



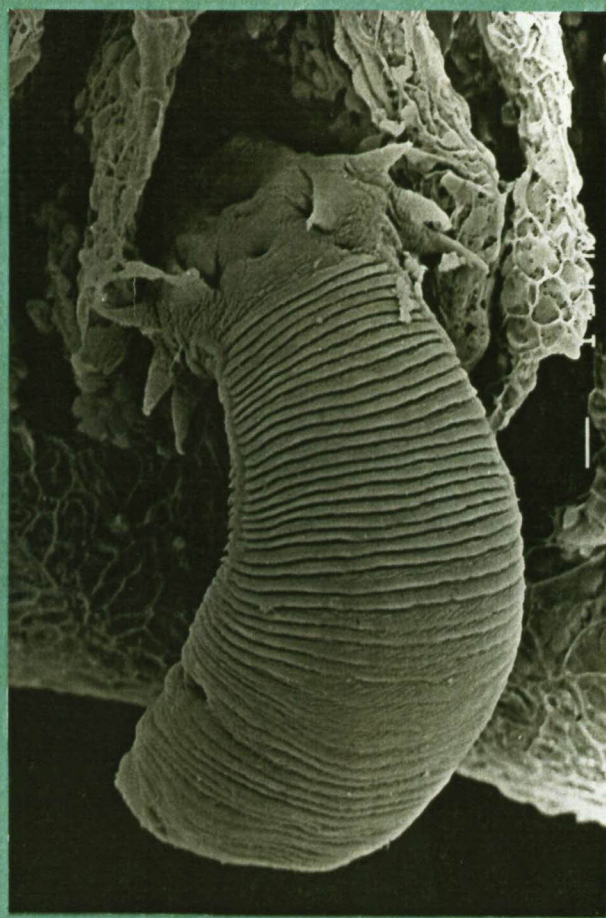
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**BRANCHIAL MONOGENEAN PARASITES  
(MONOGENEA: DACTYLOGYRIDAE) OF CHARACIN  
FISHES FROM THE OKAVANGO RIVER AND DELTA,  
BOTSWANA**

**By**

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*Dissertation submitted in fulfilment of the requirements for the degree  
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# CHAPTER 1





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# INTRODUCTION

## THE OKAVANGO DELTA

The Okavango Delta is situated in north-western Botswana, in the midst of the Kalahari Desert, and is one of the last great African wetland wildernesses. The area of the delta fluctuates from 15 000 km<sup>2</sup> during the flood season to 6 000 – 8 000 km<sup>2</sup> during the dry season. There is much speculation about where and when the Okavango was formed. According to Bailey (1998) it is certain that its development spanned millions of years, and was closely interwoven with the creation of its neighbour and host, the Kalahari, and of the succession of massive water systems that cover the area. According to Merron (1991) the Okavango as it is today is a geologically young system, which before major uplifting, formed a drainage channel into a great lake called Makgadikgadi. Presently the Okavango is the only large river of the world, which forms an inland delta.

The Okavango River originates from a series of headwater streams on the southern slopes of the Angolan highlands. These streams flow south and south-eastwards, then gather to form a large mainstream (the Cubango), which turns eastward shortly after reaching the Angola-Namibia border. A second major branch of the system (the Cuito) also rises in the Angolan highlands and joins the mainstream, which after crossing Namibia's Caprivi Strip, enters Botswana at Molembo. Upon entering Botswana, the Okavango is a single broad river, approximately 100 km long, 150 m wide and 4 m deep. In a series of exaggerated S-bends, the river meanders between two high forested banks of Kalahari sand set about 15 km apart, within a broad riverine floodplain, colloquially termed the riverine panhandle. The panhandle is bound by fault lines running south-easterly from the Namibian border. According to Bailey (1998) about 11 billion cubic metres of water flow through the panhandle annually, reaching its peak towards the end of summer (February to March), months after the rains have fallen in the Angolan highlands far to the north-east.

It is only after the confines of the riverine floodplain that the Okavango branches out to form the anastomoses of the delta. Beyond the village of Seronga, the nature of the Okavango River changes dramatically as it passes over the Gumare Fault. This fault forms the north-western edge of the depression which contains the permanent swamp, a 6 000 km<sup>2</sup> wetland where the Okavango assumes the character for which it is famed, a confusion of channels, floodplains, lagoons and islands (Bailey, 1998).

Merron (1991) divides the Okavango Delta into five major ecological regions namely the riverine floodplain, permanent swamp, seasonal swamp, drainage rivers and sump lakes based on the ecological communities of mixed vegetation formed by the overlapping of adjoining communities. The riverine floodplain and perennial swamp which cover approximately two-thirds of the area of the delta, have surface waters up to 3 m deep and are covered with a dense growth of papyrus *Cyperus papyrus*, reeds *Phragmites australis*, bulrushes *Typha latifolia capensis* and the fern *Cyclosorus interruptus*. In the riverine floodplain, the mainstream channel is approximately 150 m wide and the substrate is sandy. There are numerous tributaries and oxbow lagoons associated with the mainstream channel. These areas are lined with dense stands of aquatic macrophytes including *Nymphaea capensis*, *Potamogeton thumbergi* and *Elodea densa*.

Upon entering the permanent swamp, the waters of the Okavango flow as a river for the last time. The slightly convex form of the land, causes the mainstream channel to split into three distributary systems, the Thoage, Nqoga and Jao which serve as the arteries of the delta, supplying the life giving waters that sustain the permanent swampy areas (Figure 1.1). According to Bailey (1998) the gradient along which the water flows from here is very slight, the water dropping only 65 m along its 250 km journey to Maun. The Thoage is the western most distributary, which prior to 1960 served as the major drainage channel. However, due to seismographic shifting which resulted in a decreased flow rate, numerous blockages built up which have now choked this river below Nokaneng (Merron, 1991). The Nqoga extends along the Maunachira and Khwai Rivers and during extremely high floods, empties into the Mababe salt pan. Since 1960, the Jao has become the primary distributary of the central delta and after passing through Xo lagoons is called the Boro River. According to Bailey (1998) the Jao-Boro System

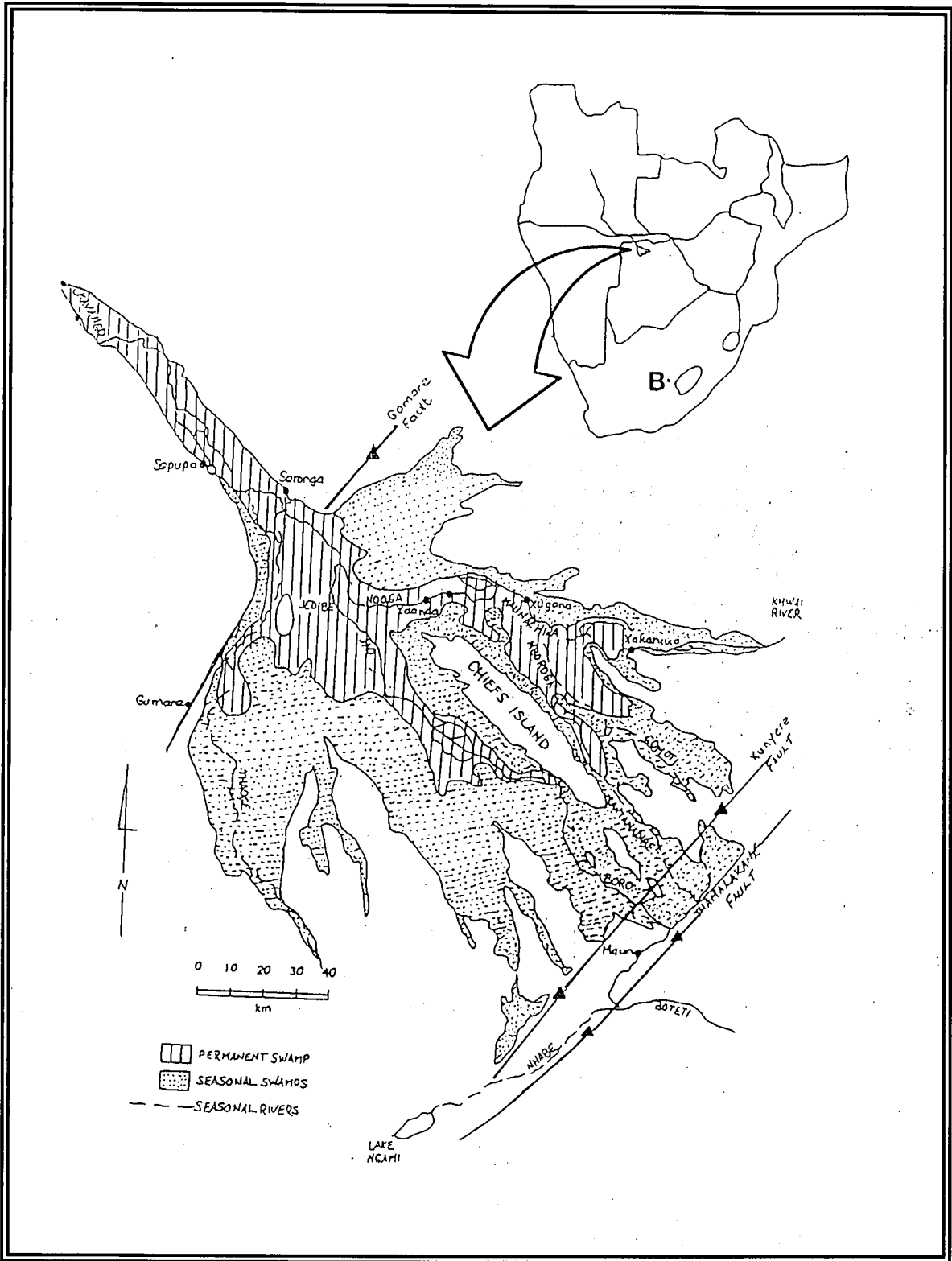
currently takes about 25 % of the Okavango's flow and is the main arterial channel to the south of Chief's Island in the central delta area.

The southern seasonal swamp covers about one-third of the area of the delta and is characterised mostly by shallow grass and sedge-covered floodplains. The southern swamp is a seasonally inundated swamp, which varies markedly in surface area, depending on the magnitude of the annual flood from Angola and the amount of local rainfall. At the south-east end of the Okavango Delta, the main drainage channels, the Boro and the Santanadibe, re-unite along a fault line to form the south-west flowing Thamalakane River, which abruptly changes its course to the south-east at its confluence with the Nhabe and Boteti Rivers (Figure 1.1).

## **ANNUAL FLOOD CYCLE**

The mean annual inflow into the delta from Angola is  $11 \times 10^9 \text{ m}^3$ , with local rainfall contributing on average  $5 \times 10^9 \text{ m}^3$  (Merron, 1991). Although these figures look impressive, most of this water is lost to the thirsty Kalahari sands or to evaporation. The loss of water to evaporation and transpiration is about 96 % of the total input of water. A further 1.8 % is lost to ground water seepage resulting in approximately only 2 % of the inflow into the swamps reaching the Thamalakane River.

The floodwaters, which are dependent on the rainfall patterns in the Okavango catchment, usually begin to arrive at Shakawe in January and reach Maun, at the southernmost part of the delta in June. The slow flood cycle causes water to reach the southern parts of the swamp during the coldest months when water temperatures are lowest (average June temperature  $16 \text{ }^\circ\text{C}$ ) (Merron, 1991). The changes with respect to water quality, temperature, and oxygen content, brought about annually by the flood, impact directly on the animals dependent on the delta.



**FIGURE 1.1** Map of the Okavango Delta Showing major ecotones, rivers and drainage systems (redrawn from McCarthy, *et al*, 1997) (B-Bloemfontien).

The major physical factor determining the distribution and abundance of fishes appears to be habitat preferences, with the physical characteristics of the environment playing a major role. The permanence of the water and the nature of its flow are two of the most obvious ecological factors affecting community structure. These two factors affect other physical and chemical parameters such as substrate type, extent of emergent, submergent and floating macrophyte cover, dissolved oxygen levels and water temperatures, which in turn affect the distribution of the fish (Merron, 1993).

According to Skelton, *et al.* (1985) the rise and fall of the annual floodwaters is one of the major driving forces in the Delta. The floods create vast shallow areas that are suitable for breeding and feeding by many species and cause large amounts of detritus, from other sources, to enter the food chain. The arrival of the floods are also responsible for supplying the stimulus for spawning and or migration of certain fish species in the delta (Merron, *et al.*, 1990; Skelton, 1993; Ross, 1987), and also provide a means of distributing the fish throughout the system. This increased water flow clears away biological blockages caused by rafts of papyrus. Many of the sump lakes and drainage rivers rely on the floods for their water. The timing and duration of flooding determines to a large extent the recruitment, growth and survival rates of wetland fish stocks (Welcomme, 1979) and according to Skelton, *et al.* (1985) is likely to be the case in the Okavango swamps as well.

Many of the above mentioned phenomena have evolved over time as a response to the natural annual flood regime. Without the natural fluctuation in water levels in the Okavango, the entire area would take on a different character, most likely one that is not as rich in species diversity and biotic processes.

## **OKAVANGO FISH PARASITE PROJECT**

Fish form an important part of the Okavango ecosystem. Very few of the fish species that occur in the Okavango are dependant on plankton as a source of nutrients. Most of the fish are either herbivorous or piscivorous. This in turn places the fishes as some of the chief secondary producers and primary consumers within this ecosystem.

Not only fish are dependent on fish for food, but many of the other animals occurring in the Delta also make use of fish as their primary diet. From insects like dragonfly larvae and the giant water bug to a variety of birds to other animals including otters, crocodiles and terrapins are dependent on fish to at least supplement their diet. The fishes of the Okavango Delta also more importantly represent a valuable natural resource for the people of Botswana.

Recently fisheries scientists and local fisherman have reported a dramatic decline in the fish numbers of the Okavango Delta. The main causes for this decline according to Bruton & Merron (1985) and Merron & Bruton (1986) are manipulation of the flood regime, effects of insecticides, invasion by alien plants and animals, encroachment on the floodplain and interference with nutrient cycles. Although many causes have been identified and a variety of further reasons can be found for this fish population decline, parasites and diseases cannot be ruled out as at least a contributing factor.

The current knowledge on the Okavango ichthyoparasite fauna is limited with only very few papers concerning Okavango fish parasites or fish parasites from similar related water bodies namely Oldewage & Van As (1988), Basson & Van As (1989); Van As (1992); Van As & Basson (1992); Douellou (1993); Douellou & Chishawa (1995) and Van As & Van As (1996) have been published.

In the light of this scientists from the University of the Orange Free State, headed by Professor J. G. Van As, submitted a project proposal to address their concern about the health status of the fish populations in the Delta.

In August 1997, the Ministry of Agriculture of Botswana approved the Okavango Fish Parasite Project as an official project within this Ministry, to be carried out under the auspices of the Kalahari Conservation Society. Permits to conduct this research were issued by the office of the President of Botswana (Appendix A). A comprehensive grant, to finance this research, was obtained from the donation fund of Debswana Diamond company in Botswana and further support was provided by Land Rover South Africa. Additional financial assistance is provided by the Foundation for Research Development,

South Africa, under the Inland Resources programme with emphasis on inland biodiversity and conservation.

This study aims to:

1. Determine the health status of the fish populations of the Okavango Delta.
2. To compile a data base on the occurrence and distribution of fish parasites in the Okavango Delta.
3. To determine if any parasite could become a potential threat to any species of fish or to the fish community as a whole.
4. To determine if potential pathogenic organisms could impact on the population density of any fish species.
5. To determine if any parasite could be a potential threat to aquaculture.
6. To determine if any parasite could be a potential threat to human consumers.
7. To determine if this system harbours any alien or translocated fish parasites.
8. To elucidate the systematics and life cycles of new parasite species.
9. To expand the knowledge on the ichthyoparasite fauna of African inland waters.
10. To develop local expertise in fish health management programmes.

During the initial stages of the project 52 species of fish have been collected out of the 82 species which occur in the Okavango Delta. The parasites recorded represent a wide diversity of taxa. Various representatives of the protozoan sub-class Peritrichia were collected from the skin and the gills of fish. Myxosporidian cysts were also recorded from the gills of numerous fish species. An *Ichthyobodo* Pinto, 1928 species and various suctorians were also found. The crustacean parasites were represented by a variety of copepod parasites collected from the gills of the fish. Two branchiuran genera were also present, a *Dolops* Audouin, 1837 species was collected from the gills of *Synodontis nigromaculatus* Boulenger, 1905 and from *Sargochromis greenwoodi* (Bell-Cross, 1975) and a new *Chonopeltis* Thiele, 1900 species was recorded from the western bottlenose, *Mormyrus lacerda* Castelnau, 1861 (Van As & Van As, in press). Various nematodes and acanthocephalans were also recorded in both their larval and adult stages. Cestodes and a variety of digenean trematode life-cycle stages were also quite abundant. The most

numerous helminth parasites recorded were the monogeneans. These parasites occurred in large quantities on both the gills and skin of a large variety of fishes.

The present study forms an integral part of the Okavango Fish Parasite Project and the data and results presented here will contribute directly to the achievement of the aims set out by the project as well as contribute to the information collected about the Okavango Delta as a whole. Besides the recent study, the project has also produced the following results, which have been published along with two conference contributions, Van As & Van As (in press); Christison, Van As & Basson (1998); and Reed, Van As and Basson (1998).

### **THE CLASS MONOGENEA**

According to Bychowsky (1957) the locations of the monogeneans are very diversified, they are parasitic on elasmobranch and teleost fish in addition to amphibians, reptiles, and parasitic crustaceans and are even known to exist on cephalopod molluscs and aquatic mammals. Those parasitic on fish usually attach on the gills, in the gill chamber and buccal cavity, on the body surface, on the fins, in the cloacal cavity and its vicinity, in the ureters and body cavities and as an exception in the heart. According to Bychowsky (1957) and Cone (1995) the majority of the parasites attach on the gills and each is located differently thereon. Most occur on the gill filaments, few on the gill rakers and some on the lateral surfaces of the gill arches. Those attached to the gill filaments are distributed differently on the filaments, many occur on all four gill arches, others are mostly or even exclusively located on the second and third arches. Different species have favoured places of location within the limits of a single gill arch.

Monogeneans are also site specific in the buccal cavity with some occurring on the lips, the palate, the tongue and even the beginning of the oesophagus. Many species are found attached to the outer surface of the body and here preference to site of attachment also occurs. Some settle mainly on the surfaces of the head whereas others settle on the ventral and dorsal surfaces of the body. Many of the lower monogeneans live on the fins of the fish, these species occur more often on the pectoral than the dorsal and more rarely the caudal, ventral and anal fins.



Monogeneans in general have a life span that vary from a few days to several years. Many are, however, incapable of living a short time after the death of the host (Schmidt & Roberts, 1977). The life cycles of a few species of monogeneans have been well studied with little or nothing being known about the rest. Apart from the viviparous Gyrodactylidae Cobbold, 1864, monogeneans usually have a short uncomplicated life cycle, involving an egg, oncomiracidium and an adult.

### **SYSTEMATICS OF THE CLASS MONOGENEA (VAN BENEDEEN, 1858)**

The first author to recognise the monogeneans as a separate group was Van Beneden (1858), who divided the class Trematoda into two divisions, namely the digénèses and the monogénèses (Wheeler & Chisholm, 1995). The French term monogénèses was thought to be vernacular and according to Wheeler & Chisholm (1995) was changed to Monogenea by Carus (1863) who was the first author to refer to the group by this name. However, the change from monogénèses to Monogenea is simply an emendation from the original French to a latinised suffix, in accordance with standard nomenclatural practice. Such a minor orthographic change does not justify attributing authorship of the name to Carus (Bychowsky, 1957). Van Beneden established the group as a distinct taxon and gave it the scientific name still used today, albeit without a latinised suffix, authorship of the Monogenea should still be attributed to Van Beneden (1858).

The classification system used by Price (1937) was based on the idea that all monogeneans are divided into two large groups, those having a true vagina, but do not have a genito-intestinal canal and those having a ductus vaginalis and a genito-intestinal canal as proposed by Odhner (1912). Odhner (1912) gave these groups sub-ordinal taxonomic status and named them Monopisthocotylea Odhner, 1912 and Polyopisthocotylea Odhner, 1912 respectively.

Based on the monogenean opisthaptor, which possesses hooks, and the cercomer in the ontogeny of the cestodes, amphilinideans and gyrocotylideans, Bychowsky (1937, 1957) suggested that these four groups were more closely related to each other than to the digeneans. Using this Bychowsky (1937) elevated the Monogenea from the rank of

order to that of class and changed the name to Monogenoidea, although he still credited the authorship to Van Beneden and dismissed the objections of Price (1937) and other workers who still attributed the authorship to Carus. According to Wheeler & Chisholm (1995), most specialists in the former Soviet Union and some workers in other countries adopted Bychowsky's nomenclature for the group, although most specialists in the West continued to use the name Monogenea. Bychowsky's (1957) hypothesis on monogenean evolution was based on comprehensive ontogenetical and anatomical results taking into account the possible co-evolution between the hosts and their monogeneans (Malmberg, 1990). The monogenean classification of Bychowsky (1937) has been one of the main systems proposed. It was developed in the mid-thirties and was based on features of larval development and the structure of the hooks in the various groups of monogeneans. The class was hence divided into two sub-classes namely Polyonchoinea (Bychowsky, 1937) and Oligonchoinea (Bychowsky, 1937).

