, 1963	1998	2	323, 300	0				Xaro Mainstream
CHARACIDAE								
<i>Brycinus lateralis</i> (Boulenger, 1900)	1998	5	97(87-105)	0				Lloyds Lagoon
<i>Hydrocymus vittatus</i> (Castelnau, 1861)	1998, 1999	9	373(165-540)	3	33	Gill operculum, gill arch	<i>Myxobolus hydrocyni</i> Kostoingue & Toguebaye, 1994	Xaro & Etsatsta Mainstreams
<i>Micralestes acutidens</i> (Peters, 1852)	1999	4	13, 42, 28, 31	0				Mohembo Floodplain, Duba Lagoon
<i>Rhabdalestes maunensis</i> (Fowler, 1935)	1999	1	45	0				Etsatsta Mainstream
HEPSETIDAE								
<i>Hepsetus odoe</i> (Bloch, 1794)	1998, 1999	28	301(230-430)	7	25	Gills	<i>Myxobolus africanus</i> Fomena, Bouix & Birgi, 1985	Lloyds, Mokoro & Thoage Lagoons
SCHILBEIDAE								
<i>Schilbe intermedius</i> Rüppell, 1832	1998, 1999	79	193(18-270)	51	64.5	Gills	<i>Henneguya</i> sp. D	Lloyds, Guma, Thoage & Duba Lagoons

Table 7.1 continued: Summary of results and infections of myxosporeans collected in June/July 1998 and 1999 from the Okavango River System in Botswana.

FISH HOST	YEAR	N	S	INF	P	O	M	L
CLARIIDAE								
<i>Clarias gariepinus</i> (Burchell, 1822)	1998, 1999	9	556(430-740)	4	44	Gills, supra-branchial organ, ovaries	<i>Henneguya branchialis</i> Ashmawy, Abu-Elwafa, Imam & El-Orfi 1989, <i>Henneguya</i> sp. A, <i>Myxobolus</i> sp. A	Lloyds & Duba Lagoons
<i>Clarias theodora</i> Weber, 1897	1999	1	150	1	100	Gills	<i>H. branchialis</i>	Duba Lagoon
MOCHOKIDAE								
<i>Synodontis nigromaculatus</i> Boulenger, 1905	1998, 1999	4	200, 250, 230, 247	0				Xaro Mainstream, Thoage Lagoon
<i>Synodontis thamalakanensis</i>	1998	1	162	0				Lloyds Lagoon
<i>Synodontis woosnami</i> Boulenger, 1911	1998	1	160	0				Lloyds Lagoon
CYPRINODONTIDAE								
<i>Aplocheilichthys hutereaui</i> (Boulenger, 1913)	1999	28	23(12-33)	0				Mohembo Backwaters, Xaru Backwaters, Etsatsta Mainstream
<i>Aplocheilichthys johnstoni</i> (Günther, 1893)	1999	3	40,23,45	0				Etsatsta Mainstream
<i>Aplocheilichthys katangae</i> (Boulenger, 1912)	1999	1	23	0				Etsatsta Mainstream
CICHLIDAE								
<i>Oreochromis andersonii</i> (Castelnau, 1861)	1998	7	122 (105-146)	6	86	Gill arch, buccal cavity	<i>Myxobolus camerounensis</i> Fomena, Marqués & Bouix, 1993	Xaro Mainstream
<i>Oreochromis macrochir</i> (Boulenger, 1912)	1998	1	173	0				Lloyds Lagoon
<i>Pharyngochromis acuticeps</i> (Steindagner, 1866)	1998, 1999	3	90, 114, 140	0				Lloyds Lagoon, Mohembo Backwaters
<i>Pseudocrenilabrus philander</i> (Weber, 1897)	1999	16	25(18-63)	0				Mohembo Floodplains, Xaru Backwaters
<i>Sargochromis carlottae</i> (Boulenger, 1905)	1998	1	180	0				Lloyds Lagoon
<i>Serranochromis angusticeps</i> (Boulenger, 1907)	1998	1	134	0				Lloyds Lagoon
<i>Tilapia rendalli rendalli</i> (Boulenger, 1896)	1998, 1999	8	117(34-173)	3	38	Gills	<i>Henneguya</i> sp. B, <i>Myxobolus</i> sp. D	Lloyds Lagoon, Mohembo Floodplains
<i>Tilapia ruweti</i> (Poll & Thys van den Audenaerde, 1965)	1999	1	100	1		Gill arch	<i>M. camerounensis</i>	Etsatsta Mainstream
<i>Tilapia sparrmanii</i> Smith, 1840	1999	10	127	0				Xaro Backwaters

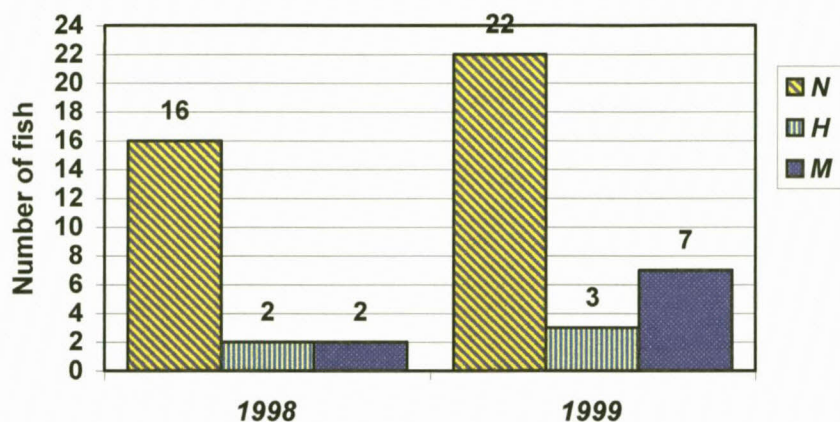


Figure 7.2: Histogram showing the number of Okavango fish species infected with *Henneguya* species (**H**) and those infected with *Myxobolus* species (**M**) (**N** = Total number of fish species examined).

Of the five *Henneguya* species collected only one was positively identified as *H. branchialis*. The remaining four species were allocated letters in the alphabet in order to distinguish between them (see Chapter 5).

HENNEGUYA BRANCHIALIS was found within the cartilage of the suprabranchial organ (Fig. 7.9A) of *Clarias gariepinus*, the sharptooth catfish (Fig. 7.11A). This is probably the most widely distributed fish in Africa, being found throughout the woodland savanna zones of the Afro-tropical region from the Nile, to as far south as the Orange River system and the Umtavuna river on the East coast (Skelton 1993). It occurs in almost any habitat, but favors floodplains, large sluggish rivers, lakes and dams. These fish may be described as having strong bodies that are compressed towards the caudal fin. They may reach 1.4m in length and have a very large, bony, depressed head with small eyes and a large mouth containing bands of fine pointed teeth (Skelton 1993).

The prevalence of *H. branchialis* in the suprabranchial organ of *C. gariepinus* was 11.1% (1/9). None of the three fish collected during 1998 from Lloyds Lagoon were infected and only one of the six fishes collected from Duba lagoon during 1999 was infected. Six plasmodia were found situated within the tips of cartilage in the

infected. Six plasmodia were found situated within the tips of cartilage in the suprabranchial organ of the infected individual, showing a X infection level (Fig. 7.10A). *Henneguya branchialis*, found by Ali (1996) in the gills of *C. gariepinus* in Egypt, showed complete replacement of the cartilaginous tissue in the suprabranchial organ, either by pressure atrophy or by phagocytosis.

Henneguya branchialis was also found in the gills of the snake catfish, *Clarias theodorae* (Fig. 7.11B) during this study. This fish species is widely distributed throughout all the major river systems in southern Africa, such as the Cunene, Okavango, upper Zambezi, Limpopo as well as some coastal rivers in northern Natal (Skelton 1993). These fish prefer dense marginal vegetation along the banks of slow flowing rivers and floodplain lagoons and are characterised by a relatively small head, with long barbels reaching to behind the head. They have a slender, elongated body with a long anal fin. Only one individual infected with *H. branchialis* was collected from Duba Lagoon during the 1999 field trip showing a X infection level. The size of the plasmodia was significantly smaller than in *C. gariepinus*.

Both these *Clarias* species were not readily collected. In a number of cases catfish that were trapped in the gill nets had been dead for far too long and were consequently not suitable for examination since post-mortem had already set in. The gills of catfish are reduced, but the suprabranchial respiratory organ allows them to survive in low oxygen conditions and to extract oxygen from the air. Thus when they are trapped in the gill nets in low oxygen lagoons, they suffocate easily since they are prevented from swimming to the surface to gulp air.

HENNEGUYA SP. A was found also within the primary gill filaments of *C. gariepinus*. The prevalence of *Henneguya* sp. A in this fish species was 22.2% (2/9). None of the three fish collected during 1998 were infected. Two of the four fish collected from Duba Lagoon during 1999 were infected. One to four plasmodia were found in the primary gill lamellae of the infected individuals (Fig. 7.9B) showing a X infection level. These plasmodia could affect the respiratory function of the gills if higher infections occur. The large plasmodia take up approximately a third of the gill filament.

HENNEGUYA SP. B was found in the gills of one individual redbreast tilapia, *Tilapia rendalli rendalli* (Fig. 7.11C). This fish species is widely distributed in the Cunene, Okavango and Zambezi system as well as in the east coastal rivers south to the Phongolo (Skelton 1993). They are tolerant of a wide range of temperatures and salinity, preferring quiet water such as backwaters, floodplains or swamps. Mature specimens are olive green to brown and have five to seven dark olive bars on the body, with a bright red throat and belly. Seven uninfected individuals were collected from Lloyds Lagoon during 1998, with a single infected individual collected during 1999 from Mohembo Floodplains. Combining the data on this fish species for both years, the prevalence of *Henneguya* sp. B was 12.5% (1/8) with an average infection level of X.

HENNEGUYA SP. C was found infecting one of the most predominant fish species collected during both 1998 and 1999, i.e. the bulldog, *Marcusenius macrolepidotis* (Fig. 7.11D) which is very widely distributed throughout southern Africa. It can be found in the Cunene, Okavango and Zambezi systems as well as in the east coastal rivers south to the Umhlatuzi in Natal (Skelton 1993). The bodies of these fish are moderately long, with median fins set well back, including a dorsal fin shorter than and originating behind the anal fin. Their color varies from light golden brown to dark olive with grey or bronze flecks (Skelton 1993). They reach 300 mm in length and are found mostly in muddy well-vegetated habitats of rivers and floodplains.

During 1998, 10 individuals were collected from Lloyds Lagoon in the riverine panhandle and 15 individuals were collected from Duba Lagoon in the upper permanent swamp region during the next year. There was an overall infection prevalence of 80% for the total 25 individuals collected. The levels of infection averaged XX over both years. The infection prevalence of the individuals collected in 1998 from Lloyds Lagoon was 50% (5/10) compared with a 100% (15/15) prevalence found in Duba Lagoon during 1999 (see Fig. 7.3). The 100% prevalence in Duba Lagoon consisted largely of X infections, with one high infection of XXX. In Lloyds Lagoon, most infections were XX, with a few X and none that were extremely high.

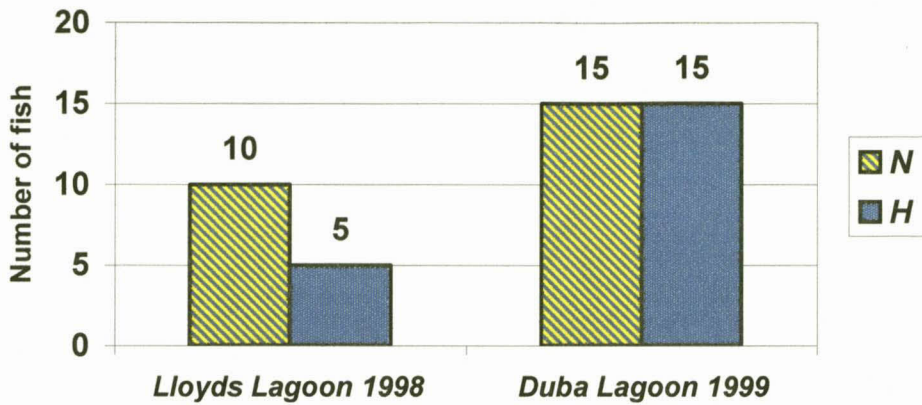


Figure 7.3: Histogram comparing the number of *Marcusenius macrolepidotis* (Peters, 1852) (N) infected with *Henneguya* sp. C (H) in different localities (N = Total number of individuals examined).

Lloyds 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 & 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. The oxygen values in these slow flowing parts are even less and can fall below 10% saturation when the waters recede (Merron & Bruton 1986). Fish collections were conducted in June and July each year, 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 and subsequently higher myxosporean infection prevalence.

A normal host/parasite relationship is when a number of individuals in the sample size are not infected, a number of individuals are moderately infected and few individuals are highly infected. Combining the data from 1998 and 1999 and then comparing fish lengths versus the number of plasmodia on the gills reveals a normal host/parasite distribution pattern (Fig. 7.4).

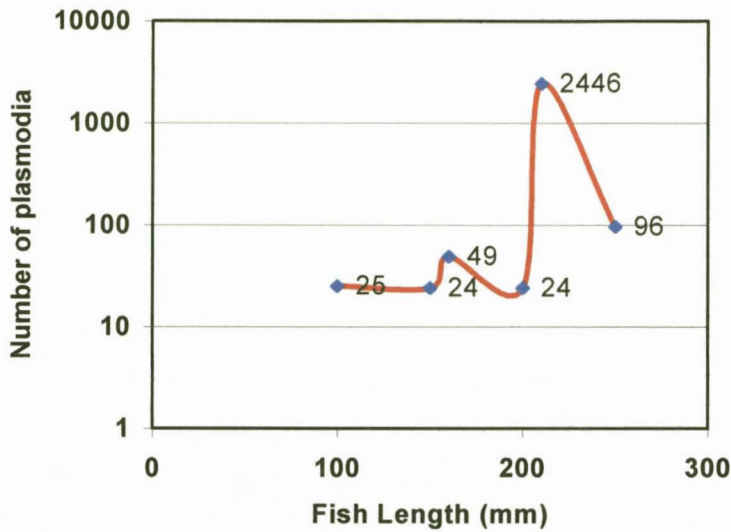


Figure 7.4: Logarithmic graph showing the number of plasmodia per *Marcusenius macrolepidotis* (Peters, 1852) gill arch versus the fish lengths for six individuals.

All of the *Henneguya* sp. C plasmodia were found infecting the gills of *M. macrolepidotis*. In Figure 7.5 it can clearly be seen that there is prevalence for the first two gill arches as well as the tips of the gill filaments. *Marcusenius macrolepidotis* specimens have very small and narrow gill slits, with the gills situated quite deeply. Myxosporean plasmodia situated 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, rather than be trapped in the gill chamber. Myxosporean plasmodia in the first two gill arches would also have the advantage of being nearest the gill slit, at the time of spore release.

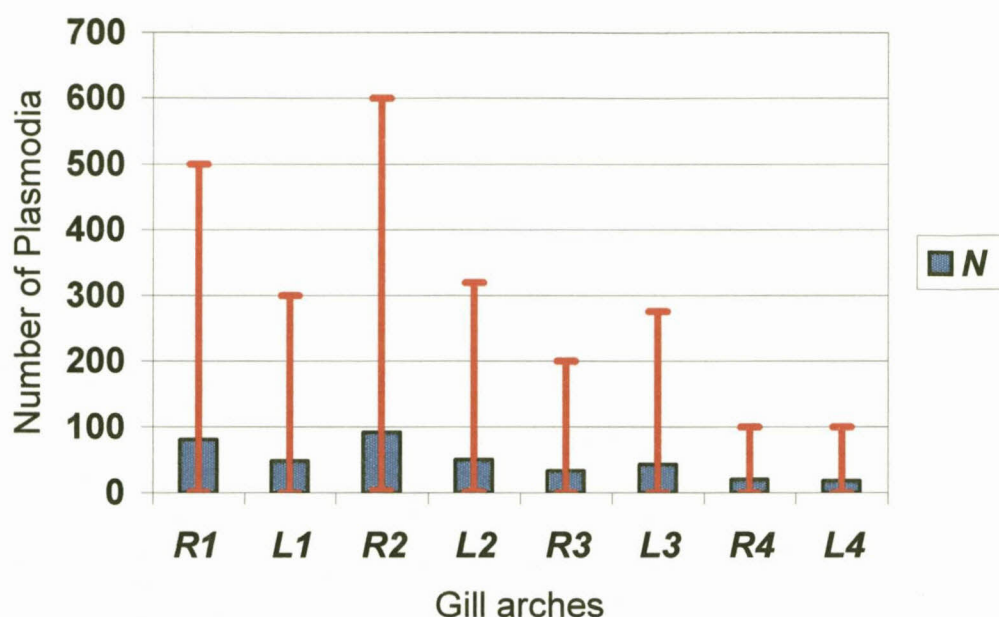


Figure 7.5: Histogram showing the average number of plasmodia (N) per gill arches of seven *Marcusenius macrolepidotis* (Peters, 1852) specimens examined (Y-error bars = range, L = Left gill arches, R = Right gill arches, gill arches numbered 1-4).

HENNEGUYA SP. D was found in the gills of the butter barbel, *Schilbe intermedius* (Fig. 7.12A) which was the most abundant fish species collected during both surveys. This fish species is very widely distributed throughout southern Africa, occurring in the Cunene, Okavango and Zambezi systems southwards to the Phongolo in northern Zululand (Skelton 1993). These fish are found mostly in shoals, usually in standing or slow flowing open water with emergent or submerged vegetation. They are generally more active at night and may reach 160 mm in length, with an elongated body that is compressed with a tapered caudal fin. The skin is smooth and the dorsal and pectoral fins have sharp, finely serrated spines. This is a very important subsistence species and is occasionally kept in aquariums (Skelton 1993).

A total of 79 individuals of *Schilbe intermedius* were collected from four different localities in 1998 and 1999. The localities included Lloyds Lagoon, Guma Lagoon, Thoage Lagoon and Duba Lagoon showing an overall infection prevalence of 64.5%.

This prevalence was more or less the same for all the localities in which sampling was conducted. In Lloyds Lagoon the prevalence was 66.7% (20/31), in Guma Lagoon it was 65.2% (12/19), in Thoage Lagoon it was 64.7% (11/17) and in Duba Lagoon it was 66.7% (8/12) (Fig. 7.6). Thus in all the fish populations examined, at least 60% of the population was always infected with this myxosporean.

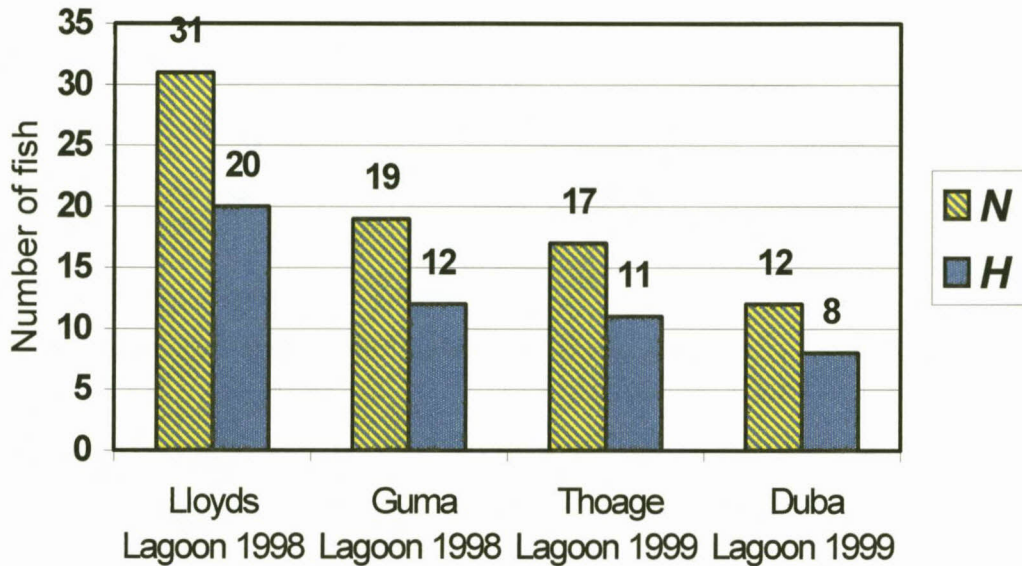


Figure 7.6: Histogram showing the number of *Schilbe intermedius* Rüppell, 1832 specimens infected with *Hennegya* sp. D (H) in different localities (N = Total number of individuals examined).

The number of plasmodia per gill arch showed no particular preference for a certain gill arch (Fig. 7.7). The gills and gill slits of these fish are not deeply situated, spores could equally well be released successfully from most of the gill arches. A relatively normal host/parasite pattern was also noted, with one individual in the sample size having an extremely high infection of more than 1104 plasmodia on the gills (Fig. 7.8). It appears as if fish ranging in length between 180 and 200mm are more highly infected, but this is due to the one individual having such a high infection prevalence.

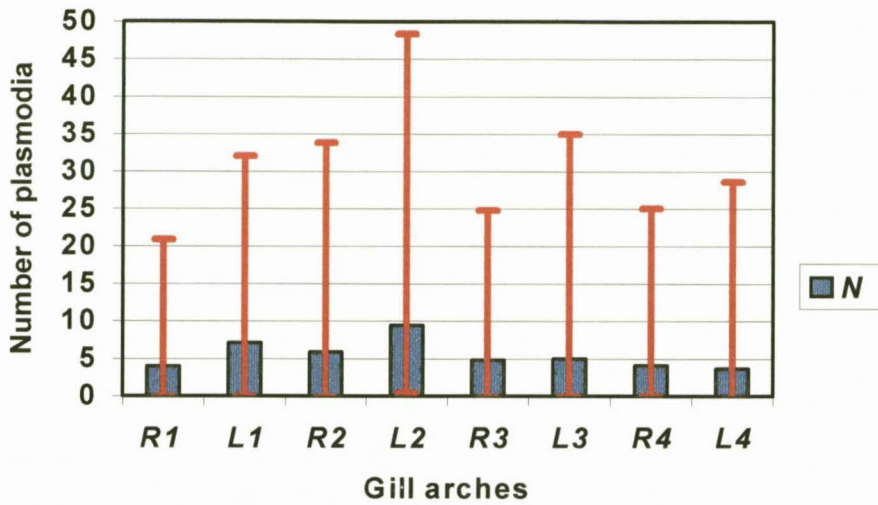


Figure 7.7: Histogram showing the average number of plasmodia (N) per gill arches of 14 *Schilbe intermedius* Rüppell, 1832 specimens examined (Y-error bars = fish length range, L = Left gill arche, R = Right gill arch).