According to Yamaguti (1963) most of the authors before him based their classification on the external morphology, particularly the cuticularised or sclerotised parts of the body, such as the haptor anchors, clamp sclerites, copulatory apparatus, etc. Although the hard parts are of taxonomic importance, Yamaguti (1963) also included the internal morphology particularly that of the genitalia to represent what he described as a more natural classification of the Monogenea. This classification system, which was merely an elaboration of the scheme proposed by Odhner (1912) and Price (1937) was used as a standard in the literature for many years.

In their cladistic studies of the spermatozoon ultrastructure and spermiogenesis of monogeneans, Justine *et al.*, (1985) and Justine (1991) found interesting similarities in terms of phylogenetic relationships amongst the monogeneans with Lebedev's (1988) classification, which was based on morphology. The problem with these studies is that they proposed a potential phylogeny of the monogeneans based on the characters of a single structure or organ. As suggested by Justine (1991), these results should be tested against data coming from the analysis of other characters of the monogeneans.

Malmberg (1990) proposed a classification scheme based on the ontogeny of the opisthaptor in which he suggested that the main trend in monogenean evolution is progressive, meaning that there is an increase of marginal hooks during evolution. He further suggested that the theories of Bychowsky, Lebedev, Lewellyn, Euzet and Lambert assumed a reduction of the number of marginal hooks during evolution, i.e. a regressive evolution.

According to Malmberg (1990), Justine, *et al.* (1985) also suggested that monogenean evolution was progressive using evolutionary trends in monogenean spermatozoon patterns. Justine (1991) stated that the results of comparative spermatology show disagreement with Malmberg's classification as sperm pattern is indicated for each family, but is not used for the erection of higher ranking taxa used in his classification.

In 1988, Lebedev put forward a classification system based on a development of Bychowsky's approach with regard to other authors views and new faunistic additions. The main difference of this classification system from the others is the addition of an independent subclass Polystomatoinea, which was placed by the previous authors amongst either the lower Monogenea (Polyonchoinea, or Monopisthocotylea), or the higher Monogenea (Oligonchoinea, or Polyopisthocotylea). Another significant difference was the introduction of orders within the Monogenea for the first time.

A common factor between the above mentioned systems is that they all make use of a single or a few sets of characters, paying less attention to other potentially useful homologies within the group. Boeger & Kritsky (1993) subjected the monogenean families to cladistic analysis to examine their evolutionary relationships based on a variety of anatomical and ultrastructural characters, this led to a classification system based on the phylogenies within the group. Lebedev (1995) proposed an emended version of his 1988 classification system, which is more or less congruent with Boeger & Kritsky (1993). There are, however, a few minor differences which Lebedev (1995) attributes to the definition of homologous character series or the choice of pleisomorphies and apomorphies and agrees that both his, as well as the Boeger & Kritsky (1993) hypothesis still need to be tested. In 1997, Boeger & Kritsky proposed a revised hypothesis of

monogenean phylogeny, specifically the Polyonchoinea, based on new ultrastructural and anatomical data. The resulting hypothesis was used to determine co-evolutionary events associated with the families of Monogenea and the higher taxonomic categories of their hosts.

Since Bychowsky (1937), there has been continuous debate about whether the class of Platyhelminthes, comprising the monogenetic flukes, should be called Monogenea or Monogenoidea. A round table discussion entitled "Monogenea: problems of systematics, biology and ecology" was convened at the Fourth International Congress of Parasitology (ICOPA IV) in Warsaw, Poland in 1978. Thirty specialists from 11 countries participated in the ICOPA round table discussion, which was an attempt to reach consensus on a number of problems in the nomenclature, taxonomy and terminology of monogeneans (Wheeler and Chisholm, 1995). At that occasion, all the participants agreed to adopt Monogenea as the name of the class rather than Monogenoidea. Although this decision was flawed, the ICOPA Round table nevertheless adopted the Monogenea as the preferred name, which has not since been changed by any similar gathering of specialists. In agreement with Wheeler & Chisholm (1995), the name to be applied to higher taxa should be determined by consensus among specialists, as the "International Code for Zoological Nomenclature" has no rules governing the names of taxa above family level.

The classification of the class Monogenea (Table 1.1) for the rest of this dissertation will be according to Boeger & Kritsky (1997), as this system is the most recent and most representative in terms of the phylogenetic relationships within the group. The subclass designation will be according to Bychowsky (1937) and Lebedev (1986), namely Polyonchoinea, Polystomatoinea and Oligonchoinea. Besides some differing opinions of the name designated to the class, the following monogenean specialists (pers. comm.) have agreed that the system adapted here is the most appropriate: M. Beverly-Burton (Canada), L. Du Preez (South Africa), D. Gibson (United Kingdom), D. Kritsky (United States), B. Lebedev (Russia), T. Littlewood (United Kingdom) and I. Whittington (Australia). Although they still form two schools as to what the class should be called, it is my opinion that the class should be called Monogenea in accordance with the ICOPA

round table decision. Whether or not there is any validity in changing the name to Monogenoidea is purely semantic and probably has no scientific base, as there are no set rules governing the higher taxa. The class will thus be referred to as Monogenea in accordance with Wheeler & Chisholm (1995).

**TABLE 1.1 Classification of the class Monogenea (Van Beneden, 1858) adapted from Boeger & Kritsky (1997)**

SUBCLASS	ORDER	SUBORDER	INFRAORDER	SUPERFAMILY	FAMILY			
Polyonchoinea (Bychowsky, 1937)	Monocotylidea				Monocotylidae			
					Loimoidae			
	Capsalidea				Dionchidae			
					Capsalidae			
	Motchadskyellidea				Montchadskyellidae			
	Lagarocotylidea				Lagarocotylidae			
	Gyrodactylidea				Bothitrematidae			
					Tetraonchoiidae			
					Anoplodiscidae			
					Gyrodactylidae			
					Acanthocotylidae			
	Dactylogyridea		Calceostomatinea		Calceostomatidae			
			Neodactylodiscinea		Neodactylodiscidae			
			Amphibdellatina		Amphibdellatidae			
			Tetraonchina			Sundanonchidae		
					Tetraonchidae			
					Neotetraonchidae			
		Dactylogyriina		Dactylogyridae				
				Diplectanidae				
				Psuedomurraytrematidae				
Polystomatoinea (Lebedev, 1986)	Polystomatidea				Polystomatidae			
					Sphyranuridae			
Oligonchoinea (Bychowsky, 1937)	Chimaericolidea				Chimaericolidae			
	Diclybothriidea				Diclybothriidae			
					Hexabothriidae			
	Mazocraeidea		Mazocraeina		Plectanocotylidae			
					Mazoplectidae			
					Mazocraeidae			
					Anthocotylina		Anthocotylidae	
							Psuedodielidophoridae	
					Gastrocotylina	Gastrocotylina	Protomicrocotylidea	
								Allodiscocotylidae
								Psuedomazocraeidae
							Chauhaneidae	
							Bychowskycotylidae	
					Gastrocotylidae			
					Neothoracocotylidae			
					Gotocotylidae			
			Discocotylina		Discocotylidae			
					Diplozoidae			
			Hexostomatinea		Octomacridae			
					Hexostomatidae			
Microcotylina				Microcotylidea	Axinidae			
						Diplasiocotylidae		
					Heteraxinidae			
					Microcotylidae			
				Allopyragraphoroidea		Allopyragraphoridae		
				Diclidophoroidea		Diclidophoridae		
				Pyragraphoroidea		Pterinotrematidae		
				Rhinecotylidae				
				Pyragraphoridae				
				Heteromicrocotylidae				

## MONOGENEAN RESEARCH IN AFRICA

Of the five families of the class Monogenea that infest African freshwater fishes, three are representatives of the subclass Polyonchoinea, namely Gyrodactylidae, Dactylogyridae Bychowsky, 1933 and Diplectanidae Bychowsky, 1957. Only two families of the subclass Oligonchoinea, namely Diplozoidae, Tripathi 1959 and Diclidophoridae Cerfontaine, 1859, have been found infesting African freshwater fishes (Khalil & Polling, 1997).

The first record of monogeneans from African freshwater fish was Wedl (1861) who described a dactylogyrid, *Dactylogyrus gracilis* Wedl, 1861, from *Hydrocynus forskalii* (Cuvier, 1819). This monogenean was later placed in the genus *Neodactylogyrus* Price, 1938. The generic diagnosis of this monogenean was again emended by Paperna (1973) who placed it in the genus *Annulotrema* Paperna & Thurston, 1969, based on the tegumental annulation and opisthaptor hook arrangement. Monogenean research in Africa has relied chiefly on the works of a few scientists who have conducted studies in north and west Africa.

Since the late sixties to early eighties, Paperna laid the foundation for monogenean research in Africa. In this time he described numerous species and also created 11 genera. Paperna concentrated his work to Uganda and Ghana and also did some work in Tanzania and Kenya.

Apart from Paperna, many French scientists like Birgi, Euzet, Guegan, Lambert and their co-workers made meaningful contributions from the late seventies to the present. These contributions are, however, concentrated to the West African countries, which were previously colonised by the French.

The monogenean research conducted in southern Africa, which includes countries like Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Swaziland, Zambia and Zimbabwe, is very sparse. According to Khalil & Polling (1997) there are no monogenean records for Angola, Botswana, Lesotho, Mozambique, Namibia and Swaziland. The rest of the southern African countries do have monogenean records,

which are represented by one off studies and hence do not represent many species. Zimbabwe has the most records (25 species) of monogeneans in southern Africa due to the work of Douellou in the early nineties, followed by South Africa (16 species), Zambia (3 species) and Malawi (2 species).

The 16 species recorded from South Africa are representatives of five genera. *Annulotrema*, *Cichlidogyrus* Paperna, 1960, *Dactylogyrus* Diesing, 1850, *Gussevstrema* Price & McClellan, 1969 & *Gyrodactylus* Von Nordmann, 1832. The earliest records of monogeneans from South African freshwater fishes are a series of publications by Price and his co-workers in which they described monogeneans from freshwater fishes in the Kwazulu-Natal area (Price, Korach & Pott, 1969; Price & McClellan, 1969; Price, McClellan, Druckenmiller & Jacobs, 1969; Price Peebles & Bamford, 1969). In 1977, Prudhoe & Hussey described *Gyrodactylus transvaalensis*. The most recent work done is that of Mashego (1983) in which he described seven new species of the genus *Dactylogyrus* and included a key for the South African species of this genus.

As can be seen there is an immense lack of knowledge concerning specifically the monogenean fauna of southern African freshwater fishes. The present study in part undertakes to expand the information available about these parasites.

After a pilot survey in October 1997, large numbers of branchial monogeneans of the genus *Annulotrema* were found infesting Okavango tigerfish. In view of this, the present study was undertaken to determine the association between branchial monogeneans and Okavango Characiform fishes.

The present study was undertaken to address the following specific objectives;

- to review the systematics of the branchial monogeneans infesting characiform fish from the Okavango System
- to review the two genera *Annulotrema* and *Characidotrema* Paperna & Thurston 1968
- to determine if these parasites are potential pathogens and whether they could impact on the population density of their fish hosts



- to contribute to the results and findings of the Okavango Fish Parasite Project
- to compile a data base on the occurrence of monogenean fish parasites in the Okavango System and southern Africa

In Chapter 2, the Okavango Delta will be discussed with respect to the various habitats encountered and sampled. The collection sites will also be indicated on a map of the Delta. The methods employed to collect the monogeneans will also be discussed as well as the further preparation of the material for various microscopic techniques. There will also be a short explanation of the terms used. Chapter 3 provides some background information on the Okavango characins, shedding some light into their life strategies and on the monogenean-host association. The two genera *Annulotrema* and *Characidotrema* are reviewed in Chapter 4 where information as to the distribution of the species of these genera, and a brief historical overview of the two genera is provided. A checklist of the currently known species representing these two genera is also included. Brief summaries of the taxonomic characters of all the species of the two genera are also supplied.

Chapter 5 provides a review of the taxonomic characters of both the species of the genera *Annulotrema* and *Characidotrema* as well as the description of *Annulotrema micralesti* sp. n. and *A. rhabdalesti* sp. n. In Chapter 6 the statistical information obtained with respect to monogenean infestation are used to determine the association between the host and parasites as well as the site preferences of the various species. Due to the vast numbers of monogeneans infesting the gills of the Okavango characins, the potential pathology of the monogeneans on the fish host is discussed in Chapter 7. Chapter 8 is a generalised discussion in which the data collected during this study is used to compile comments on the association between these parasites and their hosts.

# CHAPTER 2



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# MATERIALS AND METHODS

## FIELDWORK

The Okavango Delta is approximately 2 000 km from Bloemfontein. This journey usually takes place over two to three days. Due to the vast distance that has to be travelled, field trips are usually no shorter than one month and usually continue for two to three months. The implication of such extensive field trips is that all equipment and luggage has to be transported there.

The accommodation for the duration of these trips is either in the tented camps provided by the various tourist lodges on the banks of the river (e.g. Drotsky's Cabins, Xaro Lodge and Guma Lagoon), or in two-man tents. Working from the tented camps limits the diversity of the sampling localities. In order to sample a diversity of habitats, sampling is frequently done from remote sites, where there are no facilities and which are unreachable by road. These sites are reached by boat, which is limited for space. On trips like these, a reduced field laboratory is used and an electricity generator is used as a power supply for the microscopes.

As most processing of the material takes place in the field, fixation and preservation methods are kept as simple as possible. The fieldwork is conducted by the Aquatic Parasitology study group from the Department of Zoology and Entomology, University of the Orange Free State, Bloemfontein, South Africa. Each member of the group concentrates on a different group of parasites and hence each fish that is collected is optimally utilised.

## COLLECTION LOCALITIES

For the purpose of this study, the Okavango System was divided into different habitats provided by the ecological regions proposed by Merron, (1991) namely; the riverine floodplain, the permanent swamp, the seasonal swamp, drainage rivers and the sump lakes. The different habitats that were sampled are as follows:

- **Mainstream** - This habitat is characterised by fast flowing water with a sandy substrate. This habitat is found in the panhandle or in the major distributary rivers where the river is deep and fast flowing.
- **Channels** - This habitat type is very similar to that of the mainstream. It differs from the mainstream in being narrower and shallower. These channels are open-ended and originate from a mainstream habitat and terminate in the same habitat further downstream. The channels are also characterised by flowing water. These habitats are frequently blocked by papyrus rafts and are cleared either manually or by flooding.
- **Backwaters** - The backwaters are also mainly associated with the mainstream habitats and are represented by adjacent channel-like water bodies in which there is no current or water flow and they are not open on both ends. These water bodies are distinguished from floodplains by being permanent.
- **Floodplains** - The floodplains are usually shallow temporary water masses on the marginal land which are inundated during the floods in winter and recede progressively during the hot summer.
- **Lagoons** - These are large, deep, open water masses and are usually associated with channels or the mainstream habitats. In some cases, the channel leading to and from the lagoons block up, isolating the lagoon.
- **Permanents swamps** - These are found in the southern delta and are characterised by shallow stationary waters. These swamps are littered with islands and are always inundated with water and form the low water mark at the end of summer before the floods.

- **Temporary swamps** - Temporary swamps are found at the margin of the permanent swamps and are also characterised by shallow, stationary water. These swamps vary in size according to the magnitude of the flood. When in flood they represent the high water mark of the flood and recede gradually throughout the following year.

All of these habitats were sampled during the two surveys in October 1997 (early summer) and in June - August 1998 (late winter). Base camps were set up at various sites within the Okavango System to ensure optimum exposure to all possible habitat types (Figure 2.1).

The northern most sampling locality was at Mohembo (4). This locality provided access to both floodplain and backwater habitats. Moving south down the panhandle the next sampling locality was the habitats around Drotsky's Cabins (1) and Xaro Lodge (8) from where access to the mainstream, floodplain, backwater, lagoon and channel habitats was possible. At both Nxamaseri (6) and Ngarange (5) only the floodplain habitat was accessible and sampled.

Three localities, which are not situated in the panhandle were also sampled. Two of these, Guma Lagoon (3) and Pepere Island (7), provided access to lagoon, channel and floodplain habitats, whereas the other locality Film Camp (2) was the only sampling locality that provided permanent and temporary swamp habitats.

## **COLLECTION OF FISH**

The collection methods for the fish varied according to their habitat preferences. When the water was very shallow and formed small pools as encountered in the floodplains and swampy areas, a variety of hand held scoop nets were used (Figure 2.2A). In slightly deeper water, like that of the backwaters, lagoons, swamps and the margins of the main channel over sandbanks, cast nets (Figure 2.2B) were effective for the collection of a wide variety of fish hosts. Gill nets (Figure 2.2C) were also effective in deep lagoons, channels or backwaters. These nets consisted of a graded series of lengths, each 10 m long and each of a different mesh size. The minimum mesh size was 40 mm and the

maximum of 140 mm (40 mm, 70 mm, 90 mm, 100 mm, 110 mm, 120 mm & 140 mm). These nets were set at dusk, left overnight and lifted the following morning at sunrise.

Other collection methods were also used with varying degrees of success. Seine nets (Figure 2.2D) were occasionally used in floodplain pools that were too large for the hand held nets to be effective. Using a fishing rod (Figure 2.2E) was particularly effective for collecting species like the tigerfish which are found in the mainstream channel, where the current is too strong for nets to be effective. Electro-fishing apparatus (Figure 2.2F) was also used and was effective in the marginal areas of the mainstream and over sandbanks. This method, however, was not excessively used as the above mentioned methods were far more effective and less labour and time consuming.

The permit for the collection and examination of the fish was obtained prior to the 1997 survey from the office of the President of Botswana (Appendix 1)

## **EXAMINATION OF HOSTS**

After collection, the fishes were taken to a field laboratory where they were examined. As far as possible the fish were kept live and were placed in temporary holding tanks for examination. Upon examination the fishes were anaesthetised and the gills were removed. Using a dissection microscope, the individual monogeneans were counted and their exact position on the specific gill arch was noted.

The gill arches were classified according to their position in the fish. The first distinction between the gills was the side on which they occurred, i.e. either left or right. The next distinction was according to their orientation with respect to the gill operculum. The gill arch closest to the operculum was numbered 1 and the gill arch closest to the mouth, or furthest from the operculum, was numbered 4. Each gill arch was then further subdivided into three separate regions. The anterior region was section A, the bend in the arch where the filaments are slightly shorter in length was section B and the posterior region was section C.

After the live observations and counting of the monogeneans, the gill arches were placed in a 1: 4 000 formalin solution for about half an hour. This solution is insufficient to fix the monogeneans, but will kill them in a relatively short time. After the monogeneans were dead, they were fixed in a 10 % neutral buffered formalin solution, still attached to the host tissue. This method of killing and fixing ensures that very few monogeneans contract on contact with the formalin and most of the specimens collected were relaxed.

In the laboratory in Bloemfontien, the parasites were treated in a variety of ways. Some were used for light microscopy, other specimens were used for scanning electron microscopical (SEM) study. Some infested gill arches were sent to the department of Anatomical Pathology, Faculty of Medicine, University of the Orange Free State, for histological sectioning and some gill arches were prepared for transmission electron microscopical (TEM) study.