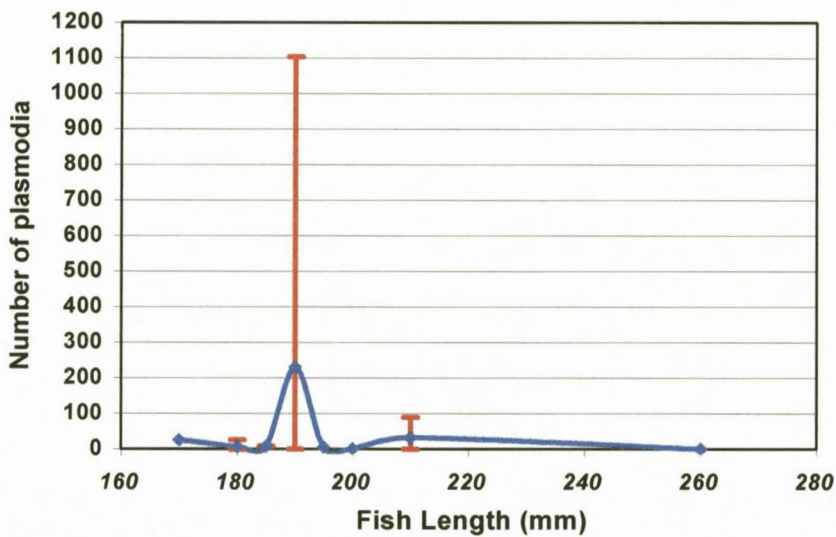


Figure 7.8: Line graph showing the relationship between the fish length and the average number of plasmodia (A) for 14 *Schilbe intermedius*. (Y-error bars = length range)

As mentioned before, one individual in 1998 was collected with more than 1104 plasmodia on a single gill arch. A number of secondary pathological effects may result from infections such as this. Histological sections of these gills (Fig. 7.10B) reveal no apparent host response. The sheer size of the plasmodia, however, significantly distorts the shape of the secondary gill lamellae between which they develop.

The presence of these large plasmodia also seems to result in a significant compression of the surrounding gill lamellae. In the case of a number of plasmodia infecting a single gill filament, the compressed gill lamellae surrounding the plasmodia may result in a large decrease of surface area of the entire gill filament. Reduction of gill surface area must certainly result in a respiratory deficiency for the fish. Since the oxygen values in the water at the time of the receding flood levels have been recorded as being low, the fish might already be stressed. Consequently, living in an environment with an already decreased oxygen concentration, high myxosporean infections in the gills could influence the productivity of the fish population. Finally, secondary bacterial and fungal infections may incur when the plasmodia rupture to release the spores.

Of the eight *Myxobolus* species collected, only five were positively identified. The remaining species collected were also allocated letters in the alphabet in order to distinguish between them (see Chapter 6).

MYXOBOLUS AFRICANUS was the first *Myxobolus* species collected during this project. This species was found in the gills of *Hepsetus odoe* (Fig. 7.12B). The African pike is an endemic African fish and has a wide spread distribution throughout southern Africa, occurring in the Cunene, Okavango, upper Zambezi and Kafue systems (Skelton 1993). In the Okavango River, this species prefers quiet backwaters and is common in floodplains throughout the system (Merron *et al.* 1990). The pike is one of the few non-cichlid, nest-guarding freshwater fish species in Africa and is characterised by an elongate body with the dorsal and anal fins set well back. An adipose fin is present and the head is pointed with prominent jaws and unevenly protruding sharp teeth (Skelton 1993). They may reach 250 mm in length and are an excellent angling species and is also used in subsistence fisheries (Skelton 1993).

During 1998 and 1999 a total of 28 fish were examined, of which 27 were collected during 1998 from Lloyds Lagoon and Mokoro Lagoon and one from Thoage Lagoon in 1999. *Myxobolus africanus* was only found parasitising the gills of these fish during the 1998 survey. The prevalence of infection for both years is thus 25% (7/28), with most individuals only having X infection. The plasmodia were found randomly in the gills of these fish and were not found in any other fish species.

MYXOBOLUS CAMEROUNENSIS was found infecting two different host species. The first, *Oreochromis andersonii* or threespot tilapia (Fig. 7.12C) was only collected during 1998 from Lloyds Lagoon. The distribution of these fish in southern Africa is mainly in the Cunene, Okavango, upper Zambezi and Kafue systems and occasionally from the middle Zambezi (Skelton 1993). These are hardy fish, tolerating fresh and brackish waters, preferring slow flowing or standing water such as in pools, backwaters and floodplain lagoons (Skelton 1993). The adults of this species are blue-grey with light scale borders and reach 450 mm in length. The fins are also blue-grey and the margins of the dorsal and the anal fins are bright red. This fish is a very valuable aquaculture, fisheries and angling species.

Seven individuals were collected in 1998 from Xaro Mainstream, of which the buccal cavities and gill arches (Fig. 7.10C) of six were infected with *M. camerounensis*, giving a prevalence of 86% (6/7). The infections were not abnormally high and varied between X and XX.

Myxobolus camerounensis was also found during 1999 from the gill arch of a single Okavango tilapia, *Tilapia ruweti* (Fig. 7.12D) collected from Etstasta mainstream. This was the only individual of this species examined during 1999 and it showed a moderate infection, with one to four plasmodia found in each of the gill arches (Fig. 7.10D). Okavango tilapias are restricted to the Okavango River, upper Zambezi and the southern tributaries of the Zaire system (Skelton 1993). These fish are found in swamps and floodplains, especially in well-vegetated shallow littoral margins.

MYXOBOLUS HYDROCYNI was collected during 1999 from the tigerfish, *Hydrocynus vittatus* (Fig. 7.13A) caught in Xaro Mainstream and Etstasta Mainstream. The tigerfish is a predatory characin that is distributed throughout Africa from the Nile and

the major rivers of West Africa, south through the rift valley lakes to the Congo (Bruton 1984). According to Skelton (1993) the distribution of the tiger fish in southern Africa is limited to the Okavango, Zambezi and lowveld reaches south to the Phongolo. They may be described as having a fusiform body and pointed fins with a large bony cheek head with characteristically very strong jaws, each with eight sharply pointed teeth and with eyes that have vertical adipose sleeves (Skelton 1993). These fish prefer warm, well-oxygenated water, mainly in larger rivers and lakes breeding during the summer months. The adults migrate to suitable spawning sites along flooded riverbanks and may reach 700 mm in length (Skelton 1993). Tiger fish are a major angling and commercial species.

Over the course of two years nine tigerfish were examined for the presence of myxosporeans. Three individuals collected during 1999 were infected with *M. hydrocyni*. The infections were localised on the gill operculum and gill arches of the fish, with the number of plasmodia varying between one and three per fish, showing an infection level of X.

MYXOBOLUS NYONGANA was found during 1999 in the gills of a single dashtail barb, *Barbus poechii* (Fig. 7.13B). In southern Africa these fish are found in the Cunene, Okavango and Upper Zambezi systems (Skelton 1993). They are common in riverine floodplains and often associated with the striped robber (*Brycinus lateralis*). These two fish species are very similar in appearance being silvery, olive brown with a prominent black dash on the caudal peduncle, suggesting some form of mimicry (Skelton 1993). *Barbus poechii* are often used for bait and is suitable for aquariums, only reaching 110 mm in length.

The infected individual was collected during 1999 from Etstasta Mainstream with a XX gill infection. The plasmodia were scattered across the filaments, with no apparent preference region. The plasmodia in the gills of *B. poechii* appear to be situated in between the secondary gill lamellae (Fig. 7.10E), which appear to be compressed.

MYXOBOLUS SP. A is the third myxosporean species that was collected from *Clarias gariepinus*. Two of the nine individuals of *C. gariepinus* collected had ovary (Fig.

7.9C) infections showing a prevalence of 22.2%. Only fishes collected during 1999 from Duba Lagoon were infected with this myxosporean and in each case at least 16 plasmodia were seen distributed throughout the ovaries. Infections in the reproductive organs of fish are sometimes serious because, even though they are not visible externally, they will most probably have effects on the reproductive potential of the fish. These large plasmodia in the ovaries of this catfish appear to be situated in the blood vessels of the ovaries. Such high numbers of plasmodia blocking the blood vessels and depriving the ovaries of circulating blood might result in the sterilization of the individual.

MYXOBOLUS SP. B was found in the gills of a single Thamalakane barb, *Barbus thamalakanensis* (Fig. 7.13C). The distribution of this species in southern Africa is concentrated in the Okavango and Upper Zambezi systems (Skelton 1993). These fish are translucent brown above and silvery white on the sides and below with a regular black stripe running from the tip of the snout to the base of the caudal fin. They only reach 40 mm in length and are mainly found in shallow, well-vegetated streams, floodplains or marshes (Skelton 1993). They are commonly used as attractive aquarium fish. The infected individual was collected during 1999 from Etsatsta Mainstream and a very low infection of X was recorded with only a few *Myxobolus* sp. B plasmodia noted on the gills of this tiny fish.

MYXOBOLUS SP. C was collected during 1999 from five straightfin barbs, *Barbus paludinosus* (Fig. 7.13D). A total of seven fish were examined. One of the individuals was collected from Etstasta mainstream and six from Duba Lagoon, giving a total of seven fish examined and a prevalence of 71%. The single individual collected from Etstasta mainstream was highly infected with a XXX infection on the gills, while the other four individuals were infected with XX. No specific region on the gills appeared to be preferred, with the small plasmodia being randomly scattered between the gill filaments (Fig. 7.10F).

MYXOBOLUS SP. D was collected from the gills of a single *Tilapia rendalli rendalli* collected during 1999 from Mohembo Floodplains. A total of eight fish were collected from both Lloyds Lagoon and Mohembo Floodplains. This fish was also infected with *Henneguya* sp. B.

HOST SPECIFICITY

In many cases, the myxosporean species collected from the Okavango River in Botswana were only collected from one host species or from a single individual of a particular species. This makes it difficult to distinguish any sort of pattern regarding the host specificity of these myxosporeans.

Henneguya branchialis was originally described from the suprabranchial organs and gills of *Clarias lazera* in Egypt by Ashmawy *et al.* (1989). According to Skelton (1993) the North African *Clarias lazera* has been synonymised with *C. gariepinus*. A number of authors have subsequently recorded *H. branchialis* from the gills and suprabranchial organ of *C. lazera* in Egypt [Alyain *et al.* (1994), Ghaffar *et al.* (1995) Ali (1996)]. From this available literature, it does appear that *H. branchialis* shows some form of host, and even organ specificity, since it has only been found in the suprabranchial organ and gills of *C. gariepinus* / *C. lazera*. The occurrence of this parasite in the gills of *C. theodorae* is thus a new record and may indicate a preference for the genus *Clarias*, rather than specifically for the species *C. gariepinus* / *C. lazera*.

Other *Henneguya* species found parasitising the gills of *C. gariepinus* in the Okavango River was *Henneguya* sp. A. This species was not recorded from any other host, but since nine individual *C. gariepinus* were examined, it would not be possible to conclude any form of host specificity.

In Israel *Clarias lazera* has also been found parasitised by *Henneguya laterocapsulata* Landsberg, 1987 (Landsberg 1987) and in Chad, *Clarias anguillaris* was found parasitised by *Henneguya fusiformis* Kostoingue, Fall, Faye and Toguebaye, 1999 (Kostoingue *et al.* 1999).

A myxosporean from the genus *Myxobolus*, *Myxobolus* sp. A has also been recorded from the ovaries of *Clarias gariepinus* in the Okavango in Botswana. Again, since only nine *C. gariepinus* were investigated it is not enough to make final deductions regarding host specificity. In the rest of Africa, two other *Myxobolus* species have been described from two *Clarias* hosts. These include *Myxobolus clarii* from the testis of *C. lazera* in Egypt by Mandour, Galal and Abed (1993), and *M. comoei* from

the gills of *C. anguillaris* in Burkina Faso by Kabré, Sakiti, Marqués and Sawadago (1995).

A number of African cichlids or tilapiines are infected with myxosporeans. The tilapiines are divided into two genera namely *Tilapia* and *Oreochromis*. In the Okavango River in Botswana a single *T. rendalli rendalli* was found infected with both *Henneguya* sp. B and *Myxobolus* sp. D and *M. camerounensis* was found in both *O. andersonii* and *T. ruwetti*. *Myxobolus camerounensis* was originally described from *Oreochromis niloticus* in Cameroon and since *M. camerounensis* has not subsequently been found in other hosts, other than tilapia species, it may be that this myxosporean shows a degree of specificity for the tilapias. Many *Myxobolus* species have been recorded from *Tilapia* hosts in Africa (Table 2.1-Chapter 2) and of the approximately 46 myxosporeans from the genus *Myxobolus* at least 11 have been described from tilapia hosts.

Henneguya sp. C infecting the gills of *Marcusenius macrolepidotis* in Botswana was never found associated with any other host. Since quite a number of *M. macrolepidotis* specimens were examined it does seem as if this parasite shows some form of host specificity. This, however, needs confirmation with more material collected from other mormyrid hosts occurring in the Okavango River in Botswana. The main reason for this is that collections during 1998 and 1999 did not focus on the habitats in which these fish occur. The other mormyrids found in the Okavango in Botswana are *Mormyrus lacerda*, *Hippopotamyrus ansorgii*, *Hippopotamyrus discorhynchus*, *Petrocephalus catostoma* and *Pollimyrus castelnaui*.

Fomena and Bouix (1996a) described *Henneguya nyongensis* and *Henneguya odzai* from the gills of *Marcusenius moorii* and *Myxidium petrocephali* Fomena and Bouix, 1986 from *Petrocephalis simus* in Cameroon. The kidneys of *Petrocephalis simus* were also infected with *Sphaerospora sangmelimaenis* Fomena, Marqués and Bouix, 1993 in Cameroon.

Henneguya sp. D infecting the gills of *Schilbe intermedius* was never found associated with any other host in the Okavango River in Botswana. *Schilbe intermedius* is the only member of the Schilbeidae family living in the Okavango, with the only other

member belonging to the genus *Eutropius*, a subgenus in the genus *Schilbe* Oken, 1817, known only from a single locality in the upper Zambezi (Skelton 1993). It does appear as if *Henneguya* sp. D shows some form of host specificity, but to determine this, the other member of the Schilbeidae would also have to be examined.

Another myxosporean infecting a member from this host group includes *Henneguya camerounensis* from the gills of *Eutropius multitoeniatus* in Cameroon (Fomena & Bouix 1987). The infection in *S. intermedius* thus marks the second record of a myxosporean infection in members of this fish family.

Myxobolus africanus was described originally from the gills of *Hepsetus odoe* from Cameroon (Fomena *et al.* 1985). This unique myxosporean species was not recorded from any other hosts during our survey. In Cameroon the kidneys of *H. odoe* have been found infected with a myxosporean species from a different genus namely, *Sphaerospora sangmelimaenis* Fomena, Marqués & Bouix 1993 (Fomena *et al.* 1993). These two myxosporean parasites appear to be the only ones infecting *H. odoe*. Since *H. odoe* is an endemic African fish, it would be essential to investigate the full extent of myxosporean infections in these fish more fully.

Myxobolus hydrocyni from the gills of *Hydrocynus forskalii* was originally described in Chad (Kostoingue & Toguebaye 1994). It does not appear as if this myxosporean has been recorded from any other hosts in Africa. Other members of the Characidae fishes in Africa infected with myxosporeans include *Brycinus longipinnis* infected with *M. kribiensis* from Cameroon and *Brycinus macrolepidotis* with a gill infection of *Myxobolus chariensis* Kostoingue, Faye and Toguebaye, 1998 in Chad.

Myxobolus nyongana was originally described from the gills of *Barbus jae* in Cameroon (Fomena *et al.* 1985). The authors also recorded a number of other *Barbus* species infected with this myxosporean from the same locality. These included *B. aspilis*, *B. campacthacanus*, *B. guirali* and *B. martorelli*. *Myxobolus nyongana* has subsequently been recorded from the gills of a number of fish species other than *Barbus* species by various authors. These hosts include *Sarotherodon melanotheron* (Sakiti *et al.* 1991), *Alestes dentex* and *Labeo parvus* (Kostoingue & Toguebaye 1994). In Botswana *M. nyongana* was recorded from *B. poechii*. Since only a single

infected specimen was examined it was not possible to distinguish a pattern, but since previous authors have recorded this myxosporean from various other hosts, it could be that this species does not specifically prefer a certain host genus, but might show some preference for cyprinids.

Myxobolus sp. B and *Myxobolus* sp. C were both found infecting two different *Barbus* species, namely *B. thamalakanensis* and *B. paludinosus*. A number of *Barbus* species have been found infected with *Myxobolus* species in Africa, examples include *M. njiei*, *M. nyongana* and *M. oloi* (Fomena *et al.* 1985, Fomena & Bouix 1994).

Most of the myxosporean species collected from the Okavango River in Botswana were found associated with a single host species, except in the case of *Henneguya branchialis* and *Myxobolus camerounensis*, which infected different hosts from the same genus or group. It may appear as if all of these infections show some form of host or host genus specificity. Since only a fraction of the fish population has been investigated in the Okavango River in Botswana, it is thus not sufficient to make any final conclusions. The same may be said for myxosporean infections throughout Africa. It does appear as if some species have certain host group preferences, but since not enough research has been conducted regarding the distribution of these parasites, it cannot be concluded at this stage, that certain species are, or are not, host specific.

Figure 7.9

Photographs of myxosporean infections in fishes in the Okavango River and Delta,
Botswana

A: *Henneguya branchialis* Ashmawy Abu-Elwafa, Imam & El-Otifi, 1989 plasmodia
in the suprabranchial organ of *Clarias gariepinus* (Burchell, 1822)