## FIGURE 2.1

**Map of the Okavango Delta illustrating the various sampling localities during the two surveys, October 1997 and June -August 1998.**

### TOWNS / VILLAGES

M - Maun

SE- Seronga

SH- Shakawe

### SAMPLING LOCALITIES

1- Drotsky's Cabins

2- Film Camp

3- Guma Lagoon

4- Mohembo

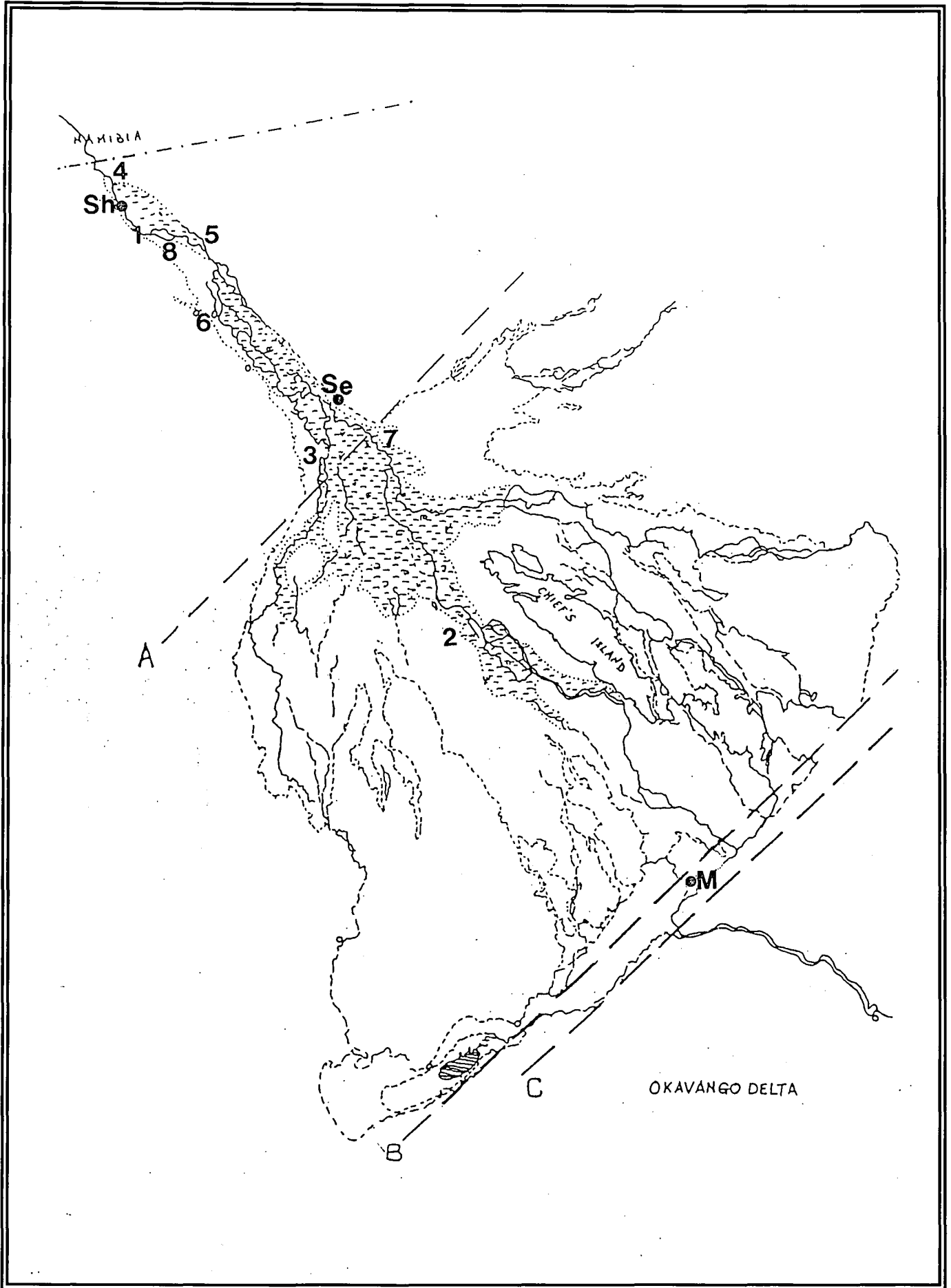
5- Ngarange

6- Nxameseri

7- Pepere Island

8- Xaro Lodge





## FIGURE 2.2

**Various methods used to collect fish in the Okavango during the two surveys, October 1997 and June-August 1998.**

- A. Using hand nets in a floodplain habitat near Guma Lagoon
- B. Using a cast net in backwaters near Xaro Lodge
- C. Setting gill nets in the Thoage distributary channel
- D. Seine netting in a floodplain near Guma Lagoon
- E. Using a fishing rod to catch a tigerfish in the Mainstream near Xaro
- F. Electro-fishing in a backwater near Mohembo



## LIGHT MICROSCOPY PREPARATION

In preparation for compound light microscopy, the specimens were removed from the gill tissue individually and mounted either in an Ammonium Picrate solution similar to that used by Malmberg (1957), to study the opisthaptoral armature, or stained in Gomori's trichrome (Kritsky, pers. com.) and mounted in Eukitt mounting medium for the study of the internal organs. The latter method had limited success and hence the former was used almost exclusively as in some specimens, the internal structures were also visible.

### AMMONIUM PICRATE

Neutral Buffered Formalin 10 %	1 part
Glycerine	9 parts
Picric acid	

Mix formalin and glycerine. Add 1 drop of the Picric acid for every 10 ml solution.

### GOMORI'S TRICHROME

Chromotrope 2R (C. I. 16570)	0.6 g
Aniline blue WS (C. I. 42780)	0.6 g
Phosphomolybdic acid	1.0 g
Distilled water	100.0 ml
Hydrochloric acid	1.0 ml

Dissolve stains in distilled water, add hydrochloric acid, allow to stand for 24 hours, store in dark container, DO NOT filter. It is recommended that the stain be stored in a refrigerator.

## SEM PREPARATION

Using a fine probe, some monogeneans were removed from the gill filaments and were placed in phosphate buffer. The phosphate buffer removes the excess mucous and debris from the monogeneans without causing any damage to the tegument of the monogeneans. The debris that remained after leaving the monogeneans in the phosphate buffer overnight was gently brushed off by holding the monogenean with a fine brush and brushing it with another.

After cleaning the specimens, they were dehydrated in a graded ethanol series of increasing concentration (30 % -100 %). The specimens were left in 100 % ethanol for approximately 10-15 minutes after which they were critical point dried.

After the dehydration and drying process, the specimens were mounted on aluminium stubs and coated with gold.

The specimens were examined using a JEOL WINSEM JSM 6400 scanning electron microscope at an acceleration voltage of 10 kV.

### PHOSPHATE BUFFER

#### Solution A

$\text{Na}_2\text{HPO}_4 \cdot 12\text{H}_2\text{O}$  35.814 g/l

$\text{Na}_2\text{HPO}_4$  14.19 g/l

#### Solution B

$\text{KH}_2\text{PO}_4$  13.610 g/l

Add 80 parts of solution A to 20 parts of solution B. Keep refrigerated.

### **TEM PREPARATION**

The infested gill filaments were removed from the formalin solution in which they were originally fixed. The specimens were then washed in phosphate buffer twice for 10 min each. Secondary fixation was achieved by placing the specimens in 1 % buffered osmium tetra-oxide for 90 min. After secondary fixation, the specimens were dehydrated by placing them in a graded acetone series of increasing concentration from 70 % to 95 %. The final dehydration was achieved by placing the specimens in 100 % acetone, renewing the acetone three times for 10 min each. The specimens were then placed in a 1:1 acetone: imbedding medium for 90 min at room temperature. SPURR'S imbedding medium was used. The filaments were then placed in pure imbedding medium for 30 min at room temperature and then for 30 min at 50 °C. The specimens were again placed in pure imbedding medium for 1hr at 50 °C. Polymerisation was achieved by leaving the specimens in the imbedding medium overnight at 70 °C.

Sections of 70-90  $\mu\text{m}$  were prepared using an ultra-microtome with a glass knife. The sections were mounted on a grid and stained for 30 min in uranylacetate after which they were thoroughly rinsed. The grids were again stained in lead citrate for 5 min and rinsed again.

The sections were studied using a Philips 301 transmission electron microscope at 60 kV.

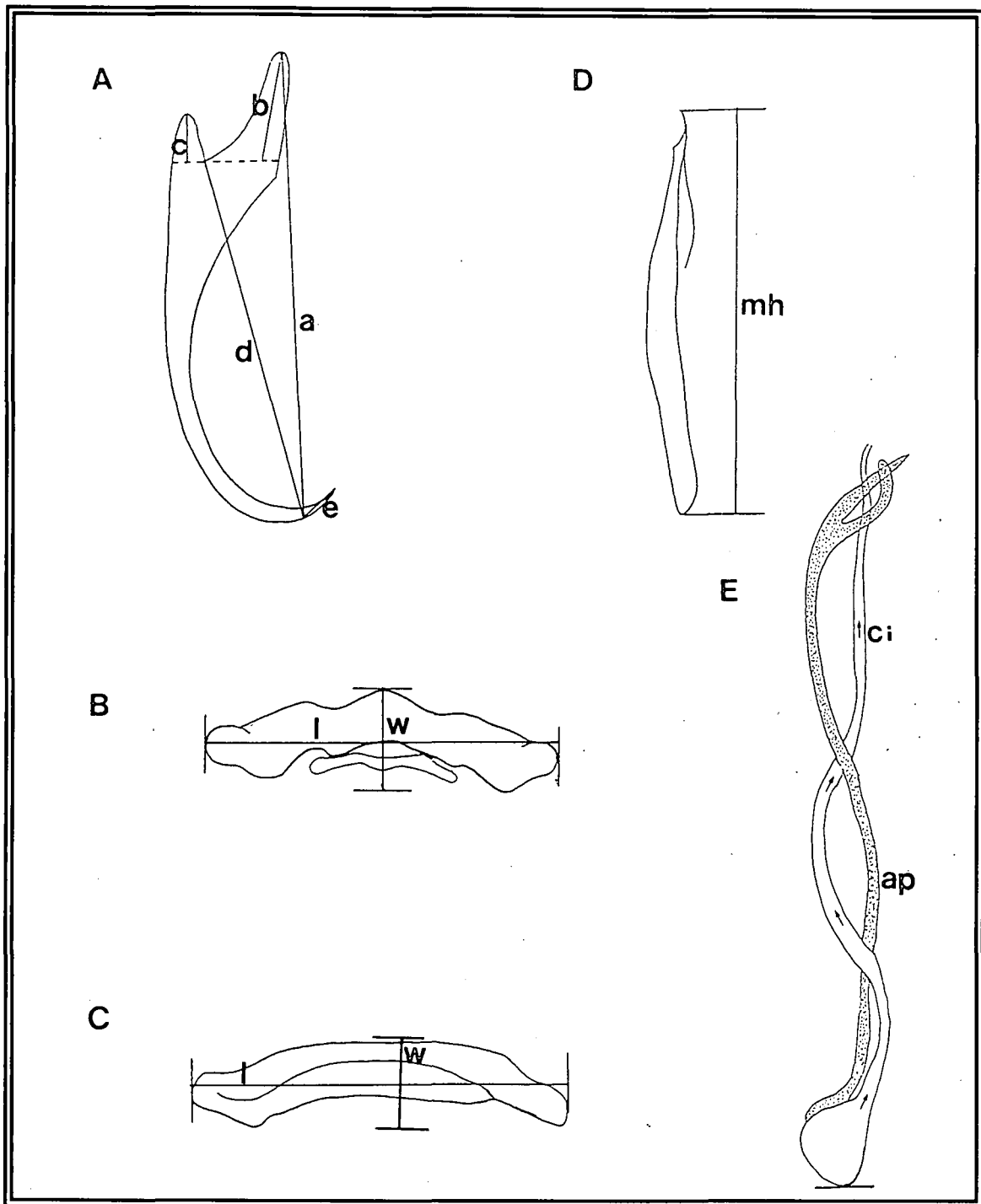
## HISTOLOGICAL PREPARATION

Some infested gill arches were sent to the Department of Anatomical Pathology at the Faculty of Medicine at the University of the Orange Free State for histological sectioning. Both hematoxylin and eosin stains were used to colour the specimens. The sections of 4  $\mu\text{m}$  were examined and photographed using a Zeiss Axiophot Photomicroscope. This analysis was used in conjunction with other techniques to examine the level of pathogenicity of the monogeneans.

## MORPHOLOGICAL MEASUREMENTS

Measurements of the sclerotised parts of both *Annulotrema* and *Characidotrema* specimens were according to N'Douba, *et al.* (1997). Five basic measurements, i.e. total length (a), inner root (b), outer root (c), shaft (d) and the tip (e) were obtained from the opisthaptor anchors (Figure 2.3A). The dorsal and ventral bars were measured in terms of their total length (l) and width (w) (Figures 2.3B, 2.3C). The marginal hooklets (mh) (Figure 2.3D) were numbered according to the system proposed by Malmberg (1990) and only their total length was measured. The total length of the cirrus as well as the accessory piece were measured and not only the length of their axis (Figure 2.3E).

The measurements of at least 10 specimens of each species found in the Okavango were measured, compared and were used as a basis to make taxonomic diagnoses. These measurements as well as the microscope projection drawings were made using a Zeiss compound microscope fitted with a drawing tube.



**FIGURE 2.3** Illustration of the measurements of the sclerotised parts of the Okavango monogeneans.

A- Anchor, a- total length, b- inner root, c- outer root, d- shaft, e- tip. B- Dorsal bar, l- length, w- width. C- Ventral bar, l- length, w- width. D- Marginal hooklet, mh- marginal hooklet length. E- Copulatory organ, ci- cirrus, ap- accessory piece

## **TYPE AND REFERENCE MATERIAL**

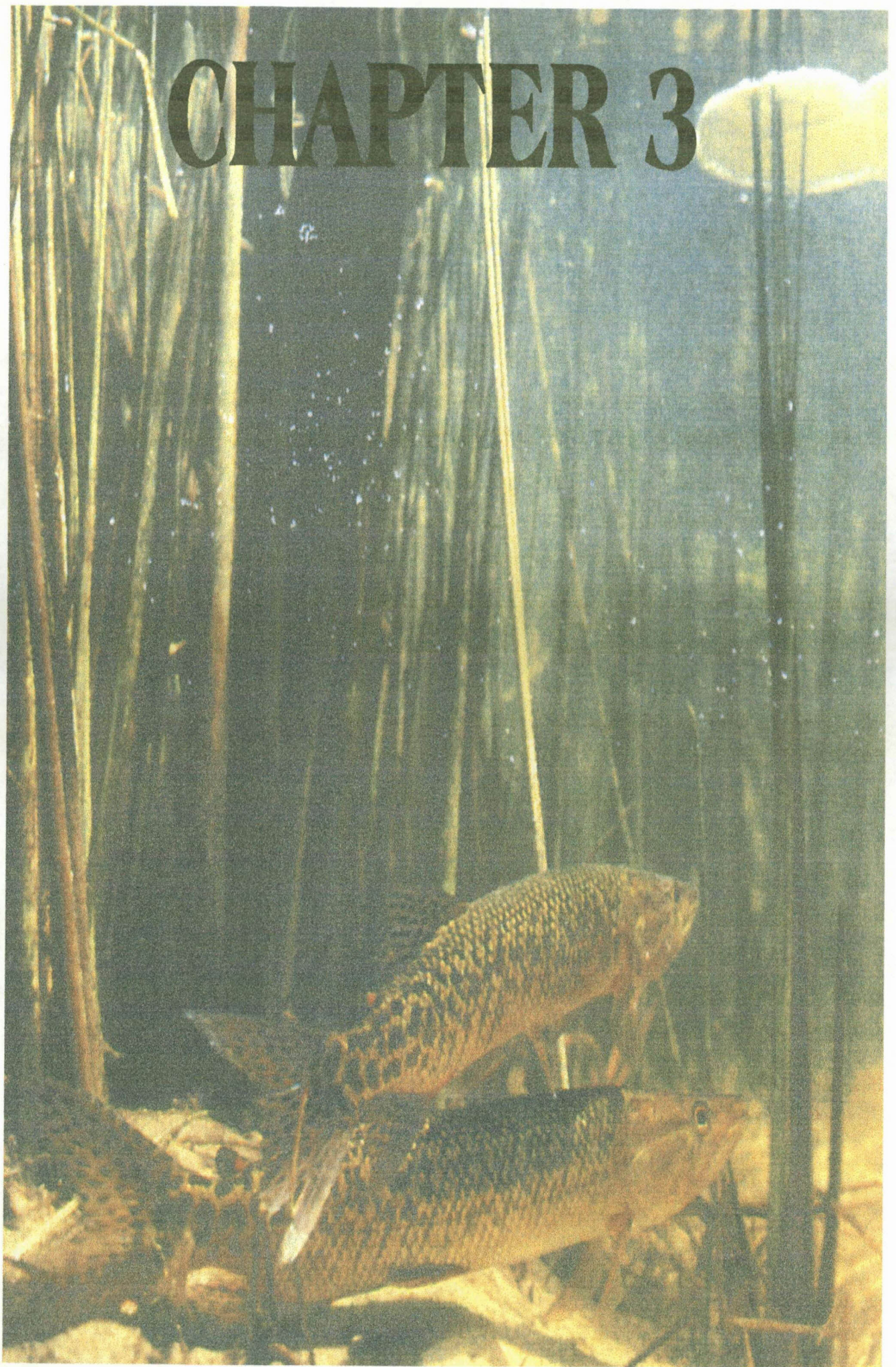
All type material was deposited in the collection of the National Museum, Bloemfontein. All reference material was placed in the collection of Aquatic Parasitology, Department of Zoology and Entomology, University of the Orange Free State.

## **DATA ANALYSIS**

Raw data (Appendix 2-8) was analysed to determine the parasite-host relationships. This data was determined in the field and were processed further in the lab in Bloemfontein. The results of this analysis are represented in chapter 6.



# CHAPTER 3



# THE OKAVANGO CHARACINS

## (PISCES: CHARACIFORMES)

The characins are a large order of strictly freshwater fishes from Africa and South and Central America. These fishes were previously thought to be most closely related to the cypriniform fishes, but it is now more generally accepted that they are more closely related to the catfishes. Jaws and teeth are very notable in the characins with some species, like the tigerfish and piranha, being notorious for their teeth. African characins include four families, nearly 40 genera and over 200 species. Three of the four families, with 12 species, occur in southern Africa (Skelton, 1993).

Representatives from all three southern African families were recorded from the Okavango. One genus *Hemigrammocharax* Pellegrin, 1923, of the family Distichodontidae is represented by two species, namely *Hemigrammocharax machadoi* Poll, 1967 and *Hemigrammocharax multifasciatus* Boulenger, 1923. As very few specimens of *H. machadoi* and *H. multifasciatus* were collected and no branchial monogeneans were recorded from either species, they will not be discussed further in this dissertation. In the Okavango, the family Characidae is represented by four species, namely *Brycinus lateralis* (Boulenger, 1900), *Micralestes acutidens* (Peters, 1852), *Rhabdalestes maunensis* (Fowler, 1935) and *Hydrocynus vittatus* Castelnau, 1861. All of the species of the family Characidae were infested by branchial monogeneans of the genus *Annulotrema* and only *Brycinus lateralis* was infested by branchial monogeneans of the genus *Characidotrema*. The monospecific family Hepsetidae is also present in the Okavango and is represented by *Hepsetus odoe* (Bloch, 1794) which was also infested by branchial monogeneans of the genus *Annulotrema*.

**THE STRIPED ROBBER, *Brycinus lateralis* (Boulenger, 1900)**

PHYLUM: Pisces

ORDER: Characiformes

FAMILY: Characidae

GENUS AND SPECIES: *Brycinus lateralis* (Figure 3.1A)

The genus *Brycinus* is represented by 30 species in Africa of which two species occur in southern Africa, namely *B. imberi* (Peters, 1852) and *B. lateralis*. These fishes according to Skelton (1993) are small to moderately sized shoaling fishes, which resemble miniature tigerfish in appearance and habit. *Brycinus lateralis*, where present, is regarded as being extremely common and has been recorded from the Zambezi System, the Okavango, the Cunene and Buzi Rivers and also from the St. Lucia catchment in KwaZulu-Natal, South Africa. According to Bell-Cross & Minshull (1988), a relict population of *B. lateralis* has also been located in a small stream tributary to the Luapula River in the Zambia-Zaire System.

*Brycinus lateralis* is a slender fish, which can easily be recognized by a prominent, black caudal dash, which extends through the caudal fin. Each jaw has two rows of sharp tricuspid teeth with 16 teeth in the upper jaw and 10 in the lower jaw. The body has a bluish dorsal surface with a silvery mid-body. The fins are tinged with a bright yellow to orange colour, which is more prominent on the adipose and caudal fins than the dorsal, pectoral and pelvic fins. The anal fin of the adult males have extended leading rays resulting in a slightly rounded, concave anal fin. The females and juvenile males on the other hand, have anal fins with straight edges (Bell-Cross & Minshull, 1988; Skelton, 1993).

According to Bell-Cross & Minshull (1988), *B. lateralis* is an omnivorous feeder, which will eat almost any other smaller living organisms, both terrestrial and aquatic, that it encounters. It is a shoaling species which migrates upstream in the rainy season, or when the floods arrive in the Okavango. These migrations are probably correlated with spawning although no confirmatory evidence of this is yet available. According to Skelton (1993), *B. lateralis* is often found occurring together with the dashtail barb, *Barbus poechii* Steindachner, 1911, and the threespot barb, *Barbus trimaculatus* Peters,

1952. The close similarity of these three species suggests mimicry between them. The preferred habitat of *B. lateralis* is usually in slow flowing well-vegetated waters. When occurring sympatrically with *Hydrocynus vittatus*, its distribution range seems to be restricted to the shallower, sandy or marshy areas.