B: *Henneguya* sp. A plasmodia in the gills of *C. gariepinus*

C: *Myxobolus* sp. A plasmodia in the ovaries of *C. gariepinus*

Scale bar: 10 mm

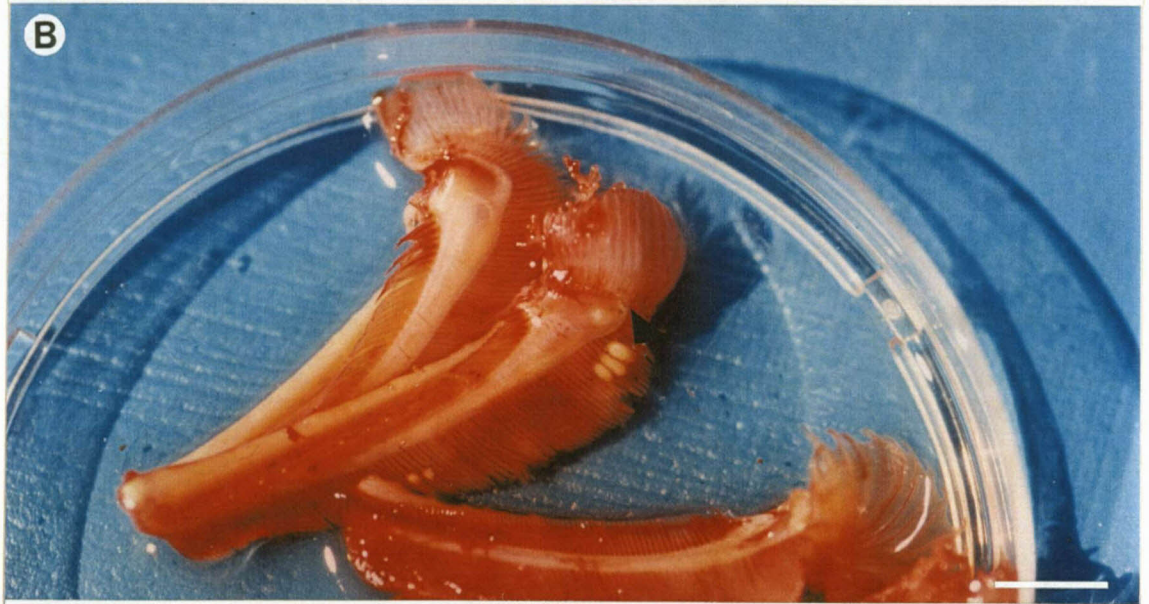
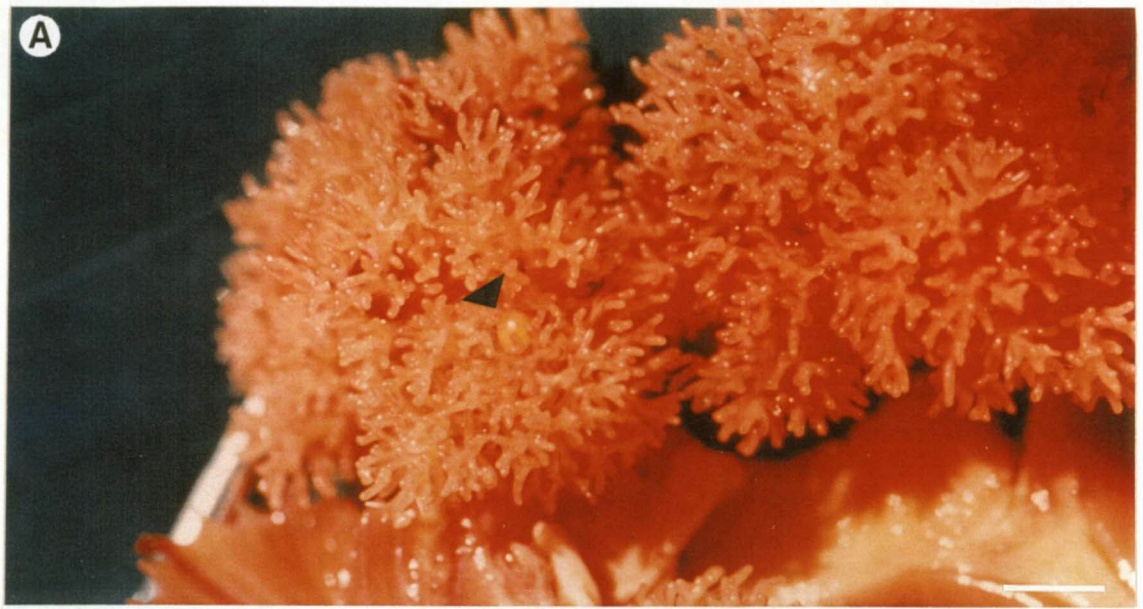
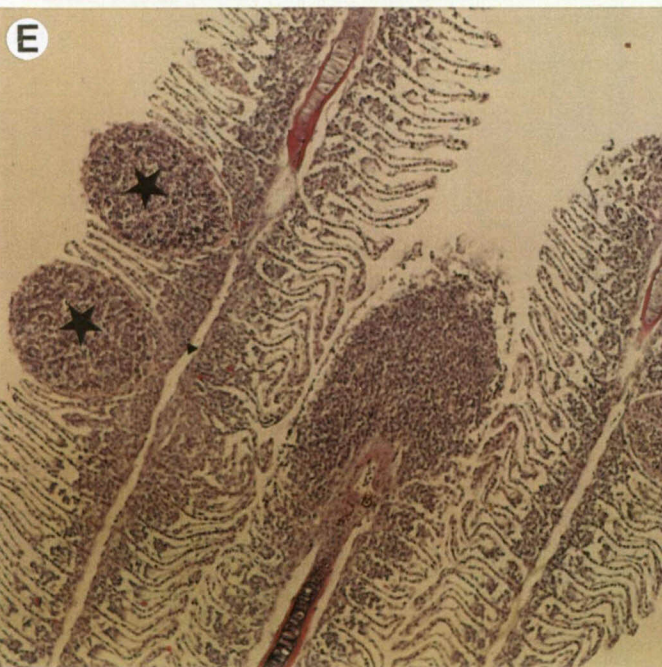
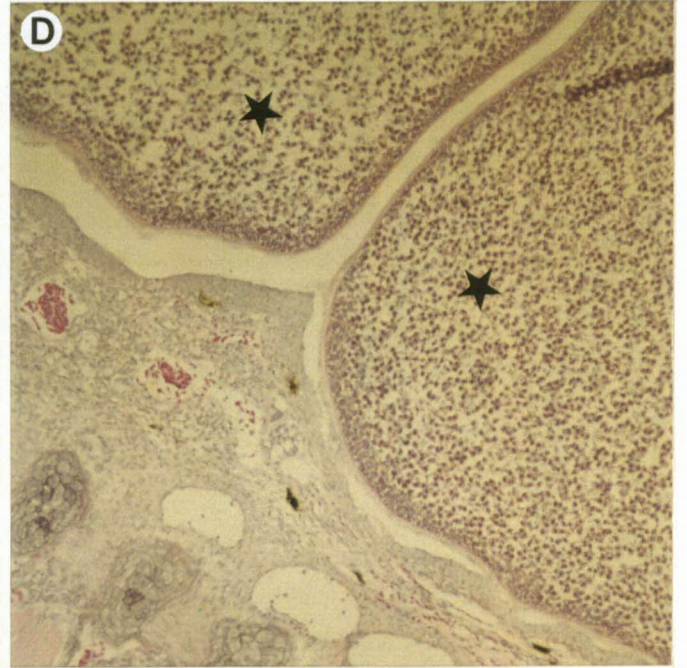
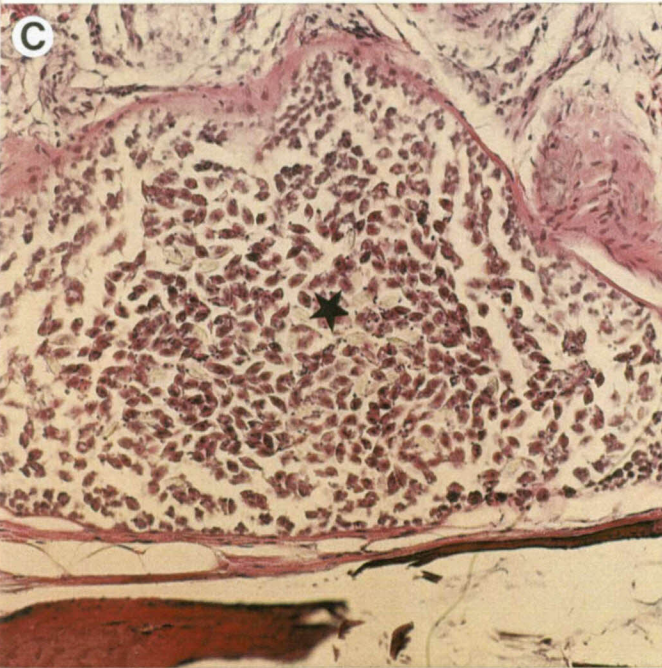
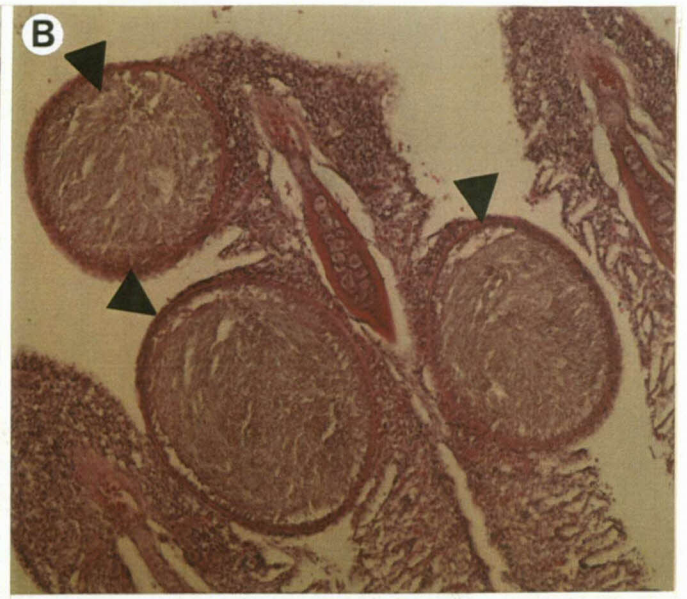
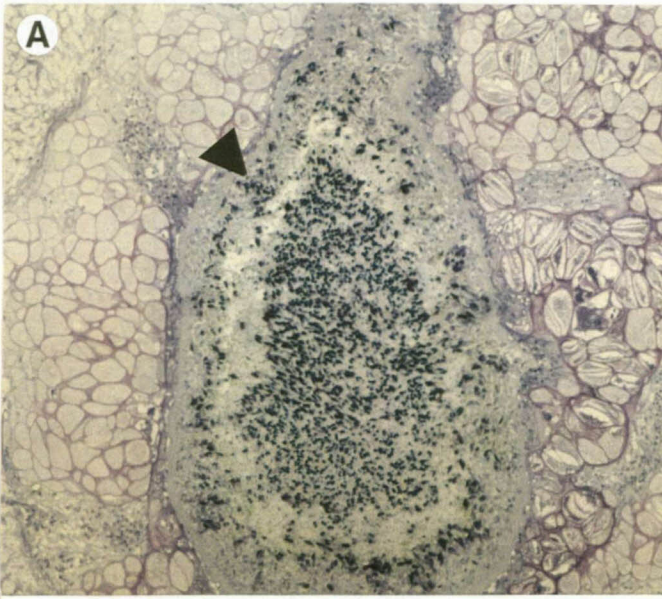


Figure 7.10

Histological sections of the organs of fishes from the Okavango River and Delta, Botswana infected with myxosporeans

- A: Histological section through the tip of the suprabranchial organ of *Clarias gariepinus* (Burchell, 1822) showing the plasmodia of *Henneguya branchialis* Ashmawy, Abu-Elwafa, Imam & El-Otifi, 1989 (10X magnification)
- B: Histological section through the gills of *Schilbe intermedius* Rüppell, 1832 showing three large plasmodia of *Henneguya* sp. D (10X magnification)
- C: Histological section through the gill arch of *Oreochromis andersonii* (Castelnau, 1861), showing the plasmodia of *Myxobolus camerounensis* Fomena, Marqués & Bouix, 1993 (20X magnification)
- D: Histological section through the gill arch of *Tilapia ruweti* (Poll & Thys van den Audeaerde, 1965), showing the plasmodia of *M. camerounensis* (20X magnification)
- E: Histological section through the gills of *Barbus poechii* Steindachner, 1911 showing the plasmodia of *Myxobolus nyongana* (Fomena, Bouix & Birgi, 1994) (10X magnification)
- F: Histological section through the gills of *Barbus paludinosus* Peters, 1852 showing the plasmodia of *Myxobolus* sp. C (10X magnification)



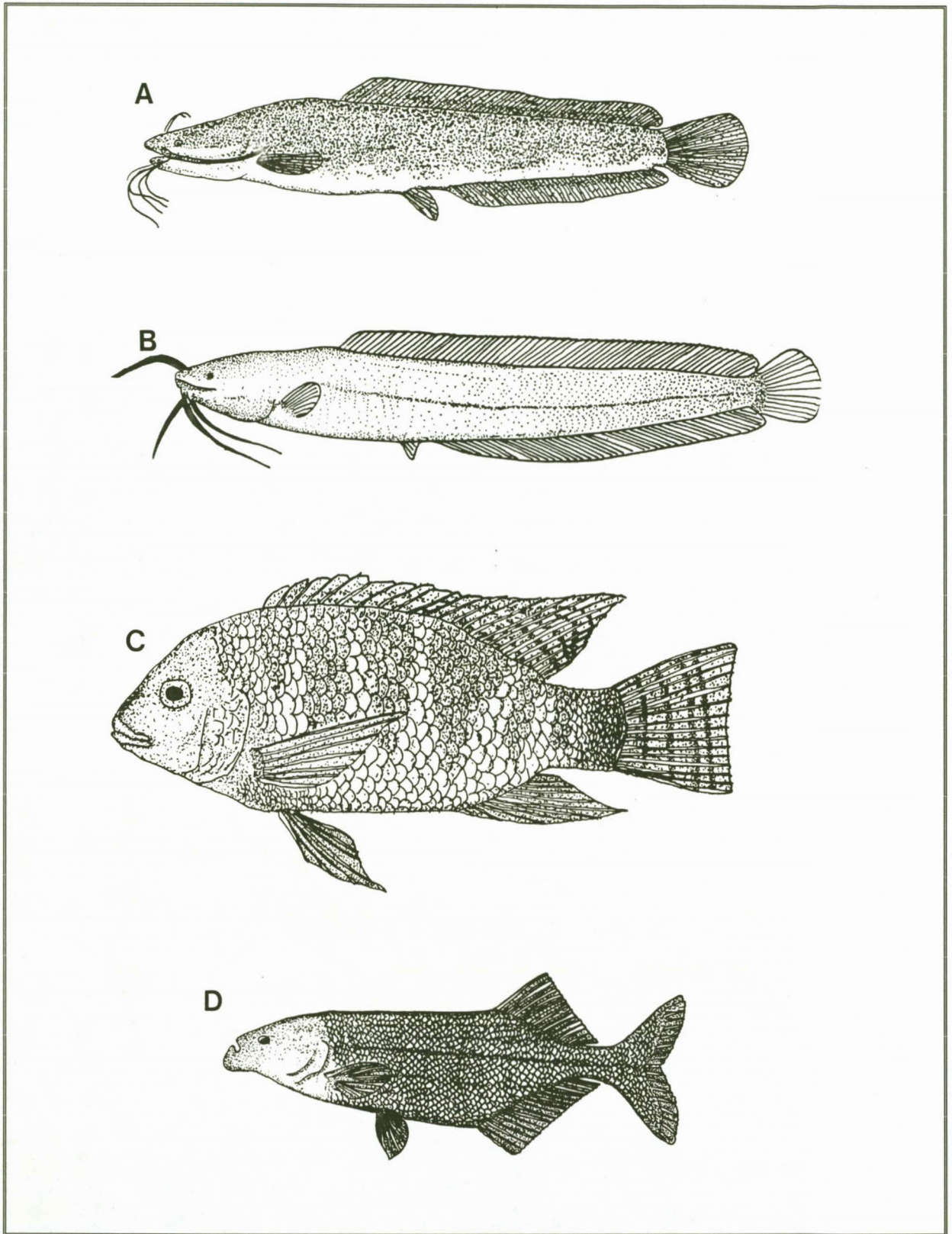


Figure 7.11: Line drawings of **A**-*Clarias gariepinus* (Burchell, 1822), **B**-*Clarias theodoarae* Weber, 1897, **C**-*Tilapia rendalli rendalli* (Boulenger, 1896), **D**-*Marcusenius macrolepidotis* (Peters, 1852) [Redrawn from Skelton, Bruton, Merron & Van der Waal (1985) and Skelton (1993)]. Not drawn to scale.

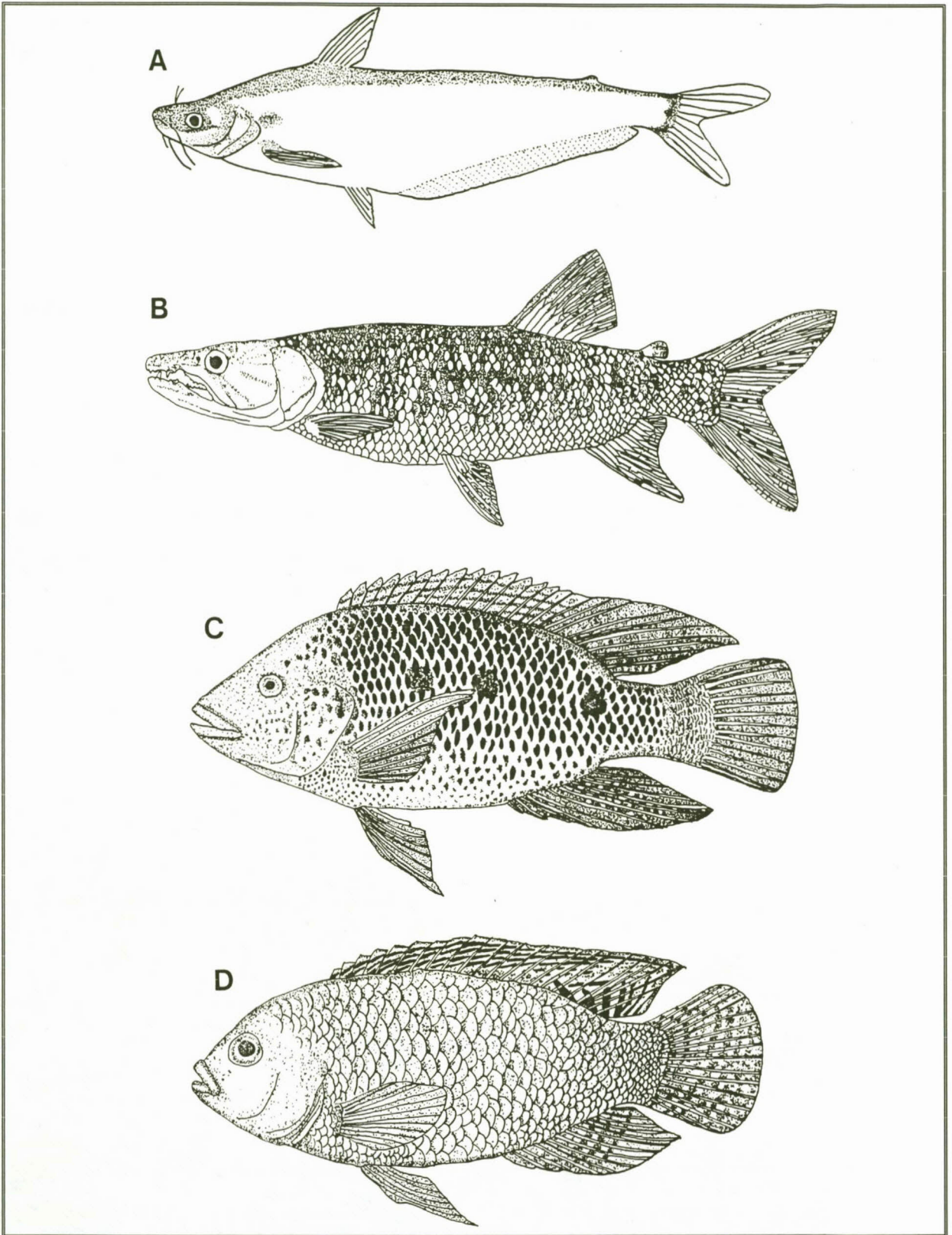


Figure 7.12: Line drawings of **A**-*Schilbe intermedius* Rüppell, 1832, **B**-*Hepsetus odoe* (Bloch, 1794), **C**-*Oreochromis andersonii* (Castelnau, 1861), **D**-*Tilapia ruweti* (Poll & Thys van den Audenaerde, 1965) [Redrawn from Skelton (1993)].
Not drawn to scale.

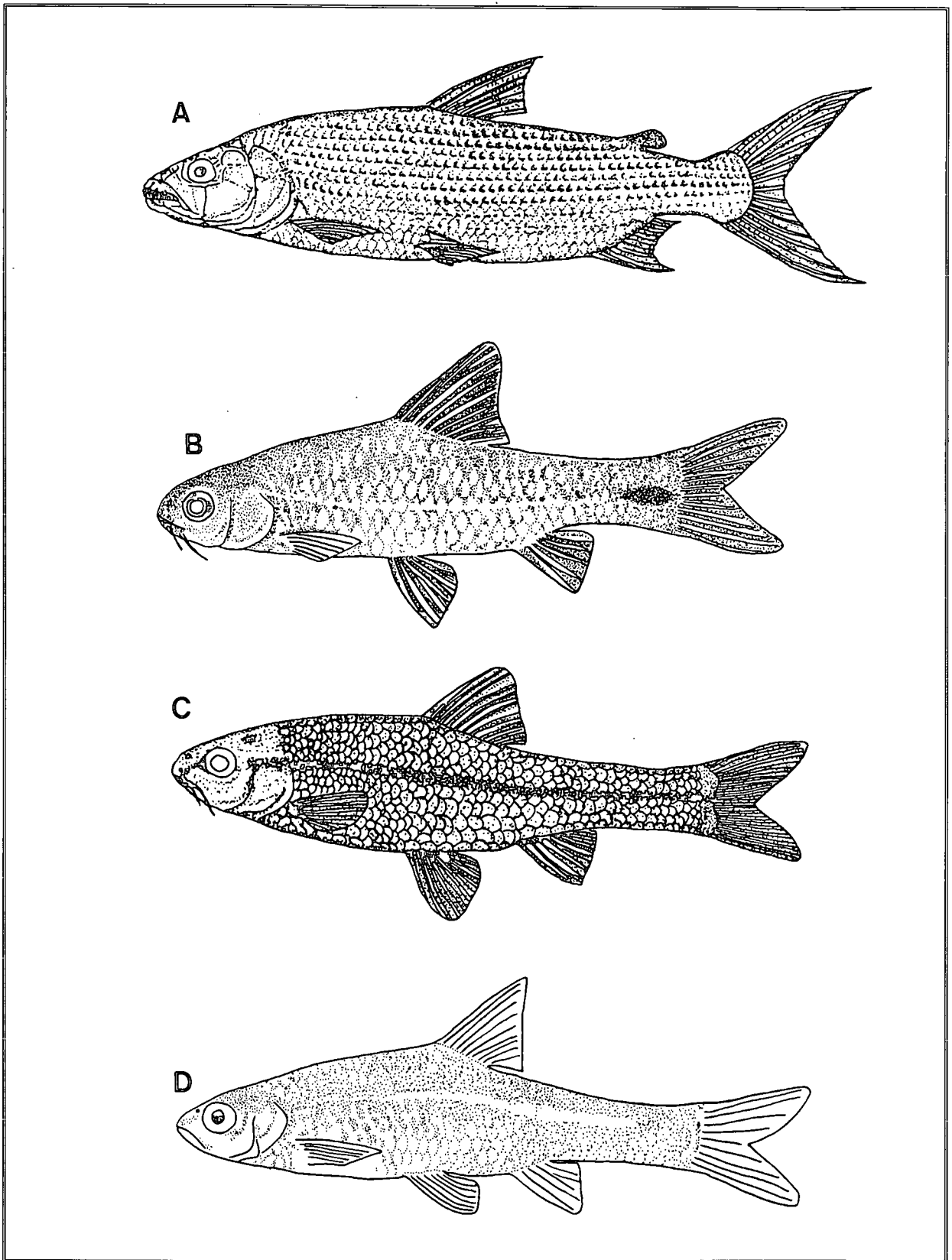


Figure 7.13: Line drawings of **A**-*Hydrocymus vittatus* Castelnau, 1861, **B**-*Barbus poechii* Steindachner, 1911, **C**-*Barbus thamalakensis* Fowler, 1935, **D**-*Barbus paludinosus* Peters, 1852 [Redrawn from Bruton (1984) and Skelton (1993)]. Not drawn to scale.

CHAPTER 8



Discussion

This pilot faunistic study on the biodiversity of myxosporeans infecting fishes in the Okavango River in Botswana has restored myxosporean research in southern Africa. Research on myxosporeans in this region has been very scanty with only seven papers appearing from South Africa during the twentieth century (see Chapter 2), none of which contained any valid species descriptions. It is thus time that the likely multitude of myxosporeans hiding in fishes and elsewhere in water bodies of southern Africa are exposed. As might be expected these preliminary investigations only give a foretaste and have most definitely uncovered many questions that still need to be answered. Considering only about half (31) of the approximate 68 species of fish in the Okavango have been investigated for the presence of myxosporean parasites, it is almost unimaginable what species still await to be discovered.

Some of the most widespread internal parasitic diseases in fish are due to myxosporean infections (Alyain *et al.* 1994). Throughout the world, myxosporeans have proven to be potential pathogens in aquaculture and fishing industries. Common diseases such as “whirling disease”, infecting trout have been reported from a multitude of countries, even from South Africa (Van Wyk 1968). Diseases such as this are known to cause a high mortality rate in young fish leading to large economical losses in especially hatchery-reared brown trout (Schmidt & Roberts 2000). *Ceratomyxa shasta* Noble, 1950, the agent of PKD as well as the myxosporean *Myxidium leei* Diamant, Lom and Dyková, 1994, are of great economic importance in the world today. Some myxosporean genera have also been associated with specific disease conditions in fish. Members of the genus *Kudoa* are of great concern to aquaculture and fisheries industries throughout the world, since they have a serious impact on product quality, resulting in accelerated degeneration or post-mortem myoliquification in the flesh of the fish (Moran *et al.* 1999).

The rearing of tilapia species is widespread throughout Africa (Fomena *et al.* 1993) and has justifiably been regarded as the backbone of *African aquaculture*. This is largely due to the relative ease of cultivation and propagation, rapid growth in some species and the general consumer acceptability of African tilapias (Obiekezie & Okaeme 1990). In fact, as a result of their ease of cultivation, African tilapias are also

being cultivated on a large scale in countries such as Taiwan, Japan and Israel. The effects of myxosporean infections in these aquaculture industries in Africa have already been experienced. Substantial losses of hybrid African catfish fingerlings have been reported from nursery facilities in Nigeria (Obiekezie & Schmahl 1993) and some species such as *Myxobolus camerounensis* were reported to form bulky plasmodia, compressing the gill filaments and disturbing the respiration of the fish (Fomena *et al.* 1993). Other species have been reported to cause serious damage to the spleen or cause partial or total loss of sight in the fish (Okaeme *et al.* 1988). In the study of the parasites of economically important fish species in Africa it is thus of major importance to prevent epizootic diseases, which could decimate fish stocks (Fomena *et al.* 1993) and result in economical losses on this continent.