### THE SILVER ROBBER, *Micralestes acutidens* (Peters, 1852)

PHYLUM: Pisces

ORDER: Characiformes

FAMILY: Characidae

GENUS AND SPECIES: *Micralestes acutidens* (Figure 3.1B)

The genus *Micralestes* is represented by small silvery characins with distinctive sharp multicuspid teeth. According to Skelton (1993), this genus is represented by 14 species in Africa of which only one, *Micralestes acutidens*, occurs in southern Africa and is also present in the Okavango System. In southern Africa, *M. acutidens* has been recorded from the Cunene, Okavango, Zambezi and East Coast Rivers south to the Pongola System and is also widespread throughout the Zaire System.

*Micralestes acutidens* can be described as a silvery, minnow sized fish with an olive coloured dorsal surface and a streak along the flanks that darkens after death (Pienaar, 1968). According to Skelton (1993), teeth are present in both the upper and lower jaws, with the upper jaw having two rows of sharp multicuspid teeth with four to six teeth in each row, and the lower jaw having eight outer and two inner teeth. The fins are pale yellow to orange in colour. The dorsal fin has a distinctive black tip and the anal and pelvic fins have white leading edges. The anal fin of the males has expanded leading edges giving them a slightly rounded concave shape. The females on the other hand have a straight or slightly concave anal fin (Pienaar, 1968; Bell-Cross & Minshull, 1988; Kenmuir, 1989; Skelton, 1993).

According to Bell-Cross & Minshull (1988), the silver robber is a hardy little fish, which does not appear to have a preferred habitat and appears to thrive in an extremely diverse range of ecological conditions. Pienaar (1968), however, indicated that it avoids excessively muddy or silt-laden waters.

The diet of *M. acutidens* includes insect larvae, winged insects, zooplankton, eggs and the fry of other fish species. According to Bell-Cross & Minshull (1988), these fish occur in shoals in deepening water downstream from sandbanks where they wait for the current to liberate food items from the sand which drift down to them in the current. *Micralestes acutidens* is one of the few small species that manages to co-exist with the tigerfish, *Hydrocymus vittatus*, although they are heavily preyed upon by the tigerfish, particularly those tigerfish approximately 450 mm in length (Bell-Cross & Minshull, 1988). In the Okavango, the floods initiate an upstream migration of these fish, where they spawn in vegetated areas. According to Pienaar (1968), Kenmuir (1989) and Skelton (1993), *M. acutidens* reaches maturity after a year when it reaches a size of about 40 mm. The longevity of this species is relatively low and the average fish lives for only three years.

### **THE SLENDER ROBBER, *Rhabdalestes maunensis* (Fowler, 1935)**

PHYLUM: Pisces

ORDER: Characiformes

FAMILY: Characidae

GENUS AND SPECIES: *Rhabdalestes maunensis* (Figure 3.1C)

The specific name of *Rhabdalestes maunensis* refers to Maun in Botswana, where this species was discovered in the Thamalakane River in the Okavango System (Bell-Cross & Minshull, 1988). Besides occurring in the Okavango System, this species also occurs in the Upper Zambezi and Cunene Rivers as well as the Kafue System. According to Skelton (1993), a similar, possibly identical species, *Rhabdalestes rhodesiensis* (Ricardo, 1943), occurs in the Zambian Zaire System in Lake Bangweulu and Lake Mweru and also in the Luapula River.

*Rhabdalestes maunensis* can easily be confused with *Micralestes acutidens*, but has a more slender body and lacks the black tip of the dorsal fin. According to Skelton (1993), *R. maunensis* is a translucent fish with a silvery head and belly. A bluish green, iridescent band extends along the body. There is a characteristic black band at the base of the anal fin. The adipose fin is yellow and the caudal fin is yellow with a black edge. The fins are pointed and the anal fin of the males has a slightly concave border whereas

that of the females is flat or slightly convex. *Rhabdalestes maunensis* has a single row of multicuspid teeth in both jaws. The upper jaw has six to eight teeth and the lower jaw has eight (Bell-Cross & Minshull, 1988; Skelton, 1993).

According to Bell-Cross & Minshull (1988), *R. maunensis* is a shoaling species, which inhabits shallow, vegetated marginal and floodplain habitats. *Rhabdalestes maunensis* has been known to migrate up river and onto floodplains during the flood season, where they spawn. Their diet consists of small aquatic insects and other invertebrates.

### **THE TIGERFISH, *Hydrocynus vittatus* Castelnau, 1861**

PHYLUM: Pisces

ORDER: Characiformes

FAMILY: Characidae

GENUS AND SPECIES: *Hydrocynus vittatus* (Figure 3.2A)

*Hydrocynus vittatus*, or literally translated water dog, according to Gaigher (1967), is referred to by quite a few vernacular names throughout its distribution in southern Africa namely; tigerfish, tiervis, ngmeshi (Upper Zambezi and Okavango), maluvali (Gwaai and Shangani rivers), mcheni (Middle and Lower Zambezi), muvanga (Lower Sabi and Lundi rivers), manga (Maphumalanga), shabani and simukuta (Mozambique) as well as uthlangi and uluthlangi (KwaZulu-Natal). *Hydrocynus vittatus* is a predatory characin which has attracted attention for three main reasons, firstly its reputation as a game fish attracts anglers from all over the world (Norman, 1990; Blackman, 1990; Balfour & Balfour, 1997). Secondly, it is considered to be an important commercial species in the commercial fishing industry in some areas of its distribution. Skelton (1993) reports that over 184 tonnes of tigerfish were taken from Lake Kariba in 1977 alone. The third reason for attracting attention is because it is one of the top freshwater predators in Africa.

Skelton (1993) describes *H. vittatus* as having a fusiform body, large head and pointed fins, of which the caudal fin is deeply forked. The head has bony cheeks and strong jaws. Each jaw has a series of eight large, protruding, sharply pointed teeth. Closer examination of the jaws reveals a set of replacement teeth in the tooth sockets, which

replace the functional teeth when lost or broken (Bell-Cross & Minshull, 1988). Under the eyes are vertical adipose sleeves. The juveniles are silvery in colour and the distinctive parallel stripes begin to show when they reach a size of about 50 mm. The adult colour is also striking; the body and head are silvery, with a bluish sheen on the back and a series of parallel longitudinal black stripes on the flanks. Characteristic of this family is the presence of the adipose fin, which is black in colour and is situated posterior to the dorsal fin. The caudal fin varies from a yellow to blood red colour at full intensity, with black trailing edges. The other fins also exhibit this yellow to red colouring especially towards their bases. The tip and trailing edge of the dorsal fin are also black. According to Bell-cross & Minshull (1988), specimens collected over a sandy substrate are slightly paler in colour when compared to those specimens frequenting waters with a rocky or muddy substrate. Males and females are similar in form, but females grow larger than 700 mm forked length (FL) while males only grow to about 500 mm FL.

*Hydrocynus vittatus* occurs in the Okavango, Zambezi and Lowveld reaches of coastal systems south to the Pongola. It also occurs in Zaire, Lake Tanganyika, Rufigi and the large Nilo-Sudanian rivers in North and West Africa. Although tigerfish are still widespread and common in most of these areas, their natural distribution has been limited and their numbers have declined due to pollution, water extraction and obstructions like dams and weirs (Skelton, 1993).

According to Skelton (1993), *H. vittatus* is a shoaling fish and it is only the very large specimens that occur on their own. Tigerfish prefer warm, well-oxygenated waters, mainly in rivers and lakes. Probably the main factor limiting the distribution of *H. vittatus* in a river system is water depth. Tigerfish seldom venture up small tributaries and according to Bell-Cross & Minshull (1988), are never encountered near the headwaters of a river. *Hydrocynus vittatus* is essentially an open water predator frequenting the surface layers of the water where it often falls prey to the African fish eagle, *Haliaeetus vocifer* (Bell-Cross & Minshull, 1988; Skelton, 1993).

Tigerfish are predators throughout their life. According to Kenmuir (1989), the newly hatched fry are pelagic and start feeding on small invertebrates or zooplankton from a length of 5 mm or five days old. During this time, the colourless juveniles develop their scales and teeth. When they reach a size of about 30 mm, they move inshore, where their diet consists of zooplankton, small aquatic insects and other small invertebrates. While in the shallow vegetated areas near the shore, they coexist with a variety of other small fish. Fish predation starts at a length of about 40 mm although this may be earlier. By the time they are adult (about 300 mm), their diet consists almost exclusively of fish.

Tooth development keeps pace with the changing diet of the young fish. Fry of 10-25 mm have conical teeth, which are replaced at a size of 25-35 mm by tricuspid teeth and again by conical teeth when the diet is becoming increasingly piscivorous. Whole sets of teeth are replaced at intervals throughout life, with replacement teeth developing in trenches on the jaws below the functional teeth (Skelton, 1993).

Tigerfish usually take whole fish, but according to Kenmuir (1989), there are numerous accounts where large specimens have bitten off the body of a hooked fish just behind the head. Prey not more than 40 % of the attacking tigerfish's size are taken from the side and swallowed whole, usually head first. Tigerfish feed on whatever prey is most abundant at a particular time, but slender-bodied shoaling fish like robbers (*Brycinus Valenciennes*, 1849 species and *Micralestes* Boulenger, 1899 species), minnows (*Barbus* Cuvier & Cloquet, 1816 species) and the sardine (*Limnothrissa* Regan, 1917 species) are favoured. Odd shaped species like *Synodontis* Cuvier, 1817 species are also sometimes taken (Bell-Cross & Minshull, 1988). Tigerfish are also reported to be cannibalistic and according to Pienaar (1968), the adults of the species are the principal enemy of especially the juveniles. According to Kenmuir (1989), tigerfish are mainly diurnal hunters, hunting by sight. Tigerfish are, however, also caught at night and in turbid waters suggesting that they also locate their prey by other means like smell.

*Hydrocynus vittatus* generally breeds in summer with the adults migrating up or down stream to suitable spawning sites along flooded riverbanks and lakeshores. The fecundity of this species is very high and large females may have as many as 780 000



ova at a time. Males mature at 2-3 years of age and 300-400 mm. Most breeding females exceed 400 mm and are generally older fish than the male group. The ripe yellow eggs vary from 0.8-1.2 mm in diameter and have an adhesive membrane, which, according to Kenmuir (1989), sticks the eggs to the substrate after shedding. The eggs hatch after about 48 hours into larvae of about 3.2 mm long. The newly hatched larvae are carried to the main water body by the receding floodwaters. Juveniles up to 30 mm are pelagic staying near the water surface during the day and descending at night. Larger juveniles (30-60 mm) change habitat to occupy marginal areas with vegetation cover. When they reach a size of about 60-80 mm, the young fish revert to the open waters. Tigerfish attain lengths of 160-200 mm in their first year and up to 300 mm by the end of the second. Although both sexes have equal growth rates, males mature quicker than females and also suffer more mortalities than females, resulting in the majority of the large specimens being female, which may have a longevity of up to 9 years (Skelton, 1993).

### **THE AFRICAN PIKE, *Hepsetus odoe* (Bloch, 1794)**

PHYLUM: Pisces

ORDER: Characiformes

FAMILY: Hepsetidae

GENUS AND SPECIES: *Hepsetus odoe* (Figure 3.2B)

The African pike, *Hepsetus odoe*, is an endemic African freshwater fish that belongs to the monospecific family Hepsetidae within the order characiformes (Merron, *et al.*, 1990). This species is widely distributed throughout west and central Africa, from Senegal southwards to Botswana, where the Okavango forms the southern most limit of its distribution. According to Merron, *et al.* (1990), *H. odoe* from the Okavango Delta prefers the quiet backwaters and is frequently encountered in the quiet, deep water, of channels and lagoons of large floodplains throughout the system.

*Hepsetus odoe* is very seldom encountered in the main stream where its distribution is limited by the threat of predation by the larger tigerfish, *Hydrocynus vittatus* (Bell-Cross & Minshull, 1988; Merron, *et al.*, 1990; Skelton, 1993; Winemiller & Kelso-Winemiller, 1994).

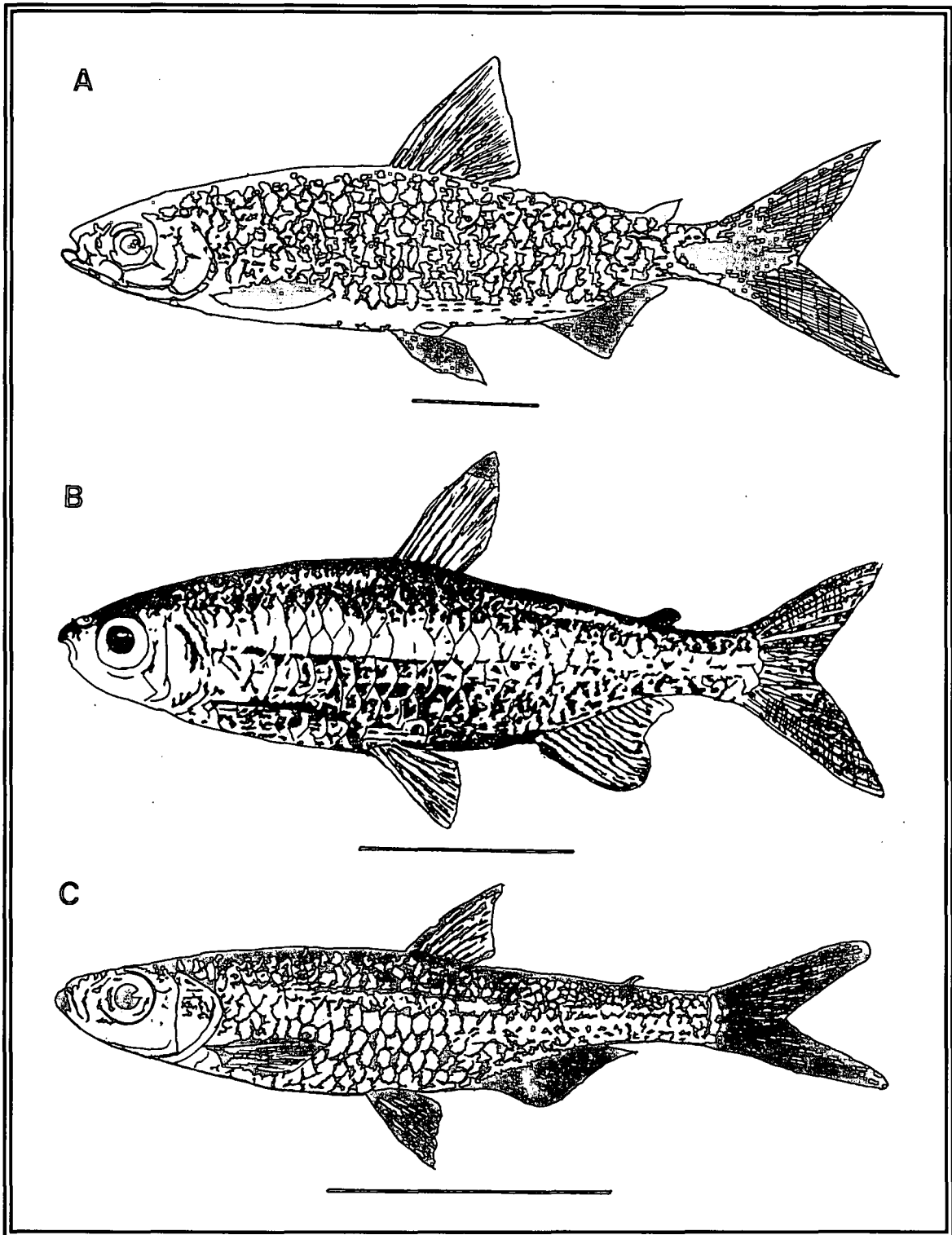
According to Skelton (1993), *H. odoe* is easily recognised by its pointed head with crocodile like jaws and its elongated body. The jaws of the pike have prominent, unevenly protruding, sharp canine teeth. The upper row of teeth are sharply pointed, with large canines present. The lower jaw possesses two rows of teeth, the outer row consisting of large canines interspersed with smaller pointed teeth (Bell-Cross & Minshull, 1988). There are two pairs of dermal flaps on the upper and the lower jaw with those on the bottom jaw being considerably larger than those on the upper jaw (Merron, *et al.*, 1990). The dorsal fin has two unbranched and seven branched rays and, like the anal fin, is set well back on the body with an adipose fin situated midway between the dorsal and the forked caudal fin. Skelton (1993) describes the basic colour of *H. odoe* to be a rich brassy olive with dark brown blotches and cream underparts. The fins have black spots and the adipose fin is orange at its base with a black tip. Three brown bands radiate posteriorly from the eye.

According to Bell-Cross & Minshull (1988), the maximum known weight for *H. odoe* is just over 2 kg, which was recorded from the Kafue River. The pike exhibits sexual dimorphism with the females growing larger than the males. Merron, *et al.* (1990) found that *H. odoe* reaches sexual maturity at a length of approximately 140 mm standard length for males and 160 mm standard length for females.

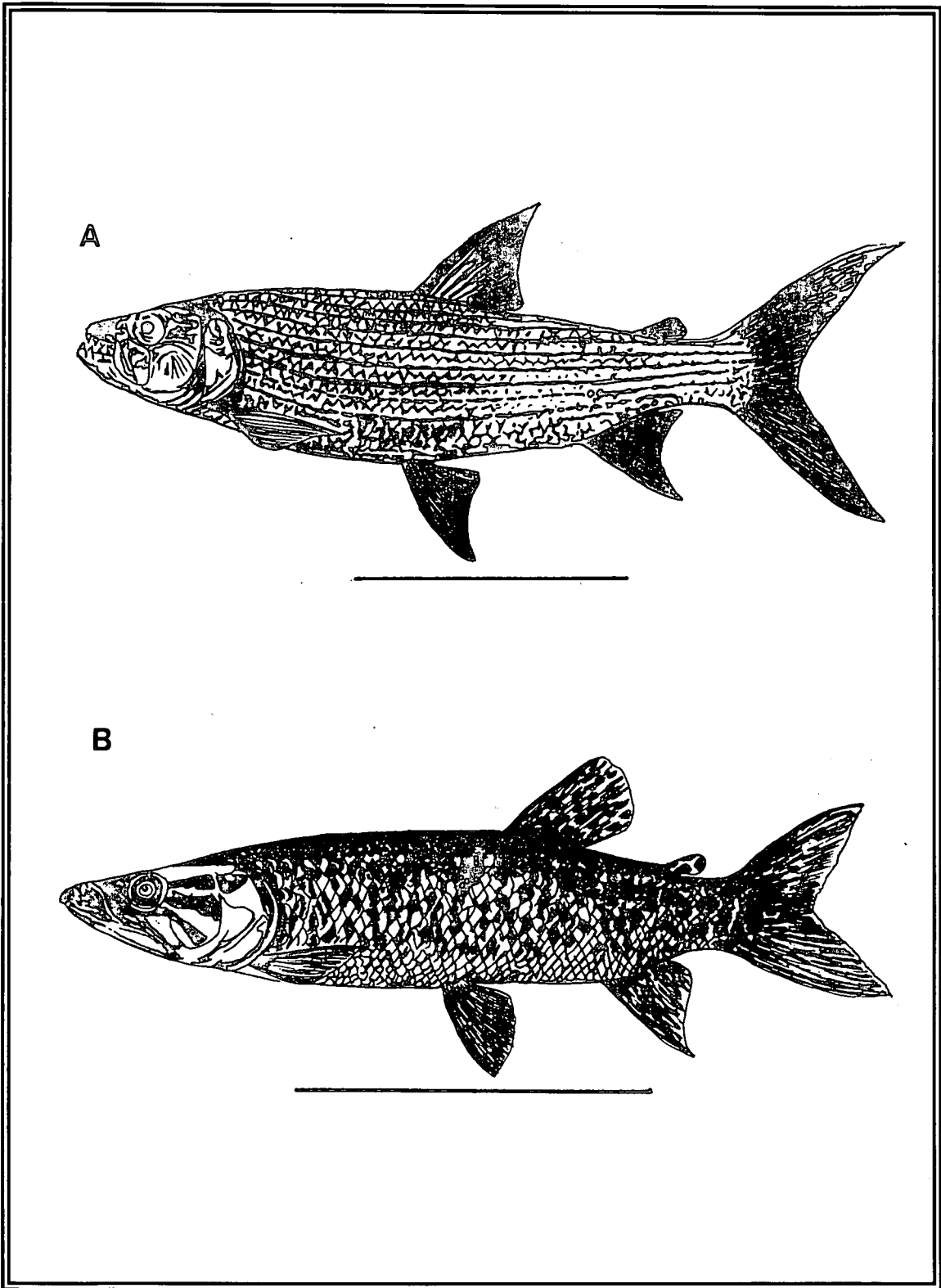
According to Merron, *et al.* (1990), an increase in gonad maturation of the pike, in the Okavango Delta, corresponds directly with the receding floodwaters and increased water temperatures between August and January. Although the arrival of the annual flood probably stimulates gonad development, spawning only occurs once the water has reached a suitable temperature in August. The life cycle of *H. odoe*, according to Merron, *et al.*, (1990), is initiated when the parents pair off and construct a foam nest which is partially built before spawning. The eggs incubate in the nest, which is closely guarded and tended by both parents. Upon hatching, the embryos wriggle their way down through the foam nest and continue their development suspended by cephalic cement glands from the lower row of bubbles of the foam nest or to surrounding vegetation. In about four days these juveniles become increasingly independent of the nest and swim to nearby, submerged stems to which they adhere, again using their cement glands. After the nest disintegrates the juveniles disperse and inhabit well-

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vegetated marginal habitats. Juveniles prey on small invertebrates and fish, whereas the adults eat mostly fish, up to about 30-40 % of their own size. Growth is rapid and the juveniles reach maturity in the second year. Having a relatively short life span of about four to five years, *H. odoe* has the ability to spawn more than once in a season.