The dependence of people in and around the Okavango River in Botswana on the fish population, whether it be for subsistence, commercial fisheries or tourism, emphasizes the need for research on myxosporean parasites infecting these fish. There are a large number of man induced and natural stresses on the Okavango. These include extended periods of drought and low water levels as well as the effects of insecticide spraying to combat largely the tsetse fly, combined with the possibility of exploitation of certain fish species. A number of important fish species that are very readily used by the people in Botswana include *Clarias gariepinus*, *Schilbe intermedius*, *Hydrocynis vittatus*, *Hepsetus odoe*, *Tilapia rendalli rendalli*, *Tilapia ruweti* and *Oreochromis andersonii*. All of these species were found infected by myxosporeans and most are also potential candidates for aquaculture industries. The possibility thus exists that in future an aquaculture industry will develop in this region. It will then be important to investigate what myxosporean species are infecting these potential aquaculture candidates in the wild, in order to try and predict possible future problems that might arise if aquaculture industries do develop in this region.

The panhandle and delta regions of the Okavango River in Botswana both contain two main habitat types. These are the *mainstream* and the *lagoon environments*. Certain differences exist in the physical conditions between these two main habitat types.

Firstly the mainstream environment has a constant flow of water, contributing to a higher oxygen concentration in these parts. Alternately the adjacent lagoons do not

have a constant flow of water and have much more decaying matter lying on the bottom, which all contributes to a lower oxygen concentration in the lagoons. A difference also exists between the panhandle lagoons and floodplain lagoons, with the latter having much lower oxygen concentrations. This could be attributed to the large amount of decaying sediment that accumulates lower down in the delta, combined with the large decrease in the rate of water flow. In general it appears as if a larger amount of fish species collected from the mainstream environment were infected with myxosporeans. Although only three fish species infected with myxosporeans were collected from lagoons in both the panhandle and delta, the sample sizes of these fish were larger than for the fish species collected in the mainstream. Six fish species collected from the mainstream environment were infected with myxosporeans, but in many cases only a single individual of a particular species was collected. In order to establish whether Okavango myxosporeans predominate in the mainstream or lagoon environment a more representative sample size of each of the fish species inhabiting both environments would have to be examined.

Henneguya sp. C infecting *Marcusenius macrolepidotis* was collected from both a panhandle mainstream lagoon, namely Lloyds Lagoon and an isolated floodplain lagoon in the delta, namely Duba Lagoon. Comparisons between the **infection prevalence** in each of these localities revealed higher infection prevalence, but lower infection level for the fishes collected from Duba Lagoon in the delta (see Chapter 7). The low oxygen concentrations in these floodplain lagoons most probably contribute to increased stress levels experienced by the fish, making them more susceptible to myxosporean and other parasite invasions. The oxygen concentrations in the panhandle are also low at the time of the receding flood levels, but do not drop as low as in the delta itself. The higher infection prevalence of these fish in the delta might indicate that the particular fish population is more sensitive to changes in the oxygen saturation of the water.

On the other hand, the prevalence of *Henneguya* sp. D infecting *Schilbe intermedius* was relatively constant in both the panhandle and delta region (see Chapter 7). Oxygen concentrations apparently had no effect on the different populations. It could be that the different *S. intermedius* populations have separately adapted to the

different environmental conditions, or it could be that this particular fish species is somehow hardier and not as sensitive to changing environmental conditions.

The annual flood cycle in the Okavango forms an intricate part of the biology and ecology of the fishes found there. *Seasonality* has been reported for a number of myxosporean species (Cone 1994, Haaparata, Tellerva & Hoffmann 1994, Molnar 1998). No deductions can, however, be made regarding the seasonal occurrence of the myxosporeans in the Okavango fishes that were found to be infected. Collections for this research project took place during June and July each year, which is the southern African winter season. This is the time of year when the floodwaters have started to recede and oxygen concentrations in this receding water have dropped. It would be interesting to determine whether the myxosporean infection levels will change at the time when the floodwaters are still high. At the time when the vanguard of the flood reaches the delta, this new water should contain higher oxygen levels and subsequently the conditions for the fish populations should be less stressful, making them less susceptible to parasite infections.

A very interesting phenomenon is reported each year when the new floodwater starts to move down the length of the Okavango River. Each year mass fish kills are reported when this water arrives. Little is known about this phenomenon, not even the period of time in which it takes place or even what species of fish are involved or what age group. If largely reproductive adult fish are affected, it could have serious effects on the fish populations. The time that the vanguard of floodwater arrives would be the time when the water and oxygen levels of the water from the previous year's flood are lowest. If the parasite loads in the gills of fishes have increased due to the higher susceptibility of the fish, it might be that the new water flowing in results in an uplifting of bottom stagnant water, decreasing the oxygen values even more. Fish with largely reduced gill surface areas due to myxosporean infections might not be able to survive such a sudden decrease in oxygen levels, resulting in masses of infected fish dying. It could be possible that the maturation of the myxosporean spores infecting fishes in the Okavango coincide with the low water levels in June and July, the time of year when the fishes are most susceptible to parasite infections.

The *life cycles* of only a small number of myxosporean species in the world have been elucidated, of which none have been described for African myxosporeans. There are a number of possible life cycle strategies that are used by myxosporeans (see Chapter 2), such as the involvement of an actinosporean intermediate stage and thus the strategies for the myxosporeans in the Okavango have an endless array of possible life cycles. The high infection prevalence of some of the fishes indicates that the specific life cycle or transmission for these Botswana myxosporeans must be very successful. Fish species such as *Marcusenius macrolepidotis* and *Schilbe intermedius* feed on a wide range of invertebrates i.e. midge or mayfly larvae, insects, shrimps, snails, plant seeds and fruits and even on small fish (Skelton 1993). The life cycle of these myxosporeans might very well involve an actinosporean stage infecting some invertebrate that forms part of the diet of these fish. The water in the Okavango River hardly contains any plankton and the sediment consists largely of sand, thus not providing ideal habitats for oligochaetes in which to live. It is possible that oligochaetes live in the matted base of the papyrus beds.

Large predatory fish such as *Hydrocymus vittatus* and *Hepsetus odoe* do not feed on invertebrates, but on other smaller fish species. Before the discovery of the alternating actinosporean life cycle, Donets (1979) showed that there is a relationship between the spores settling rates and the specific hosts and that predatory hosts feeding from the surface to midwater are characteristically infected with slow-settling spores. These predator fish of the Botswana Okavango system live in a mainstream environment with a constant strong flow of water. Slow settling spores might be washed away. Do these fish become infected by eating smaller fish species that have eaten actinosporean infected intermediate hosts, or by direct fish-fish transmission as described by Diamant (1997)? Investigations into the life cycles of Botswana myxosporeans will most definitely form part of the future research that will be conducted on this project.

Modern techniques such as DNA and RNA analysis are being used to differentiate between species as well as to determine the relationships between myxosporeans and the alternate actinosporean stages. Ultrastructure and histopathological investigations are also largely being investigated. These would be the next steps involved for the Okavango myxosporeans. Histology and histopathological evaluation of the

myxosporean infections of the fishes in the Okavango River and Delta, which are currently in the preliminary stage, as well as ultrastructural features of the infections will be one of the more important aspects of future research for this project.

Myxosporeans are undeniably one of the most diverse, complicated and extremely interesting group of parasites that are being researched in the world today. These parasites are so small that their placing under the protozoans was only recently queried, since it was established that they show a degree of multicellularity, contain nematocyst-like polar capsules and their DNA indicates that they have affinities with the Cnidarians (Siddall *et al* 1995, Smothers *et al.* 1994)! Furthermore, they are extremely common and are found in any organ of a number of hosts ranging from primitive invertebrates to highly developed vertebrate fish. The life cycles of these deceptively simple looking organisms are also incredibly complicated and diverse, with some relying on a direct fish to fish transmission (Diamant 1997) and others incorporating an intermediate stage that looks totally different and is found in a very different host (Wolf & Markiw 1984).

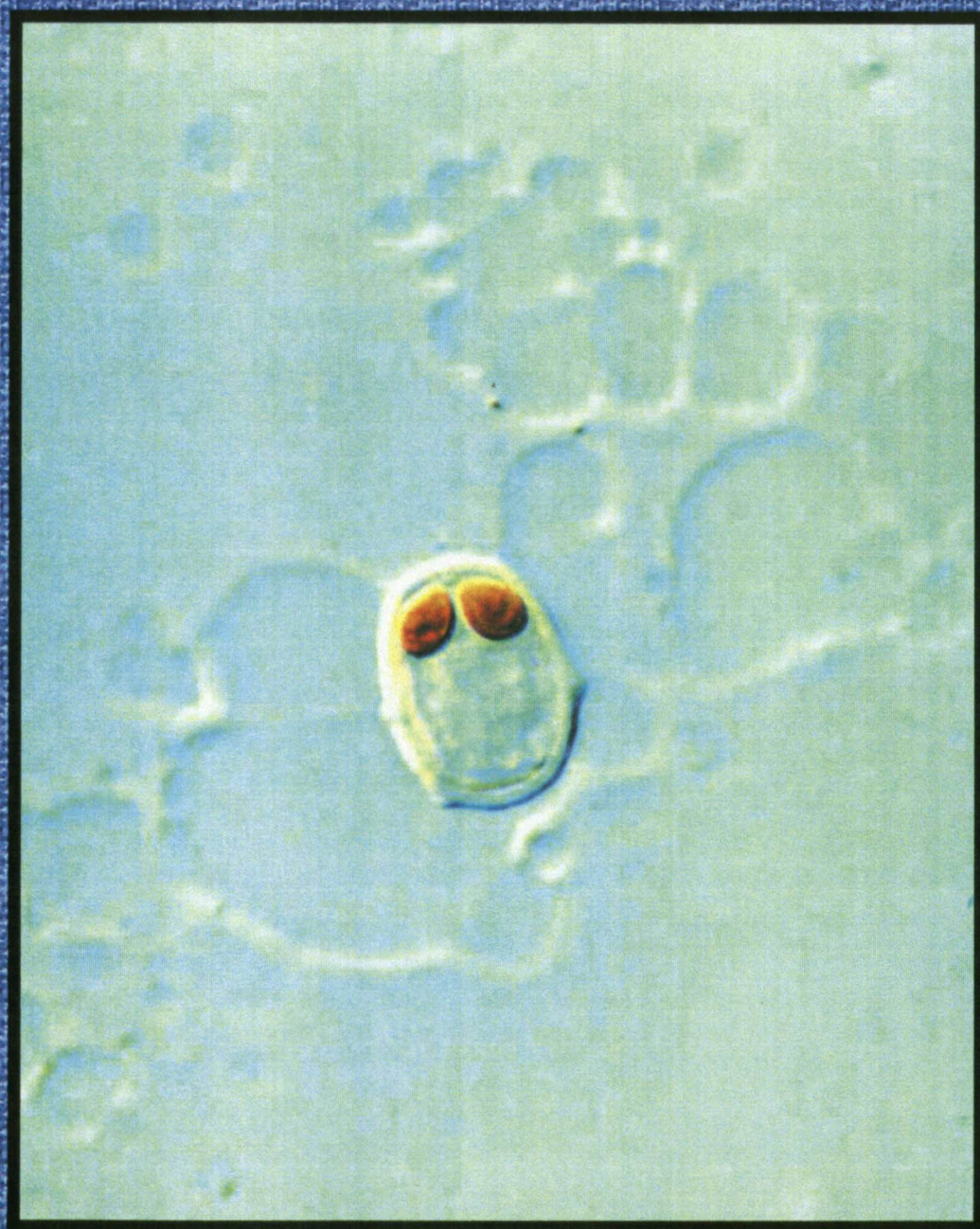
Finally, a large amount of myxosporean research has been conducted in Europe, Asia and North America. Considering the relatively low diversity of fish species and other possible myxosporean hosts in these countries and the incredible discoveries have been made regarding those myxosporeans, it is not difficult to imagine what species and peculiar features are awaiting discovery in our Africa, with its incredibly diverse fauna... *Ex Africa semper aliquid novi...*

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Abstract

The Class Myxosporea Bütschli, 1882 comprises an enormous group of spore forming obligatory parasites that are able to infect any organ of the hosts in which they are found. Myxosporeans mostly parasitise fish and to date there are more than 1300 species known from fishes throughout the world. In Africa, approximately 84 species have been described from primarily freshwater fish. Research on myxosporeans in southern Africa is very limited, with only a few publications appearing from the coast of South Africa during the early 20th century. In Botswana no research has ever been conducted on myxosporean parasites infecting fishes. Botswana contains one of the worlds largest inland delta systems formed by the Okavango River, which flows in a southeasterly direction from Angola. Knowledge on the fishes as well as their parasites is essential for the well being of a unique body of water such as this. Since myxosporean parasites of fish hold the potential to be pathogenic to their hosts and have been known to cause serious economical losses in aquaculture industries throughout the world, it is thus essential to determine the distribution and biodiversity of these parasites in the Okavango River and Delta in Botswana. The main aims of this project were to investigate the available literature regarding African myxosporeans, compile a database of species infecting freshwater fishes in Africa and to investigate the taxonomic status, species biodiversity and prevalence of myxosporeans infecting fishes in the Okavango River and Delta in Botswana. Fieldwork for this project was conducted in June and July 1998 and 1999 in the Okavango and a total of 275 fishes belonging to 31 species from nine different families were examined for the presence of myxosporean parasites. Five myxosporeans from the genus *Henneguya* Thélohan, 1892 were collected from four different fish hosts. Only one of these was identified as a known species and was described in this dissertation. A comprehensive morphological description of the four unknown species was also provided. Eight myxosporeans from the genus *Myxobolus* Bütschli, 1882 were also found infecting nine different fish hosts, of which four were identified as known species and described. Detailed descriptions of the four unknown species were provided. It was also found that some fish species showed very high gill infections of these parasites, which may cause some form of respiratory deficiency. This current investigation into myxosporean parasites infecting fishes in the Okavango River System in Botswana provided new insight into the distribution of myxosporeans in southern Africa and has also opened the door for future research in this unique group.

Opsomming

Die Klas Myxosporea Bütschli, 1882 bestaan uit 'n groot groep verpligte spoorvormende parasiete, wat in staat is om enige orgaan van die gasheer waarin hul voorkom te infekteer. Miksoporiidiums is meestal parasiete van visse en tot op hede is daar meer as 1300 spesies vanaf visse regoor die wêreld beskryf. Ongeveer 84 spesies is in Afrika beskryf, vanaf hoofsaaklik van varswater visse. Navorsing op verteenwoordigers van die miksporidiidiums in suidelike Afrika is baie beperk, met slegs enkele publikasies gedurende die vroeë 20ste eeu vanuit Suid-Afrika. Geen navorsing is egter in Botswana op miksporidiidium parasiete van visse gedoen nie. Botswana het een van die grootste binnelandse deltas, wat deur die suid-oos vloeiende Okavangorivier gevorm word. Die rivier het sy oorsprong in die hooglande van Angola. Kennis van die visse sowel as hul parasiete is noodsaaklik vir die ekologiese welstand van hierdie unieke stelsel. Miksoporiidium parasiete is potensiële patogene en daarvoor bekend dat hulle groot ekonomiese verliese in visakwakultuur reg oor die wêreld kan veroorsaak. Dit is dus noodsaaklik om die verspreiding en biodiversiteit van hierdie parasiete te bepaal. Die hoof doelwitte van hierdie studie was om die beskikbare literatuur rakende miksporidiidiums in Afrika te bestudeer, 'n data basis op te stel van die spesies wat varswater visse in Afrika infekteer, asook om die taksonomiese status, spesie biodiversiteit en besmettings statistiek van miksporidiidiums van visspesies in die Okavangorivier en- delta te bepaal. Veldwerk vir hierdie studie was gedurende Junie en Julie 1998 en 1999 in die Okavango uitgevoer. 'n Totaal van 275 visse wat tot 31 verskillende spesies en nege families behoort was vir die aanwesigheid van miksporidiidium parasiete ondersoek. Vyf spesies van die genus *Henneya* Thélohan, 1892 was van vier verskillende visgashere versamel. Slegs een is as 'n bekende spesie geïdentifiseer en beskryf. 'n Breedvoerige morfologiese beskrywing van die ander vier spesies is gedoen. Agt miksporidiidiums van die genus *Myxobolus* Bütschli, 1882 was van nege verskillende visgashere versamel. Vier van hierdie spesies was bekend en is beskryf, 'n omvattende beskrywing van die vier onbekende spesies is gedoen. Daar is ook gevind dat van die visspesies 'n baie hoë kieuinfeksie gehad het, wat moontlik tot respiratoriese disfunksie kan lei. Hierdie studie rakende die miksporidiidium parasiete, wat visse van die Okavangorivierstelsel in Botswana infekteer, werp nuwe lig op die verspreiding van miksporidiidiums in suidelike Afrika en open deure vir toekomstige navorsing op hierdie unieke groep organismes.

Appendix I: Glossary of terms used

The terms below have been compiled from Lom and Dyková (1995)

AUTOGAMY-a sexual process taking place in which two nuclei of the sporoplasm fuse together.

CAPSULOGENIC CELL-one of the cells in the sporoblast that eventually gives rise to the polar capsule.

CELL-IN-CELL ORGANISATION-myxosporean development stages where a **primary cell** contains inner **secondary cells**, which are produced by endogenous cleavage. There may also be tertiary and quaternary cells included in these secondary and tertiary cells, respectively. A cell doublet is when a primary cell contains a single secondary cell and a cell triplet is when the primary cell contains two secondary cells.

COELOZOIC-myxosporeans infecting organ cavities.

EXTRASPOROGONIC-development phase which occurs parallel to the sporogonic phase.

GENERATIVE CELL-a secondary cell within the plasmodium that will later be involved in spore production.

HISTOZOIC-myxosporeans found within tissue organs.

NEMATOCYST-a specialised cell containing a capsule with an extrudible filament.

PANSPOROBLAST-a spore producing formation that is found within a polysporic formation. It originates by the union of two generative cells, with one, the pericyte, enveloping the other, the sporogonic cell. This then divides to produce the sporoblast cells. Pansporoblasts usually produces two spores.

POLYSPORIC-a plasmodium producing several spores

POLAR CAPSULE-a thick walled vesicle in myxozoan spores containing an inverted **polar filament**, forming a coil with two or more turns.

PRESPOROGONIC STAGES-a sequence of development in the life cycle preceding sporogony.

PSEUDOPLASMODIUM-a sporogony stage that has a single vegetative nucleus producing one or two spores

SHELL VALVE-forming one of the two or more parts of the myxosporean spore wall.

SPORE-an infectuous stage consisting out of several specialised cells.

SPOROBLAST-a developmental stage preceeding the spore, with not yet fully differentiated cells.

SPOROGENIC CELL-produced by the division of sporoblast cells.

SPOROGENY-the process of spore formation.

SPOROGENIC PLASMODIUM-a multinuclear cell containing many generative nuclei involved in sprorogony.

SPOROPLASM-the amoeboid cell within the spore, which is the actual infective germ.

SUTURE LINE- the line of dehiscence, along which the shell valves adhere.

VALVOGENIC CELL-one of the cells of the sporoblast forming the shell valves.

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OFFICE OF THE PRESIDENT
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GABORONE

REPUBLIC OF BOTSWANA

REF: 46/1 LVVII (90)

August 1, 1997

Dr. Keith Leggett
Conservation Officer
Kalahari Conservation Society
P. O. Box 859
GABORONE

Dear Sir,

RE: GRANT OF A RESEARCH PERMIT:
DR.K. LEGGETT, PROF. J. G. VAN AS
AND. J. P. VAN NIEKERK

Your application dated 12 March, 1997 refers.

I am pleased to inform you that you have been granted permission to conduct research on "Parasites of Fish in the Okavango". The research will be conducted at Okavango Panhandle and Delta, Moremi Game Reserve and Ngamiland District.

The research is valid for twenty-four (24) months effective 4 August 1997.

The permit is granted subject to the following conditions:

1. Copies of any papers/books written as result of the study are directly deposited with the Office of the President, National Archives (2 copies each), Ministry of Agriculture, Ministry of Commerce and Industry, Ministry of Mineral Resources and Water Affairs, Ministry of Local Government, Lands & Housing, Department of Wildlife & National Parks, Department of Fisheries, National Library Services and National Institute for Research.
2. You work in close liaison with Ministries listed in (1) above.
3. You work with the Fisheries Department, Ministry of Agriculture.

4. You obtain a supplementary permit from the Department of Wildlife & National Parks.
5. You pay park fees.
6. You comply with all regulations governing visitor's conduct in the parks.
7. You conduct the study according to the particulars furnished in the application.
8. The research team comprises Prof. J. G. Van As, J. P. Van Niekerk, Messrs L. Basson, L. L. Van As, N. J. Smit, K. W. Christison, N. J. Grobler, H. Botes, P. A. S. Olivier, S. M. Dippenaar, N. N. Nicolaai, J. H. Viljoen, L. C. Van Nieuwenhuizen, N. M. Mokgalong, W. J. Powell and Dr. K. Leggett.
9. The permit does not give authority to enter any premises, private establishment or protected area. Permission for such entry should be negotiated with those concerned.

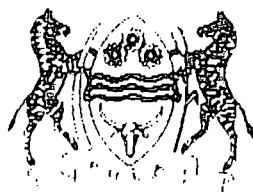
Yours faithfully


J. MOSWEU

for/PERMANENT SECRETARY TO THE PRESIDENT

- cc. Permanent Secretary
- Ministry of Agriculture
 - Ministry of Commerce & Industry
 - Ministry of Local Government, Lands & Housing
 - Ministry of Mineral Resources & Water Affairs
- Commander, Botswana Defence Force
Commissioner of Police
Director, Department of Wildlife & National Parks
Director, Department of Fisheries
District Commissioner, Maun
Council Secretary, Maun
Landboard Secretary, Maun
Government Archivist
Director, National Library Services
Director, National Institute for Research

ELEGRAMS: FULA
TELEPHONE: 350800
FLEX: 2655 BD



REPUBLIC OF BOTSWANA

OFFICE OF THE PRESIDENT
PRIVATE BAG 001
GABORONE

OP 46/1 LXXVII (74)

November 19, 1999

Mr Felix Monggae
P. O. Box 859
GABORONE

Dear Sir/Madam

RE: EXTENSION OF RESEARCH PERMIT OP 46/1 LVVII (90)

Your letter of November 10, 1999 refers.

We are pleased to inform you that your permit OP 46/1 LVVII (90) has been revalidated for a period not exceeding twelve (12) months effective from January 2000.

Kindly be reminded that all other conditions remain valid and equally binding.

Yours faithfully

A handwritten signature in dark ink, appearing to read 'J. Sothibe'.

J. Sothibe

for PERMANENT SECRETARY TO THE PRESIDENT