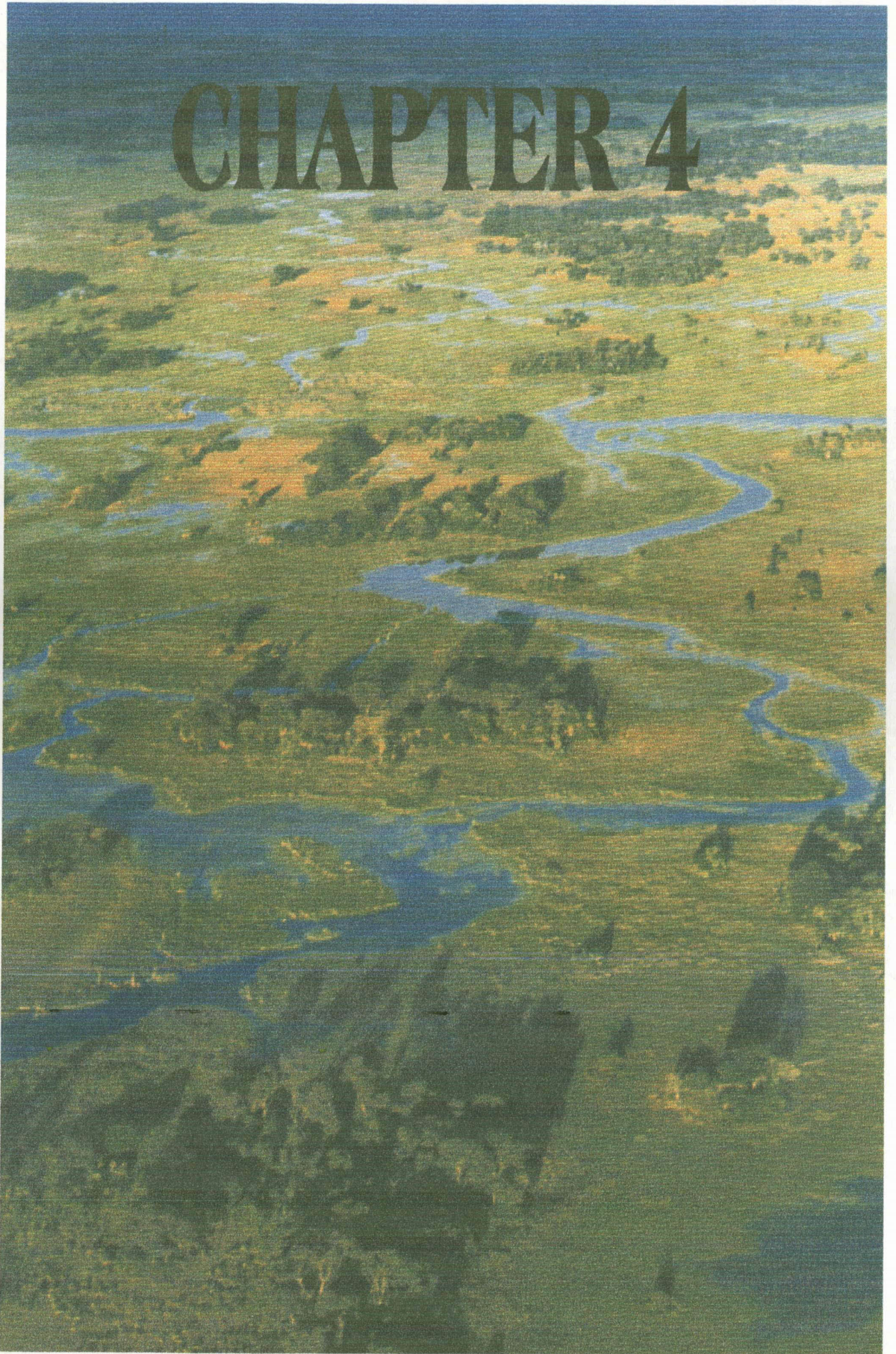


**FIGURE 3.1** Illustration of (A) the striped robber *Brycinus lateralis* (Boulenger, 1900), (B) the sliver robber *Micralestes acutidens* (Peters, 1852) and (C) the slender robber *Rhabdalestes maunensis* (Fowler, 1935) redrawn from Skelton (1993). Scale bar: 20 mm



**FIGURE 3.2** Illustration of (A) the tigerfish *Hydrocynus vittatus* Castelnau, 1861 and (B) the African pike *Hepsetus odbe* (Bloch, 1794) redrawn from Skelton (1993). Scale bar: 200 mm

# CHAPTER 4



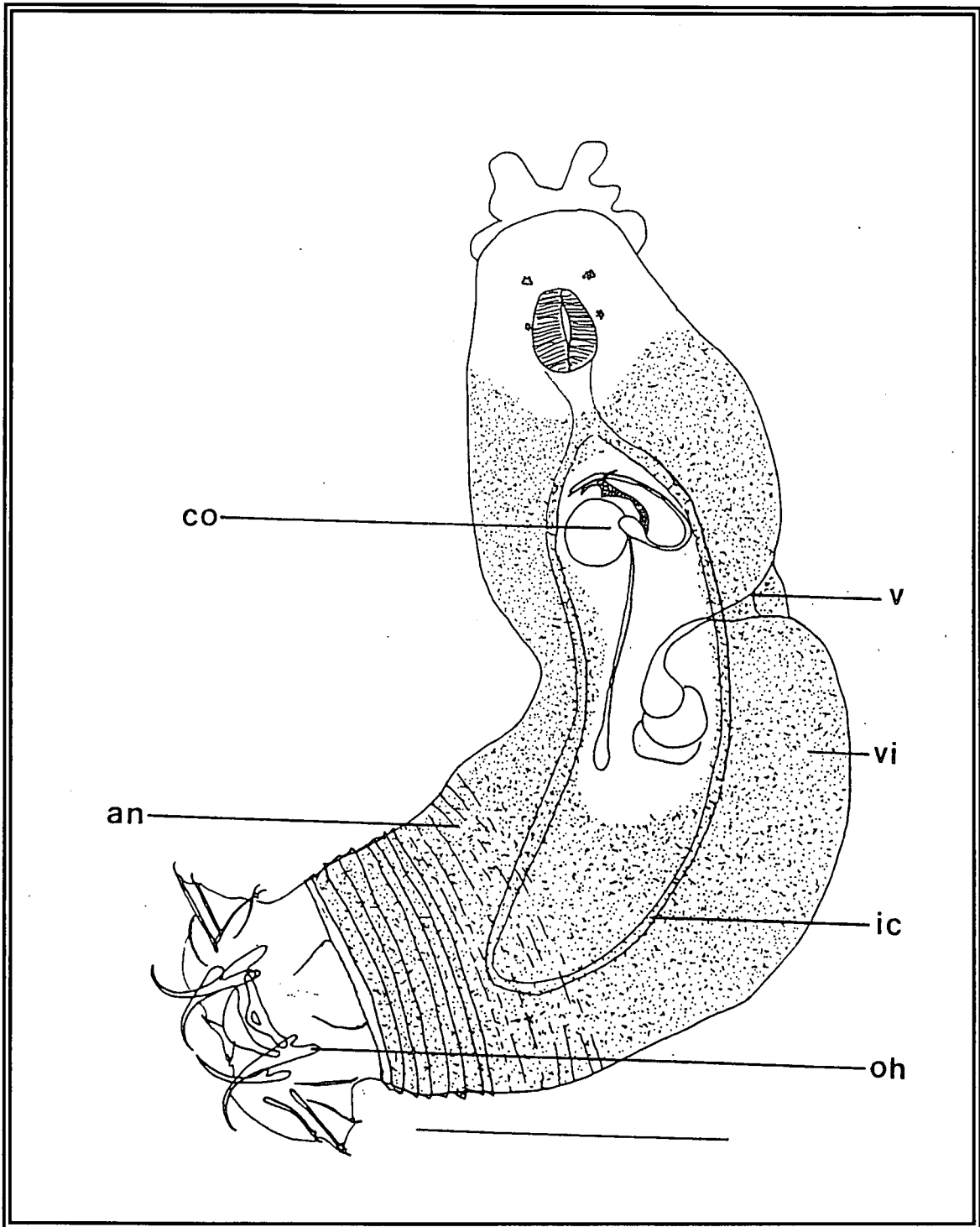
# BRANCHIAL MONOGENEANS OF AFRICAN CHARACINS

## THE GENUS *ANNULOTREMA* PAPERNA & THURSTON, 1969

The genus *Annulotrema* Paperna & Thurston, 1969, are parasites of characiform fish, particularly of the families Characidae and Hepsetidae. This genus is represented by 44 species, which have all been described from Africa. A closely related Neotropical genus, *Annulotrematoides* Kritsky & Boeger, 1995, from South America has similar host preferences and morphological characters. This, according to Kritsky & Boeger (1995), suggests that *Annulotrema* is a relatively old genus sharing a common ancestor with *Annulotrematoides* and hence supporting the hypothesis that the monogenean faunas of the Neotropical and Ethiopian biogeographical regions have ancient evolutionary relationships.

## GENERIC DIAGNOSIS

The genus *Annulotrema* as described by Paperna & Thurston (1969) (Table 4.1 & Figure 4.1), belongs to the family Dactylogyridae and sub-family Ancyrocephalinae. A thick robust annulated cuticle covers the posterior half of the body, which is more prominent in certain species. The opisthaptor can easily be separated from the rest of the body and is divided into two zones. The proximal zone consists of two lateral bunches of hooklets with seven in each bunch. The distal zone consists of two pairs of anchors, the dorsal pair and the lateral pair, and two transverse bars. The anchor shaft is usually delicate and elongated, while the spike is usually very small. The roots of the anchors are solid and well delineated from the rest of the anchor shaft. An additional small process is located between the inner and outer roots, this process may develop into an additional median root in some species or may be vestigial in other species. Four eyespots are usually present. The intestinal caeca are fused posteriorly. The copulatory organ consists of a penis (cirrus), an accessory piece, a seminal vesicle and a prostate gland. According to Paperna & Thurston (1969), the vagina opens on the sinistral side of the body. Kritsky & Boeger (1995), found that in some specimens, the vagina opened dextrally. A seminal vesicle, as well as two vitelline vesicles are present. The testis is located ventral or slightly posterior-ventral to the ovary.



**FIGURE 4.1** Illustration of the morphological features of *Annulotrema* Paperna & Thurston, 1969 species. (co- Copulatory organ, an- Tegumental annulations, v- Vagina, vi- Vitellaria, ic- Intestinal caecum, oh- Opisthaptor.) Scale bar: 100  $\mu$ m



**TABLE 4.1 Summary of the taxonomic characters of the genus *Annulotrema* Paperna & Thurston, 1969**

<i>Annulotrema</i> Paperna & Thurston, 1969	
BODY	<ul style="list-style-type: none"> <li>• Posterior half covered by thick annulated cuticle</li> </ul>
HAPTOR	<ul style="list-style-type: none"> <li>• Well delineated from body and divided into 2 zones</li> <li>• Proximal zone has 2 lateral bunches of large hooklets, 7 in each bunch</li> <li>• Posterior zone has 2 pairs of anchors and 2 bars</li> <li>• Anchor shaft usually elongated and delicate, while the spike is very small</li> <li>• Roots of anchors very solid and well delineated from anchor shaft</li> <li>• An additional small process located between inner and outer roots may develop into additional root in some species</li> </ul>
DIGESTIVE TRACT	<ul style="list-style-type: none"> <li>• Intestinal cruri united posteriorly</li> </ul>
FEMALE REPRODUCTIVE SYSTEM	<ul style="list-style-type: none"> <li>• Vagina opening sinistral</li> <li>• Seminal receptacle and 2 lateral vitelline vesicles present</li> </ul>
MALE REPRODUCTIVE SYSTEM	<ul style="list-style-type: none"> <li>• Copulatory organ consists of cirrus, an accessory piece, seminal vesicle and a prostate gland</li> <li>• Testis located ventral or slightly posterior-ventral to the ovary</li> </ul>
GENERAL	<ul style="list-style-type: none"> <li>• 4 eyes</li> <li>• Parasites of the fish of the family Characidae</li> <li>• Type species: <i>Annulotrema gravis</i></li> </ul>

## HISTORY OF THE GENUS *ANNULOTREMA*

Paperna & Thurston (1969), created the genus *Annulotrema* to accommodate three morphologically similar species of ancycrocephaline monogeneans collected from the gills of *Alestes baremoze* (de Joannis, 1835), *Brycinus nurse* (Rüppell, 1832) and *Hepsetus odoe*. In 1969, Price, Peebles & Bamford described a new *Cleidodiscus* Mueller, 1934 species from the tigerfish, *Hydrocynus vittatus*. According to Paperna (1969) this species was later to be placed into the genus *Annulotrema* based on the similarity of the structure of its haptor hooks of this species and those of *Annulotrema armorata* Paperna 1969 collected from *Hydrocynus forskalii* (Cuvier, 1819). During the same year, Paperna described five new species from this genus from the Volta Basin and south Ghana; namely *Annulotrema armorata* from *Hydrocynus forskalii*, *A. curvipenis* Paperna, 1969 and *A. longipenis* Paperna, 1969 from *Alestes baremoze*, *Annulotrema robusta* Paperna, 1969 from *Brycinus leuciscus* (Günther, 1864) and *A. spiropenis* Paperna, 1969 from *Brycinus nurse*.

Thurston (1970) also recorded three already known species namely, *A. armorata*, *A. curvipenis*, *A. spiropenis* & *A. elongata* Paperna, 1969, from Uganda.

In 1973, Paperna published a preliminary report of new species of Monogenea collected from African freshwater fish, which was just a list of their taxonomic characters without sketches. In this report he described 13 new *Annulotrema* species. The complete descriptions with the sketches of these 13 species as well as two new sub-species from the Ruahae River in Tanzania were published in Paperna (1979).

In 1988, Birgi did some work in Cameroon where he described a further 15 species. Ergens (1988) recorded four *Annulotrema* species from Egypt including three known and one new species, to which he did not allocate a specific name, but only placed it in the genus *Annulotrema*. Guegan, *et al.* (1988), described *Annulotrema pikoides* Guegan, Lambert & Birgi, 1988 from tigerfish in Mali and drew a comparison between *A. pikoides*, *A. pikei* (Price, Peebles & Bamford, 1969) and *A. pikei ruahae* Paperna, 1979.

Up to 1997, *A. hepseti*, was the only species of *Annulotrema* that was described from a host which was not of the family Characidae. N'Douba, *et al.* (1997) described two new species of *Annulotrema* and redescribed *A. hepseti* from *Hepsetus odoe* collected from the Ayamé Retention Lake, Ivory Coast.

There are currently 43 known species in this genus as well as the one described by Ergens (1988). Table 4.2 summarises these species, their locations and the hosts from where these monogeneans were described.

**TABLE 4.2 Checklist of all the currently known species of the genus *Annulotrema* Paperna & Thurston, 1969, their hosts and distribution**

SPECIES	SYNONYM	HOST	DISTRIB
<i>A. alberti</i> Paperna, 1973		<i>Brycinus macrolepidotus</i>	Uganda
<i>A. alestesimberi</i> Paperna, 1973		<i>Brycinus imberi</i>	Tanzania
<i>A. alestesnursi</i> Paperna, 1973		<i>Brycinus nurse</i>	Uganda, Ghana, Egypt
<i>A. allogravis</i> Paperna, 1973		<i>Brycinus imberi</i>	Tanzania
<i>A. amieti</i> Birgi, 1988		<i>Hemigrammopetersius pulcher</i> <i>Phenacogrammus major</i>	Cameroon
<i>A. armorata</i> Paperna, 1969		<i>Hydrocynus forskalii</i>	Uganda, Ghana
<i>A. biaensis</i> N'Douba, Pariselle & Euze,t 1997		<i>Hepsetus odoe</i>	Ivory Coast
<i>A. bilongi</i> Birgi, 1988		<i>Neolebias trewavasae</i>	Cameroon
<i>A. bouixi</i> Birgi, 1988		<i>Brycinus kingsleyae</i>	Cameroon
<i>A. combesi</i> Birgi, 1988		<i>Brycinus kingsleyae</i>	Cameroon
<i>A. cryptophallus</i> Paperna, 1973		<i>Hydrocynus forskalii</i>	Uganda
<i>A. curvipenis</i> Paperna, 1969		<i>Alestes baremose</i> , <i>Hydrocynus forskalii</i>	Ghana, Uganda
<i>A. delta</i> Paperna, 1973		<i>Brycinus nurse</i>	Uganda, Ghana, Egypt
<i>A. edeensis</i> Birgi, 1988		<i>Micralestes sp.</i>	Cameroon
<i>A. elongata</i> Paperna & Thurston, 1969		<i>Alestes baremose</i> , <i>Alestes dentex</i> , <i>Brycinus macrolepidotus</i>	Uganda, Ghana
<i>A. endjami</i> Birgi, 1988		<i>Neolebias trewavasae</i>	Cameroon
<i>A. fomenai</i> Birgi, 1988		<i>Neolebias trewavasae</i>	Cameroon
<i>A. gabrioni</i> Birgi, 1988		<i>Hemigrammopetersius pulcher</i> , <i>Phenacogrammus major</i>	Cameroon
<i>A. gracilis</i> (Wedl, 1861)	<i>Dactylogyrus gracilis</i> , <i>Neodactylogyrus gracilis</i> (Price, 1938)	<i>Hydrocynus forskalii</i>	Egypt
<i>A. gravis</i> Paperna & Thurston, 1969		<i>Brycinus jacksoni</i> , <i>Brycinus nurse</i>	Uganda, Kenya, Ghana
<i>A. helicocirra</i> Paperna, 1973		<i>Brycinus macrolepidotus</i>	Uganda
<i>A. hepseti</i> Paperna & Thurston, 1969		<i>Hepsetus odoe</i>	Ghana, Cameroon, Ivory Coast
<i>A. hydrocynusi</i> Paperna, 1973		<i>Hydrocynus forskalii</i>	Uganda
<i>A. kribiensis</i> Birgi, 1988		<i>Brycinus longipinnis</i>	Cameroon
<i>A. lamberti</i> Birgi, 1988		<i>Brycinus longipinnis</i>	Cameroon
<i>A. longipenis</i> Paperna, 1969		<i>Brycinus macrolepidotus</i> , <i>Alestes baremose</i> , <i>Hydrocynus forskalii</i>	Ghana, Uganda

TABLE 4.2 continued

<i>A. macropenis</i> N'Douba, Pariselle & Euzet, 1997		<i>Hepsetus odoe</i>	Ivory coast
<i>A. magna</i> Paperna, 1973		<i>Hydrocynus vittatus</i>	Tanzania
<i>A. magnihamula</i> Paperna, 1973		<i>Hydrocynus forskalii</i>	Uganda
<i>A. maillardi</i> Birgi, 1988		<i>Brycinus kingsleyae</i>	Cameroon
<i>A. moanko</i> Birgi, 1988		<i>Brycinus longipinnis</i>	Cameroon
<i>A. nannaethiopsis</i> Birgi, 1988		<i>Nannaethiops unitaeniatus</i>	Cameroon
<i>A. nili</i> Paperna, 1973		<i>Hydrocynus forskalii</i>	Uganda
<i>A. nili ruahae</i> Paperna, 1979		<i>Hydrocynus forskalii</i> , <i>Hydrocynus vittatus</i>	Tanzania
<i>A. noyongensis</i> Birgi, 1988		<i>Brycinus kingsleyae</i>	Cameroon
<i>A. pikei</i> (Price, Peebles & Bamford, 1969)	<i>Cleidodiscus pikei</i> (Price Peebles & Bamford, 1969), <i>A. armorata</i> (Paperna, 1969)	<i>Hydrocynus vittatus</i>	Ghana, Uganda, Natal, Pongola system, South Africa
<i>A. pikei ruahae</i> Paperna, 1979		<i>Hydrocynus vittatus</i>	Tanzania
<i>A. pikoides</i> Guegan, Lambert & Birgi, 1988		<i>Hydrocynus vittatus</i>	Mali
<i>A. robusta</i> Paperna, 1969		<i>Brycinus leucisus</i>	Ghana
<i>A. ruahae</i> Paperna, 1973		<i>Hydrocynus vittatus</i>	Tanzania
<i>A. sangmelinensis</i> Birgi, 1988		<i>Micralestes humulis</i>	Cameroon
<i>A. spiroopenis</i> Paperna, 1969		<i>Brycinus nurse</i> , <i>Hydrocynus forskalii</i>	Ghana, Uganda, Egypt
<i>A. tenuicirra</i> Paperna, 1973		<i>Brycinus macrolepidotus</i>	Uganda
<i>Annulotrema</i> sp. Ergens, 1988		<i>Brycinus nurse</i>	Egypt

### DISTRIBUTION OF SPECIES OF THE GENUS *ANNULOTREMA*

The species diversity and geographical distribution (Figure 4.2) of the genus *Annulotrema* is inaccurate as the records of species represented from this genus are localised and are representative of a few scattered parasitological surveys conducted randomly throughout Africa. A large section of central Africa is not represented in the distribution range of the genus *Annulotrema* due to the total lack of research conducted in these areas. The species diversity of this genus is also not a true indication as the host range of the genus *Annulotrema* is limited to 17 species of the family Characidae and the one species of the family Hepsetidae. The localities from where the various species of *Annulotrema* have been recorded are scattered throughout the distribution ranges, proposed by Skelton (1988), of the two host families.

According to Skelton (1988) the classification of certain characin genera and species have been revised but are still not stable. The classification of the fish hosts referred to are according to Skelton (pers. comm.). Table 4.3 illustrates the occurrence of the 44 *Annulotrema* species within the 18 host species. The two fish hosting the most *Annulotrema* species are *Hydrocynus vittatus*, which is host to six species, and *H. forskalii*, which is host to ten. The reason for the recorded abundance of these parasites among these two host species is probably the accessibility of the hosts as well as their extensive distribution and abundance. According to Skelton (1988) representatives of the genus *Hydrocynus* Cuvier 1817 occur practically throughout the range of the family Characidae in Africa, with *H. forskalii* occurring predominantly in the north of the distribution of the genus and *H. vittatus* predominantly in the south.

*Hepsetus odoe* only has three *Annulotrema* species recorded from it, which can be attributed to the limited amount of available data within its distribution range. According to N'Douba, *et al.* (1997) *Annulotrema hepseti* Paperna & Thurston, 1969 has been recorded from Ghana, Nigeria, Chad and Cameroon but *A. biaensis* N'Douba, Pariselle & Euzet, 1997 and *A. macropenis* N'Douba, Pariselle & Euzet, 1997 have only been recorded from Cameroon by N'Douba, *et al.* (1997). According to N'Douba, *et al.* (1997) the low diversity of *Annulotrema* species can probably be explained by the peculiar morphology of the cirrus which led to confusion between species. This type of narrowly spiralled cirrus is also observed in species of the genus *Enterogyrus* Paperna, 1963 (N'Douba, *et al.*, 1997).

Twenty species of *Annulotrema* have been recorded from seven species of the genus *Brycinus* Valenciennes, 1849. Of these only *Annulotrema gravis* Paperna & Thurston, 1969 was recorded from more than one host in the genus *Brycinus*. However, *Annulotrema elongata*, *A. longipenis* and *A. spiopenis* were recorded from species of *Brycinus* as well as from *Alestes* species and *Hydrocynus* species. *Brycinus macrolepidotus* (Valenciennes, 1849) and *B. nurse* are host to five species of *Annulotrema* each. The apparent parasite diversity infesting the gills of these two as opposed to the other *Brycinus* species may be due to their distribution and accessibility and is probably an inaccurate indication of the diversity of the representatives of the genus *Annulotrema* infesting members of the order Characiformes as a whole.

The geographical distribution of the genus *Annulotrema* in Africa is widespread (Figure 4.2) with species being recorded from Egypt in the north to South Africa in the south and from Mali in the west to Tanzania in the east. The species diversity of the genus *Annulotrema* within the various countries of its distribution once again is dependent on the amount of parasitological research conducted there, as well as the diversity and distribution of the host species within these countries.

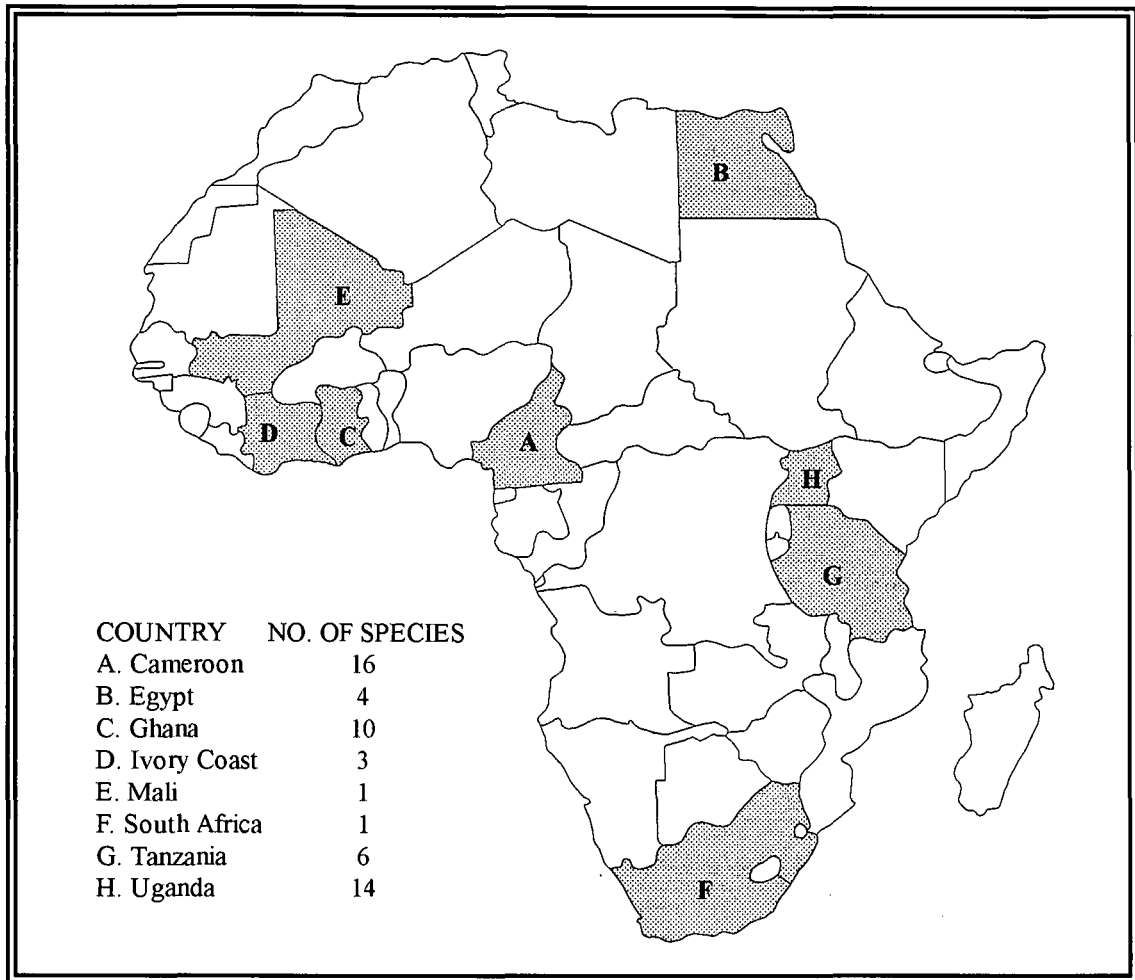
Cameroon, which has 16 *Annulotrema* species, has the highest number of species as a result of the extensive work done there by Birgi (1988) while countries like Ghana, which has 10, and Uganda, which has 14, have high numbers of species in this genus due to the works of Paperna & Thurston (1969), Paperna (1969, 1973, 1979) and Thurston (1970).

Only one species of the genus *Annulotrema* has been described from southern Africa from the tigerfish, *Hydrocymus vittatus*. Southern Africa, however, has at least seven characin species, which have not been studied. It is clear that further data from African characin fish is required for a better understanding of the number of species in, as well as the distribution, of the genus *Annulotrema*.

**TABLE 4.3** Fish hosts of species of the genus *Annulotrema* Paperna and Thurston, 1969

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>A. alberti</i>								•										
<i>A. alestesimberi</i>			•															
<i>A. alestesnursi</i>									•									
<i>A. allogravis</i>			•															
<i>A. amieti</i>										•								•
<i>A. armorata</i>												•						
<i>A. biaensis</i>											•							
<i>A. bilongi</i>																	•	
<i>A. bouixi</i>					•													
<i>A. combesi</i>					•													
<i>A. cryptophallus</i>												•						
<i>A. curvipenis</i>	•											•						
<i>A. delta</i>									•									
<i>A. edeensis</i>														•				
<i>A. elongata</i>	•	•						•										
<i>A. endjami</i>																	•	
<i>A. fomenai</i>																	•	
<i>A. gabrioni</i>										•								
<i>A. gracilis</i>												•						
<i>A. gravis</i>				•					•									
<i>A. helicocirra</i>								•										
<i>A. hepseti</i>											•							
<i>A. hydrocynusi</i>												•						
<i>A. kribiensis</i>							•											
<i>A. lamberti</i>							•											
<i>A. longipenis</i>	•							•				•	•					
<i>A. macropenis</i>											•							
<i>A. magna</i>													•					
<i>A. magnihamula</i>												•						
<i>A. maillardi</i>					•													
<i>A. moanko</i>							•											
<i>A. nannaethiopsis</i>																•		
<i>A. nili</i>												•	•					
<i>A. nili ruahae</i>												•	•					
<i>A. noyongensis</i>					•													
<i>A. pikei</i>												•	•					
<i>A. pikei ruahae</i>													•					
<i>A. pikoides</i>													•					
<i>A. robusta</i>						•												
<i>A. ruahae</i>													•					
<i>A. sangmelinensis</i>															•			
<i>A. spiropenis</i>									•			•						
<i>A. tenuicirra</i>								•										
<i>Annulotrema</i> sp.									•									

1. *Alestes baremose* 2. *Alestes dentex* 3. *Brycinus imberi* 4. *Brycinus jacksoni* 5. *Brycinus kingsleyae* 6. *Brycinus leuciscus* 7. *Brycinus longipinnis* 8. *Brycinus macrolepidotus* 9. *Brycinus nurse* 10. *Hemigrammopetersius pulcher* 11. *Hepsetus odoe* 12. *Hydrocynus forskalii* 13. *Hydrocynus vittatus* 14. *Micralestes* species 15. *Micralestes humulis* 16. *Nannaethiops unitaeniatus* 17. *Neolebias trewavasae* 18. *Phenacogrammus major*



**FIGURE 4.2** Distribution of species of the genus *Annulotrema* Paperna & Thurston, 1969 in Africa indicating the number of species recorded from each country.

## REVIEW OF SPECIES

The reviews of the following species of the genus *Annulotrema* are based on an examination of their original descriptions. These descriptions have been summarised and edited to establish uniformity in the terminology used. All measurements are reproduced exactly as they appeared in their original form and are expressed in micrometers.



*Annulotrema alberti* Paperna, 1973

**Host and Locality:** *Brycinus macrolepidotus*, Lake Albert, Uganda.

**Description and Measurements:** (according to Paperna, 1979). Total length 260-360, width 80-120. Dorsal anchors 32-40, inner root 10-16, outer root 2-5, shaft 24-28, tip 7-10. Dorsal bar 21-27, dorsal bar width 2-3. Ventral anchors 32-37, inner root 9-15, outer root 1-3, shaft 24-29, tip 7-11. Ventral bar 20-27, ventral bar width 2-4. Central hooklets 10-12, marginal hooklets 16-23 (Figure 4.3A). Cirrus 72-90, accessory piece 19-22 (Figure 4.3B).

*Annulotrema alestesimberi* Paperna, 1973

**Host and Locality:** *Brycinus imberi*, Ruahae River, Tanzania.

**Description and Measurements:** (according to Paperna, 1979). Small species, total length 300-400, width 70-100. Large anchors and hooklets. Dorsal anchors 51-59, inner root 18-20, outer root 6-11, shaft 34-39, tip 4-6. Dorsal bar 27-32, dorsal bar width 12. Ventral anchors 46-53, inner root 9-12, outer root 3-6, shaft 40-45, tip 3-5. Ventral bar 29-32. Central hooklets 26-27, marginal hooklets 25-40 (Figure 4.3C). Cirrus 19-20, small thin tube coiled three or four times. Accessory piece 12-18, ends with two or three curved hooks (Figure 4.3D). Vagina tubiform and sclerotised.

*Annulotrema aletesnursi* Paperna, 1973

**Host and Locality:** *Brycinus nurse*, Lake Albert, Uganda, Volta Lake, Ghana, Egypt.

**Description and Measurements:** (according to Paperna, 1979) Small to medium worms, total length 310-500, width 100-150. Mature specimens have large anchors and hooklets. Dorsal anchors 49-59, inner root 20-22, outer root 6-10, shaft 32-35, tip 2-3. Dorsal bar 30-36, dorsal bar width 4-5. Ventral anchors 47-53, inner root 10-18, outer root 7-11, shaft 40-42, tip 2-4. Ventral bar 30-36, ventral bar width 4-7. Central hooklets 22-28, marginal hooklets 29-45, distal hooklets 13-14 (Figure 4.3E). Cirrus 75-80, tubiform, long and looped. Accessory piece 16-25 attached to cirrus funnel and distally forms complex structure with branching spikes (Figure 4.3F). Vagina non-sclerotised.

*Annulotrema allogravis* Paperna, 1973

**Host and Locality:** *Brycinus imberi*, Ruahae River, Tanzania.

**Description and Measurements:** (according to Paperna, 1979). Small worms, total length 250-300, width 50-70. Medium sized delicate anchors with elongated shafts. Dorsal anchors 43-56, inner root 17-23, outer root 5-8, tip 5-6. Dorsal bar V-shaped rather than crescent, dorsal bar 33-41. Ventral anchors 34-44, inner root 6-9, outer root 2-5, shaft 32-43, tip 3-4. Ventral bar 28-33. Central hooklets 18-20, marginal hooklets 23-33 (Figure 4.4A). Cirrus 67-80, tubiform, thick and large. Accessory piece 25-26, bifid or trifid (Figure 4.4B). Vagina non-sclerotised.

*Annulotrema amieti* Birgi, 1988

**Host and Locality:** *Hemigrammopetersius pulcher*, *Phenacogrammus major*, Youande, Sangmélina, Cameroon.

**Description and Measurements:** (according to Birgi, 1988). Total length 400-450, width 120. Dorsal anchors 30-33, inner root 8-10, outer root 6-8, shaft 25-27, tip 4-5. Dorsal bar 30, dorsal bar width 5. Ventral anchors 35-40, inner root 8-12, outer root 5-7, shaft 30-34, tip 5. Ventral bar 30, ventral bar width 5. Marginal hooklets; I= 12-16, II= 12-15, III-IV= 20-25, V= 26-32, VI= 22, VII= 22-28 (Figure 4.4C). Cirrus 50-60 (Figure 4.4D). Vagina sclerotised 50-60.

*Annulotrema armorata* Paperna, 1969

**Host and Locality:** *Hydrocymus forskalii*, Volta Lake at the Black and White Volta confluence, Ghana, Lake Albert, Uganda.

**Description and Measurements:** (according to Paperna, 1969). Total length 500-700, width 150-200. Body armoured with annulated heavy cuticle. Proximal anchors 80-90, inner root 12-15, outer root 7-8, median root vestigial, shaft 60-70, the attached bar 40-50. Hooklets 20-30 (Figure 4.4E). Cirrus, 40, delicate, tubiform, accessory piece elongated, delicate, distally bifurcated, copulatory organ complex is embedded in muscular sheet (Figure 4.4F).

*Annulotrema biaensis* N'Douba, Pariselle & Euzet, 1997

**Host and Locality:** *Hepsetus odoe*, Ayamé Retention Lake, Ivory Coast.

**Description and Measurements:** (according to N'Douba, *et al.*, 1997). Total length 437 (279-586), width 92 (56-122). Pharynx width 30 (19-47). Dorsal anchors 46 (39-55), inner root 18 (14-25), outer root 5 (2-8), shaft 31 (28-37), tip 3 (2-4), dorsal bar 34 (26-42), dorsal bar width 5 (3-9). Ventral anchors 44 (38-52), inner root 18 (14-23), outer root 5 (3-8), shaft 38 (34-45), tip 4 (3-5), ventral bar 38 (32-48), ventral bar width 5 (4-6). Hooklets; I= 19 (15-21), II= 17 (14-22), III= 24 (22-28), IV= 26 (24-29), V= 28 (25-33), VI= 26 (23-30), VII= 22 (18-25) (Figure 4.5A). Male copulatory apparatus consists of spiralled penis 75 (61-90), number of spirals 28 (25-29). Accessory piece 13 (8-16) surrounds distal end of the penis (Figure 4.5B). Vagina, sclerotised, 20 (11-30), vagina diameter 2 $\mu$  (1-2).

*Annulotrema bilongi* Birgi, 1988

**Host and Locality:** Nkolya, Cameroon.

**Description and Measurements:** (according to Birgi, 1988). Dorsal anchors 16-18, inner root 8-10, outer root 3-4, shaft 10-12, tip 5-6. Dorsal bar 20-25, dorsal bar width 1-2. Ventral anchors 15-18, inner root 8-10, outer root 3-4, shaft 10-13, tip 4-5. Ventral bar 25-30, ventral bar width 2. Marginal hooklets; I= 15-17, II= 12-16, III-IV= 15-20, V= 19-22, VI= 15-18, VII= 13-16 (Figure 4.5C). Cirrus 15-18 (Figure 4.5D).

*Annulotrema bouixi* Birgi, 1988

**Host and Locality:** *Brycinus kingsleyae*, Cameroon

**Description and Measurements:** (according to Birgi, 1988). Dorsal anchor 30-32, inner root 5-6, outer root 12-14, shaft 20-23, tip 3-4, dorsal bar 20-28. Ventral anchors 24-32, inner root 5-7, outer root 4-5, shaft 25-30, tip 2, ventral bar 24. Marginal hooklets; I= 18, II= 10, III-IV= 20-22, V= 27-28, VI= 22, VII= 18-19 (Figure 4.5E). Cirrus 18-20, accessory piece 5 (Figure 4.5F).

*Annulotrema combesi* Birgi, 1988

**Host and Locality:** *Brycinus kingsleyae*, Cameroon

**Description and Measurements:** (according to Birgi, 1988). Total length 450. Dorsal anchors 47-50, inner root 22-25, outer root 7-8, shaft 30-33, tip 5, dorsal bar 65, dorsal bar width 5. Ventral anchors 45.5, inner root 12, outer root 5, shaft 32-37, tip 5, ventral bar 20, ventral bar width 5. Marginal hooklets; I= 50, II= 20, III-IV= 50, V-VI-VII= 60-70 (Figure 4.6A). Cirrus 55, accessory piece 20 (Figure 4.6B).

*Annulotrema cryptophallus* Paperna, 1973

**Host and Locality:** *Hydrocynus forskalii*, Butiaba, Lake Albert, Uganda.

**Description and Measurements:** (according to Paperna, 1979). Total length 280, width 80. Dorsal anchors 38-39, inner root 5-6, shaft 24-25, tip 6-8, dorsal bar 31. Ventral anchors 43-45, inner root 9-10, outer root 6-7, median root vestigial, shaft 37-40, tip 4-6, ventral bar 38. Central hooklets 13-13, marginal hooklets 28-29 (Figure 4.6C). Described from immature specimens, which already contained ovary and testis. Cirrus tubiform, coiled twice or thrice with cup shaped funnel, accessory piece absent (Figure 4.6D). Vaginal sclerotisation vestigial.

*Annulotrema curvipenis* Paperna, 1969

**Host and Locality:** *Alestes baremoze*, Volta Lake at Yeji, Ghana, *Hydrocynus forskalii*, Lake Albert, Uganda.

**Description and Measurements:** (according to Paperna, 1969). Total length 300-400, width 50-70, cuticle thin, annulation not too distinct. Dorsal anchors 50-55, inner root 15-20, outer root 5, no median root, shaft 20-25; dorsal bar 30-35. Ventral anchors 40-50, inner root 10-12, outer root 8-10, no median root, shaft 25-30, ventral bar 30-35, median part 9 wide and perforated. Hooklets 18-22 (Figure 4.6E). Cirrus 40-50, tubiform, accessory piece 20, bifurcated distally (Figure 4.6F). Vaginal pore with wide sclerotinoid plate.

*Annulotrema delta* Paperna, 1973

**Host and Locality:** *Brycinus nurse*, Lake Albert, Uganda, Volta Lake, Ghana, Egypt.

**Description and Measurements:** (according to Paperna 1979). Small worms, total length 250-320, width 60-100. Anchors small. Dorsal anchors 36-42, inner root 11-12,

outer root 6-10, shaft 24-32, tip 1-2. Dorsal bar 25-30. Ventral anchors 31-36, inner root 7-10, outer root 3-5, shaft 30-33, tip 1-2. Ventral bar 28-31, resembles Greek delta sign. Central hooklets 10-17, marginal hooklets 11-25, distal hooklets 9-9 (Figure 4.7A). Cirrus 38-46, tubiform. Accessory piece 20-30, long and distally bifid (Figure 4.7B). Vagina sclerotised and spatulate distally. Seminal receptacle, ovaly elongated.

*Annulotrema edeensis* Birgi, 1988

**Host and Locality:** *Micralestes* species, Cameroon

**Description and Measurements:** (according to Birgi, 1988). Dorsal anchors 33-35, inner root 8-9, outer root 6-7, shaft 25-27, tip 5-6, dorsal bar 30-32, dorsal bar width 7. Ventral anchors 28, inner root 8-9, outer root 3-5, shaft 22-23, tip 6-7, ventral bar 28-32, ventral bar width 4. Marginal hooklets I= 10-11, II= 8-10, III= 15, IV= 18-20, V-VI-VII= 13-16 (Figure 4.7C). Cirrus 26-30, accessory piece 28 (Figure 4.7D).

*Annulotrema elongata* Paperna & Thurston, 1969

**Host and Locality:** *Alestes baremoze*, Lake Albert, Uganda.

**Description and Measurements:** (according to Paperna & Thurston, 1969). Body elongated, total length 1.6 mm-2.0 mm, width 0.09 mm-0.12mm. Cuticular annulations well developed. Opisthaptor well delineated, 70-100 long and 50-70 wide. Dorsal anchors 75-80, inner root 25-30, outer root 12-15, shaft 30-45. Dorsal bar 35-45. Ventral anchors 65-80, inner root 20-30, outer root 10-20, shaft 40-60. Ventral bar 35-45. Marginal hooklets 25-30 (Figure 4.7E). Cirrus long and tubular (Figure 4.7F).

*Annulotrema endjami* Birgi, 1988

**Host and Locality:** *Neolebias trewavasae*, Nkolya, Cameroon.

**Description and Measurements:** (according to Birgi, 1988). Total length 350, width 150. Dorsal anchors 16-20, inner root 8-10, outer root 3-5, shaft 15-18, tip 2-3. Dorsal bar 30, dorsal bar width 2-3. Ventral anchors 28-30, inner root 10-13, outer root 5-6, shaft 30-32, tip 3-4. Ventral bar 28-30, width 3-4 (Figure 4.8A). Cirrus 60-70. Accessory piece 20-25 (Figure 4.8B). Vagina non-sclerotised.

*Annulotrema fomenai* Birgi, 1988

**Host and Locality:** *Neolebias trewavasae*, Nkolya, Cameroon.

**Description and Measurements:** (according to Birgi, 1988). Total length 300, width 140. Dorsal anchors 22-28, inner root 4-8, outer root 2-3, shaft 18-24, tip 3-4. Dorsal bar 20-24, dorsal bar width 2-3. Ventral anchors 30-38, inner root 7-12, outer root 2-3, shaft 26-30, tip 3-4. Ventral bar 30, ventral bar width 2-3. Marginal hooklets; I= 15-19, II= 16-18, III-IV= 22-25, V= 27-29, VI-VII= 20-25 (Figure 4.8C). Cirrus 22-25. Accessory piece 10 (Figure 4.8D).

*Annulotrema gabrioni* Birgi, 1988

**Host and Locality:** *Phenacogrammus major*, *Hemigrammopetersius pulcher*, Yaoundé, Sangmélima, Cameroon.

**Description and Measurements:** (according to Birgi, 1988). Dorsal anchors 30-32, inner root 8-12, outer root 4-6, shaft 25-27, tip 1. Dorsal bar 10. Ventral anchors 26-30, inner root 5-8, outer root 4-6, shaft 25-27, tip 3. Ventral bar 28-32, ventral bar width 4-5. Marginal hooklets; I= 12-16, II= 14-15, III-IV= 15-18, V= 20-21, VI= 17-18, VII= 18 (Figure 4.8E). Cirrus 20-25 (Figure 4.8F). Vagina non-sclerotised.

*Annulotrema gracilis* (Wedl, 1861)

**Host and Locality:** *Hydrocynus forskalii*, Nile, Egypt.

**Description:** According to Paperna (1979) it is clear from the original description and accompanying illustrations of *Dactylogyrus gracilis*, that this species should be placed within the sub-family Ancyrocephalinae and it is definitely not a representative of the genus *Dactylogyrus*. Paperna (1979) goes on to provisionally place it in the genus *Annulotrema* due to the shape of its anchors which are characteristic of this genus.

*Annulotrema gravis* Paperna & Thurston, 1969

**Host and Locality:** *Brycinus nurse*, Lake Victoria, Jinja, Uganda.

**Description and Measurements:** (according to Paperna & Thurston, 1969). Body stout, total length 380-450, width 80-110. Cuticular annuli 7-9 wide. Opisthaptor poorly delineated. Dorsal anchors 45-60, inner root 15-20, outer root 5-7, median root 2-4, shaft 30-40. Dorsal bar 35-40. Ventral anchors 50-70, inner root 15-20, outer root 5-8, median root 2-4, shaft 35-40. Ventral bar 30-40. Marginal hooklets 10-40 (Figure

4.9A). Cirrus 20-25, long and tubular. Accessory piece 20-25 (Figure 4.9B). Vagina opens sinistrally.

*Annulotrema helicocirra* Paperna, 1973

**Host and locality:** *Brycinus macrolepidotus*, Lake Albert, Uganda.

**Description and Measurements:** (according to Paperna, 1979). Small worms, total length 230-310, width 80-90. Small anchors and large hooklets. Dorsal anchors 34-34, inner root 12-15, outer root 12-15, shaft 22-22, tip 2-2. Dorsal bar 14-14. Ventral anchors 32-37, inner root 8-10, outer root 3-4, shaft 27-30, tip 2-3. Ventral bar 20-23. Central hooklets 15-15, marginal hooklets 18-31 (Figure 4.9C). Cirrus 103-112, long and coiled twice. Accessory piece 12-15, forms distally complex structure, prostatic reservoir ovaly elongated (Figure 4.9D). Vagina tubiform and sclerotised. Seminal receptacle pear shaped.

*Annulotrema hepseti* Paperna & Thurston, 1969

**Host and Locality:** *Hepsetus odoe*, Beira Stream, New Tafo, Ghana, Ayamé Retention Lake, Ivory Coast, Cameroon.

**Description and Measurements:** (according to Paperna & Thurston, 1969). Body stout, total length 200-300, width 80-100. Cuticular annulation narrow, each 3-5 wide. Opisthaptor large and triangular, length 40-60, width 70-90. Dorsal anchors 70-100, inner root 12-15, outer root 4-9, median root absent, shaft 50-70, dorsal bar 35-40. Ventral anchors 60-75, inner root 18-20, outer root 4-6, median root absent, shaft 40-55, ventral bar 38-42. Hooklets 40-60, except central pair 30-40 (Figure 4.9E). Cirrus and funnel enveloped by accessory piece (Figure 4.9F). Vagina opens to left.

*Annulotrema hydrocynusi* Paperna, 1973

**Host and Locality:** *Hydrocynus forskalii*, Butiaba, Lake Albert, Uganda.

**Description and Measurements:** (according to Paperna, 1979). Medium size worms with large anchors. Total length 280-450, width 70-100. Dorsal anchors 42-52, inner root 13-20, outer root 6-10, shaft 33-39, tip 2-4, dorsal bar 28-38. Ventral anchors 42-50, inner root 7-13, outer root 4-9, shaft 37-40, tip 5-7, ventral bar 32-37. Hooklets are medium sized central hooklets 16-17, marginal hooklets 20-29 (Figure 4.10A). Cirrus tubiform, looped together with elongated accessory piece, distal end of cirrus spatulate,

cirrus 70-80 $\mu$ , accessory piece 28-45 $\mu$  (Figure 4.10B). Vagina non-sclerotised.

*Annulotrema kribiensis* Birgi, 1988

**Host and Locality:** *Brycinus longipinnis*, Cameroon.

**Description and Measurements:** (according to Birgi, 1988). Total length 450. Dorsal anchors 40-41, inner root 10-12, outer root 6-8, shaft 28-30, tip 5-6, dorsal bar 18, dorsal bar width 3. Ventral anchors 42-48, inner root 8-10, outer root 5-7, shaft 28-30, tip 5, ventral bar 35, ventral bar width 5. Marginal hooklets I= 22-24, II= 10-12, III-IV=22-26, V= 37, VI= 22, VII= 32 (Figure 4.10C). Cirrus 55, accessory piece 45-50 (Figure 4.10D).

*Annulotrema lamberti* Birgi, 1998

**Host and Locality:** *Brycinus longipinnis*, Cameroon

**Description and Measurements:** (according to Birgi, 1988). Dorsal anchors 22-24, inner root 9-11, outer root 5-6, shaft 18-29, tip 6, dorsal bar 30, dorsal bar width 2. Ventral anchors 21-25, inner root 8-9, outer root 3-4, shaft 18-19, tip 3, ventral bar 30, ventral bar width 3. Marginal hooklets I= 12-13, II= 11-12, III-IV= 22-25, V=30, VI-VII= 23-25 (Figure 4.10E). Cirrus 35, accessory piece 35-39 (Figure 4.10F).

*Annulotrema longipenis* Paperna, 1969

**Host and Locality:** *Brycinus macrolepidotus*, *Alestes baremose* and *Hydrocymus forskalii*, Volta Lake, Ghana, Lake Albert, Uganda.

**Description and Measurements:** (according to Paperna, 1979). Total length 280-230, width 90-110. Dorsal anchors 39-42, inner root 12-16, outer root 2-3, shaft 29-32, tip 11-13, dorsal bar 40-43. Ventral anchors 37-39, inner root 10-13, outer root 2-4, shaft 27-30, tip 9-21, ventral bar 37-38. Central hooklets 12-13, marginal hooklets 15-23, distal hooklets 14-15 (Figure 4.11A). Cirrus 140-200, accessory piece 18-20 (Figure 4.11B).



*Annulotrema macropenis* N'Douba, Pariselle & Euzet, 1997

**Host and Locality:** *Hepsetus odoe*, Agnéby River, Ivory Coast.

**Description and Measurements:** (according to N'Douba, *et. al.*, 1997). Total length 638 (427-881), width 127 (73-219). Pharynx diameter 40 (23-64). Dorsal anchor 33 (27-36), inner root 14 (10-17), outer root 6 (4-9), shaft 23 (20-25), tip 7 (5-9). dorsal bar, V-shaped, 40 (34-48), dorsal bar width 3 (2-5). Ventral anchor 33 (26-38), inner root 15 (8-20), outer root 7 (4-10), shaft 25 (21-28), tip 6 (4-7), ventral bar much wider than dorsal bar with bulged endings, ventral bar 44 (34-50), ventral bar width 4 (2-5). Hooklets very thin; I= 29 (24-38), II= 18 (12-22), III= 27 (23-31), IV= 33 (26-40), V= 37 (28-44), VI= 36 (24-42), VII= 26 (19-29) (Figure 4.11C). Cirrus very long and spiralled, number of spirals 36 (34-38), small accessory piece surrounds distal end of the cirrus, 17 (14-22) (Figure 4.11D). Vagina sclerotised 35 (27-49), vagina diameter 1 (1-2).

*Annulotrema magna* Paperna, 1973

**Host and Locality:** *Hydrocymis vittatus*, Ruahae River, Tanzania.

**Description and Measurements:** (according to Paperna, 1979). Large worms. Total length 730-970, width 190-250. Anchors relatively small, anchor shafts solid and short. Dorsal anchors 50-67, inner root 17-30, outer root 6-10, shaft 35-39, tip 10-11, dorsal bar V-shaped, dorsal bar 42-44. Ventral anchors 42-54, inner root 13-20, outer root 4-9, shaft 37-40, ventral bar 44-45. Hooklets moderate sizes, central hooklets 25-26, marginal hooklets 26-34, distal hooklets 15-22 (Figure 4.11E). Cirrus 44-48, accessory piece 33-35, cirrus tubiform and stout, accessory piece bifid distally (Figure 4.11F). Vagina non-sclerotised.

*Annulotrema magnihamula* Paperna, 1973

**Host and Locality:** *Hydrocymus forskalii*, Lake Albert, Uganda.

**Description and Measurements:** (according to Paperna, 1979). Large worms with large anchors. Total length 540-580, width 130-180. Dorsal anchors 60-64, inner root 22-23, outer root 7-15, shaft 40-46, tip 6-9, dorsal bar 39-45. Ventral anchors 60-64, inner root 16-17, outer root 4-7, shaft 54-54, tip 6-7, ventral bar 34-36. Central hooklets 23-26, marginal hooklets 25-34 (Figure 4.12A). Cirrus delicate tube, accessory piece rudimentary, small plate attached to distal end of cirrus, cirrus 44-52, accessory piece

15-22 (Figure 4.12B). Vagina non-sclerotised.

*Annulotrema maillardi* Birgi, 1988

**Host and Locality:** *Brycinus kingsleyae*, Cameroon.

**Description and Measurements:** (according to Birgi, 1988). Dorsal anchors 45-49, inner root 20-23, outer root 5, shaft 28-30, tip 5, dorsal bar 35, dorsal bar width 3-5. Ventral anchors 38-40, inner root 3-5, outer root 8-10, shaft 28-30, tip 2-5, ventral bar 35, ventral bar width 3-5. Marginal hooklets I= 17, II= 22, III-IV= 27-29, V-VI= 25-28 (Figure 4.12C). Cirrus 35, accessory piece 18-20 (Figure 4.12D).

*Annulotrema moanko* Birgi, 1988

**Host and Locality:** *Brycinus longipinnis*, Cameroon.

**Description and Measurements:** (according to Birgi, 1988). Proximal anchors 40, inner root 15, outer root 6, shaft 25, tip 4, dorsal bar 36. Marginal hooklets I= 18, II=15, III-IV= 22, V= 28, VI-VII= 25-30 (Figure 4.13A). Cirrus 45, accessory piece 45 (Figure 4.13B).

*Annulotrema nannaethiopsis* Birgi, 1988

**Host and Locality:** *Nannaethiops unitaeniatus*, Nkolya, Cameroon.

**Description and Measurements:** (according to Birgi, 1988). Total length 220-350. Dorsal anchors 18-20, inner root 8-12, outer root 3-5, shaft 16-20, tip 2-3. Dorsal bar 26-30, dorsal bar width 2-3. Ventral anchors 30-32, inner root 6-8, outer root 3-6, shaft 26-28, tip 3-5. Ventral bar 28-32, ventral bar width 3-4. Marginal hooklets; I= 16-17, II= 17-20, III-IV= 18-22, V= 25-29, VI-VII= 18-25 (Figure 4.13C). Cirrus 40-45, accessory piece 18-20 (Figure 4.13D).

*Annulotrema nili* Paperna, 1973

**Host and Locality :** *Hydrocynus forskalii*, Butiaba, Lake Albert, Uganda.

**Description and Measurements:** (according to Paperna 1979). Medium to large worms with large anchors and hooklets. Total length 360-400, width 100-150. Dorsal anchors 44-55, inner root 16-20, outer root 5-9, shaft 31-38, tip 6-9, dorsal bar 29-36. Ventral anchors 36-45, inner root 8-13, outer root 3-6, shaft 32-40, tip 4-8, ventral bar 34-40. Central hooklets 17-22, marginal hooklets 23-36, distal hooklets 14-15 (Figure

4.14A). Cirrus tubiform and coiled, funnel is oval to cylindrical, accessory piece forms a clasper and spike-like distal complex structures, cirrus 44-52, accessory piece 15-22 (Figure 4.14B). Vagina non-sclerotised

*Annulotrema nili ruahae* Paperna, 1979

**Host and Locality:** *Hydrocynus vittatus*, *Hydrocynus forskalli*, Ruahae River, Tanzania.

**Description and Measurements:** (according to Paperna, 1979). Differs from Lake Albert type in size and pattern of the anchors being longer with elongated shafts and much longer hooklets. In *A. n. ruahae* the cirrus is much longer than that of the Lake Albert type. Total length 300-350, width 50-80. Dorsal anchors 55-66, inner root 25-32, outer root 9-13, shaft 37-40, tip 4-6, dorsal bar 33-34, width 14-19. Ventral anchors 52-62, inner root 11-15, outer root 10-13, shaft 49-52, tip 5-5, ventral bar 32-35. Central hooklets 23-25, marginal hooklets 28-47, distal hooklets 17-18 (Figure 4.14C). Cirrus 61 (Figure 4.14D).

*Annulotrema nyongensis* Birgi, 1988

**Host and Locality:** *Brycinus kingsleyae*, Cameroon.

**Description and Measurements:** (according to Birgi, 1988). Total length 100. Dorsal anchors 23-26, inner root 5-8, outer root 3-5, shaft 20-22, tip 1-2, dorsal bar 10-12. Ventral anchors 22-25, inner root 5-7, outer root 3-4, shaft 20-21, tip 7-8, ventral bar 26-30, ventral bar width 4-5. Marginal hooklets I= 15-17, II= 12-14, III-IV= 18-20, V-VI-VII= 20-23 (Figure 4.14E). Cirrus 35-38, accessory piece 8-10 (Figure 4.14F).

*Annulotrema pikei* (Price, Peebles & Bamford, 1969)

**Host and Locality:** *Hydrocynus vittatus*, KwaZulu-Natal, Pongola system, South Africa. *Hydrocynus* sp., Volta Lake, Ghana. *Hydrocynus forskalii*, Lake Albert, Uganda.

**Description and Measurements:** (Price, Peebles & Bamford, 1969). Small worm with thin cuticle, total length 256 (197-332), width 80 (69-100). Two pairs of eyespots, posterior pair larger. Four pairs of glandular cephalic organs. Pharynx muscular, prominent. Anterior and lateral cephalic lobes moderately well developed. Dorsal anchor 40 (35-43). Dorsal bar 26 (24-30). Ventral anchor 40 (36-43). Ventral bar 30

(27-33). Marginal hooks; I= 11 (10-12), II= 21 (19-23), III= 27 (26-29), IV= 19 (18-21), V= 12 (11-13), VI= 20 (19-21), VII= 18 (16-19) (Figure 4.15A). Cirrus 47 (40-52), elongate, tubular. Accessory piece 42 (38-46) (Figure 4.15B).

*Annulotrema pikei ruahae* Paperna, 1979

**Host and Locality:** *Hydrocynus vittatus*, Ruahae River, Tanzania.

**Description and Measurements:** (according to Paperna, 1979). Specimens from the Ruahae River are characterised by having a cirrus with a deep cup-shaped funnel and a vagina with sclerotised spiraloid pattern not found in the other specimens assigned to this species. Also the marginal hooklets are larger in Ruahae population (Figures 4.15C-D).

*Annulotrema pikoides* Guegan, Lambert & Birgi, 1988

**Host and Locality:** *Hydrocynus vittatus*, Niger River, Mali.

**Description and Measurements:** (according to Guegan, *et al.*, 1988). Total length 320-620, width 100-150. Dorsal anchor 44 (41-47), inner root 14 (12-16), outer root 6 (5-8), shaft 39 (32-42), tip 6 (4-7), dorsal bar 30. Ventral anchors 44 (40-48), inner root 14 (11-16), outer root 6 (5-8), shaft 40 (35-43), tip 6 (4-7), ventral bar 34. Marginal hooklets; I=17 (15-19), II=12 (8-15), III=22 (18-25), IV=29 (24-32), V=31 (28-33), VI=33 (30-36), VII=24 (20-29) (Figure 4.15E). Cirrus 87 (72-96), accessory piece present (Figure 4.15F). Vagina sclerotised.

*Annulotrema robusta* Paperna, 1969

**Host and Locality:** *Brycinus leuciscus*, Volta Lake, Uganda.

**Description and Measurements:** (according to Paperna, 1969). Total length 400-600, width 50-100. Annulation not to distinct. Dorsal anchor 60-80, inner root 18-20, outer root 5-7, median root vestigial. Dorsal bar 25-45. Ventral anchors 60-70, inner root 12-16, outer root 10, median root rudimentary, shaft 40. Ventral bar 40. Marginal hooklets 30-35 (Figure 4.16A). Cirrus 70-80. Accessory piece 50-65 (Figure 4.16B).

*Annulotrema ruahae* Paperna, 1973

**Host and Locality:** *Hydrocynus vittatus*, Ruahae River, Tanzania.

**Description and Measurements:** (according to Paperna, 1979). Small to medium worms, total length 330-400, width 60-80. Small anchors with delicate shafts. Dorsal anchor 33-42, inner root 4-8, shaft 24-29, tip 3-5, dorsal bar almost straight dorsal bar 23-28, width 8-9. Ventral anchors 36-40, inner root 8-13, outer root 5-8, shaft 29-34, tip 5-7, ventral bar 29-31. Hooklets moderate sizes, central hooklets 12-19, marginal hooklets 18-24 (Figure 4.16C). Cirrus long winding tube with large rounded funnel, accessory piece branching complex structure, cirrus 67-89, funnel diameter 8-10, accessory piece 21-23 (Figure 4.16D). Vagina non-sclerotised.

*Annulotrema sangmelinensis* Birgi, 1988

**Host and Locality:** *Micralestes humulis*, Cameroon.

**Description and Measurements:** (according to Birgi, 1988). Dorsal anchors 25-27, inner root 11-12, outer root 6-8, shaft 19-20, tip 3-4, dorsal bar 30, dorsal bar width 3-4. Ventral anchors 28-29, inner root 8-10, outer root 5-6, shaft 24-25, tip 3-4, ventral bar 30, ventral bar width 6. Marginal hooklets I= 13-15, II= 13-15, III= 15-16, IV= 18, V= 22, VI-VII= 18-20 (Figure 4.16E). Cirrus 29, accessory piece 20 (Figure 4.16F).

*Annulotrema spiropenis* Paperna, 1969

**Host and Locality:** *Brycinus nurse*, Volta Lake, Ghana, Lake Albert, Butiaba and Lower Waisoke River, Uganda. *Hydrocynus forskalii*, Uganda.

**Description and Measurements:** (according to Paperna, 1969). Total length 350-400, width 50-80, annulation distinct. Proximal anchors 55-65, inner root 12-15, outer root 8-10, median root 1, shaft 35-40, the attached bar 35. Hooklets 20-25 (Figure 4.17A). Cirrus multispiral, accessory piece, stalk 80, distal claspers 20, copulatory organ is 45-50 (Figure 4.17B). Vagina terminates as a long and coiled tube.

*Annulotrema tenuicirra* Paperna, 1973

**Host and Locality:** *Brycinus macrolepidotus*, Butiaba, Lake Albert, Uganda.

**Description and Measurements:** (according to Paperna, 1979). Small worms, total length 230-240, width 30-110. Small anchors and hooklets. Dorsal anchors 35-37. Ventral anchors 32-35, inner root 10-12, outer root 3-5, shaft 27-31, tip 1-6. Ventral

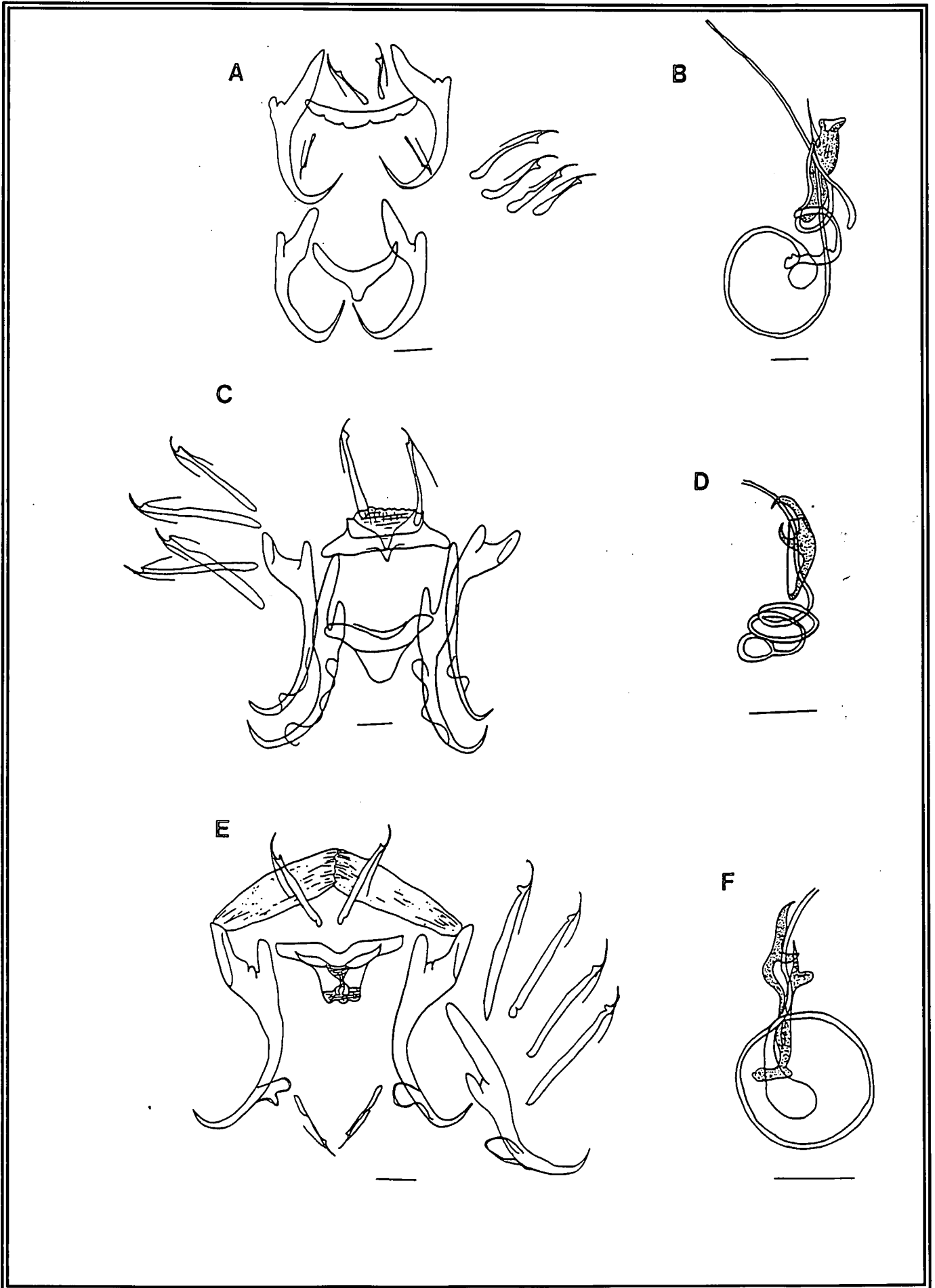
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bar 23-25. Central hooklets 15-15, marginal hooklets 18-20, distal hooklets 12-14 (Figure 4.17C). Cirrus 42-50, long delicate tube. Accessory piece 46-50, elongated rod which terminates distally in spatulate piece which embraces distal end off cirrus (Figure 4.17D). Vagina sclerotised and tubiform.

## FIGURE 4.3

- A. Diagram showing the structure of the opisthaptoral armature of *Annulotrema alberti* Paperna, 1973. (redrawn from Paperna, 1979)
- B. Diagram showing the structure of the copulatory organ of *Annulotrema alberti* Paperna, 1973. (redrawn from Paperna, 1979)
- C. Diagram showing the structure of the opisthaptoral armature of *Annulotrema alestesimberi* Paperna, 1973. (redrawn from Paperna, 1979)
- D. Diagram showing the structure of the copulatory organ of *Annulotrema alestesimberi* Paperna, 1973. (redrawn from Paperna, 1979)
- E. Diagram showing the structure of the opisthaptoral armature of *Annulotrema alestesnursi* Paperna, 1973. (redrawn from Paperna, 1979)
- F. Diagram showing the structure of the copulatory organ of *Annulotrema alestesnursi* Paperna, 1973. (redrawn from Paperna, 1979)

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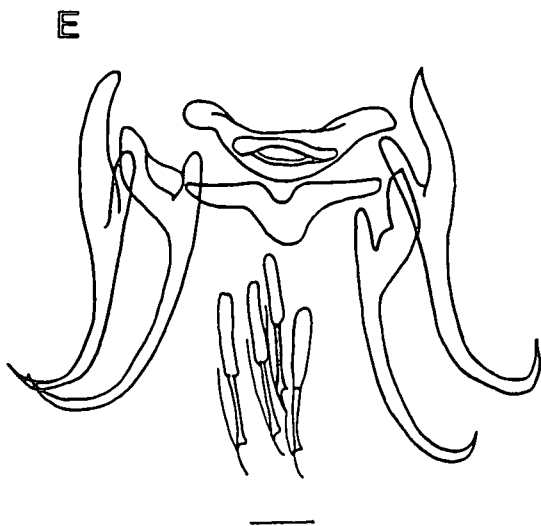
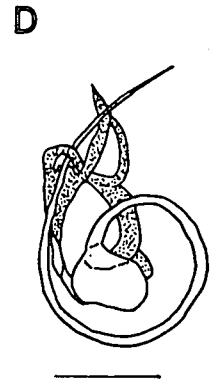
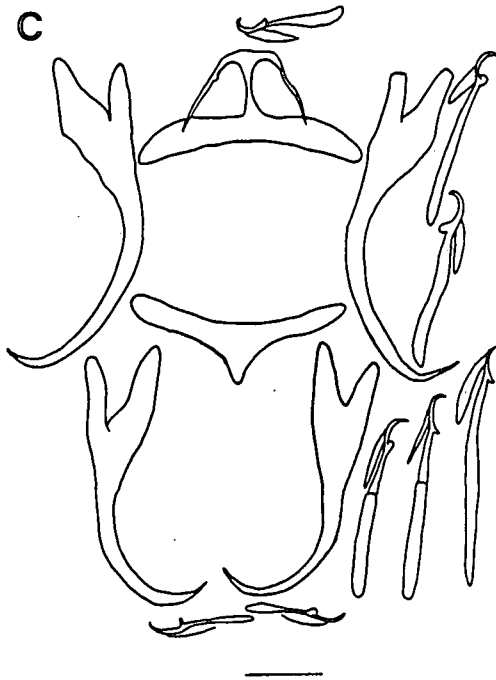
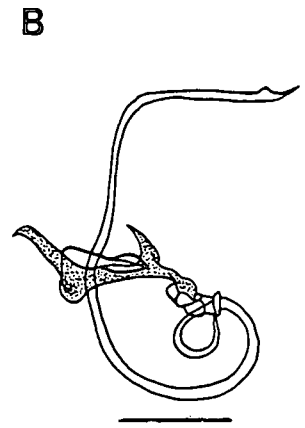
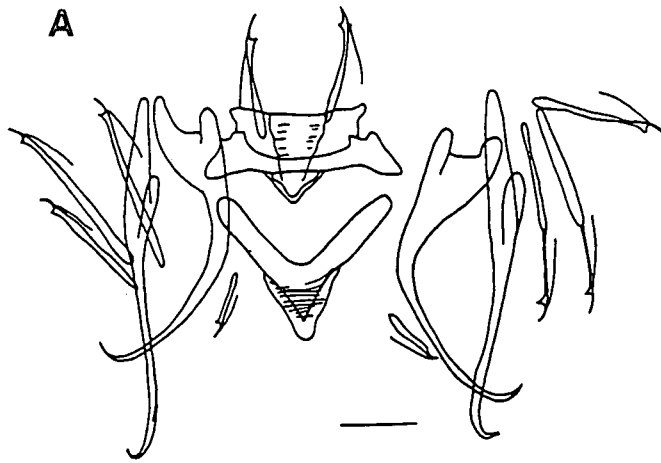




## FIGURE 4.4

- A. Diagram showing the structure of the opisthaptoral armature of *Annulotrema allogravis* Paperna, 1973. (redrawn from Paperna, 1979)
- B. Diagram showing the structure of the copulatory organ of *Annulotrema allogravis* Paperna, 1973. (redrawn from Paperna, 1979)
- C. Diagram showing the structure of the opisthaptoral armature of *Annulotrema amieti* Birgi, 1988. (redrawn from Birgi, 1988)
- D. Diagram showing the structure of the copulatory organ of *Annulotrema amieti* Birgi, 1988. (redrawn from Birgi, 1988)
- E. Diagram showing the structure of the opisthaptoral armature of *Annulotrema armorata* Paperna, 1969. (redrawn from Paperna, 1969)
- F. Diagram showing the structure of the copulatory organ of *Annulotrema armorata* Paperna, 1969. (redrawn from Paperna, 1969)

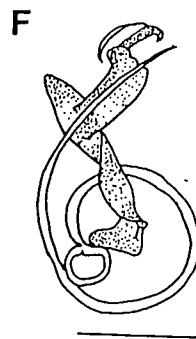
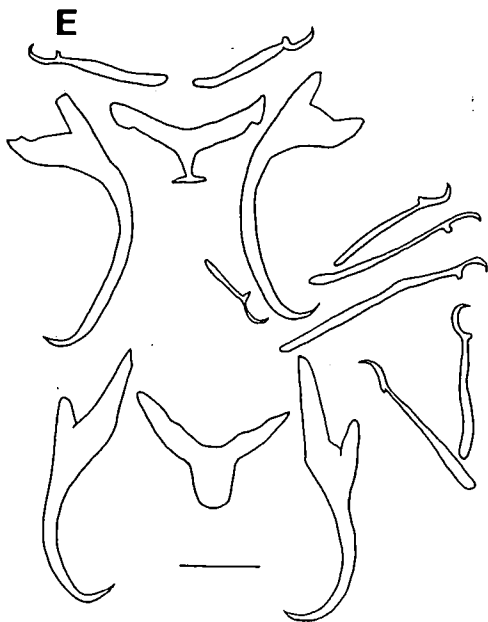
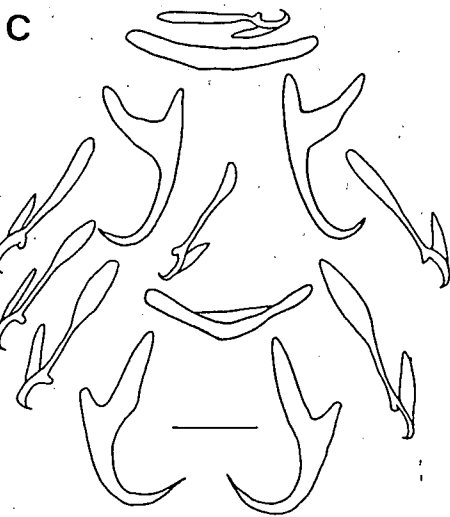
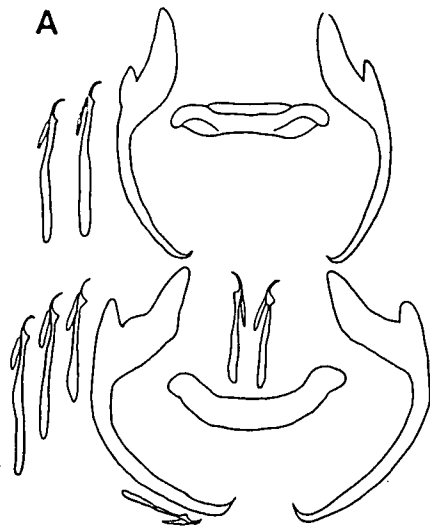
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## FIGURE 4.5

- A. Diagram showing the structure of the opisthaptoral armature of *Annulotrema biaensis* N'Douba, Pariselle & Euzet, 1997. (redrawn from N'Douba, *et. al*, 1997)
- B. Diagram showing the structure of the copulatory organ of *Annulotrema biaensis* N'Douba, Pariselle & Euzet, 1997. (redrawn from N'Douba, *et. al*, 1997)
- C. Diagram showing the structure of the opisthaptoral armature of *Annulotrema bilongi* Birgi, 1988. (redrawn from Birgi, 1988)
- D. Diagram showing the structure of the copulatory organ of *Annulotrema bilongi* Birgi, 1988. (redrawn from Birgi, 1988)
- E. Diagram showing the structure of the opisthaptoral armature of *Annulotrema bouixi* Birgi, 1988. (redrawn from Birgi, 1988)
- F. Diagram showing the structure of the copulatory organ of *Annulotrema bouixi* Birgi, 1988. (redrawn from Birgi, 1988)

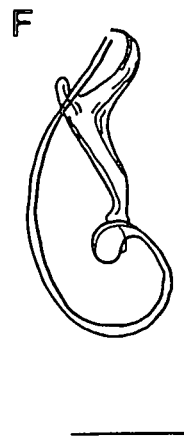
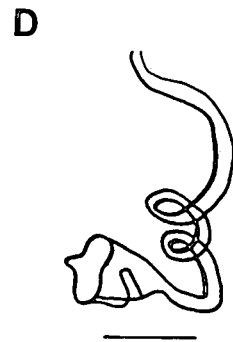
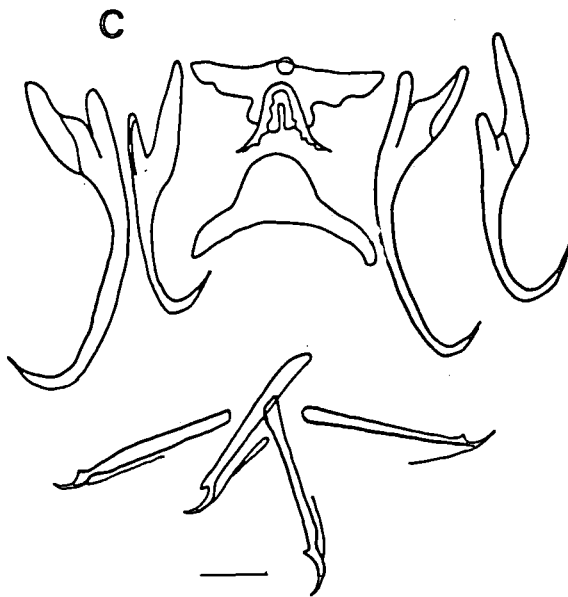
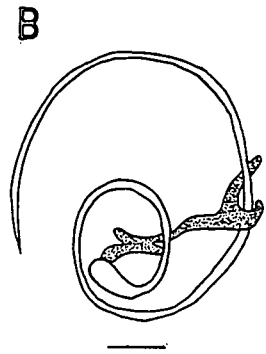
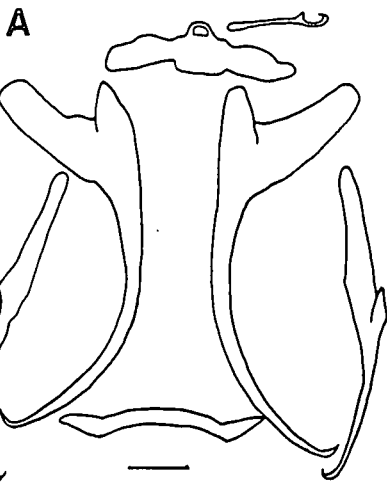
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## FIGURE 4.6

- A. Diagram showing the structure of the opisthaptor armature of *Annulotrema combesi* Birgi, 1988. (redrawn from Birgi, 1988)
- B. Diagram showing the structure of the copulatory organ of *Annulotrema combesi* Birgi, 1988. (redrawn from Birgi, 1988)
- C. Diagram showing the structure of the opisthaptor armature of *Annulotrema cryptophallus* Paperna, 1973. (redrawn from Paperna, 1979)
- D. Diagram showing the structure of the copulatory organ of *Annulotrema cryptophallus* Paperna, 1973. (redrawn from Paperna, 1979)
- E. Diagram showing the structure of the opisthaptor armature of *Annulotrema curvipenis* Paperna, 1969. (redrawn from Paperna, 1969)
- F. Diagram showing the structure of the copulatory organ of *Annulotrema curvipenis* Paperna, 1969. (redrawn from Paperna, 1969)

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## FIGURE 4.7

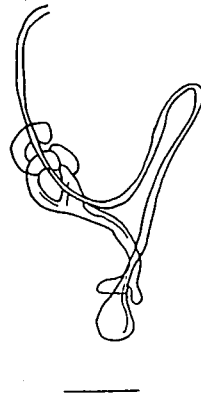
- A. Diagram showing the structure of the opisthaptor armature of *Annulotrema delta* Paperna, 1973. (redrawn from Paperna, 1979)
- B. Diagram showing the structure of the copulatory organ of *Annulotrema delta* Paperna, 1973. (redrawn from Paperna, 1979)
- C. Diagram showing the structure of the opisthaptor armature of *Annulotrema edeensis* Birgi, 1988. (redrawn from Birgi, 1988)
- D. Diagram showing the structure of the copulatory organ of *Annulotrema edeensis* Birgi, 1988. (redrawn from Birgi, 1988)
- E. Diagram showing the structure of the opisthaptor armature of *Annulotrema elongata* Paperna & Thurston, 1969. (redrawn from Paperna & Thurston, 1969)
- F. Diagram showing the structure of the copulatory organ of *Annulotrema elongata* Paperna & Thurston, 1969. (redrawn from Paperna & Thurston, 1969)

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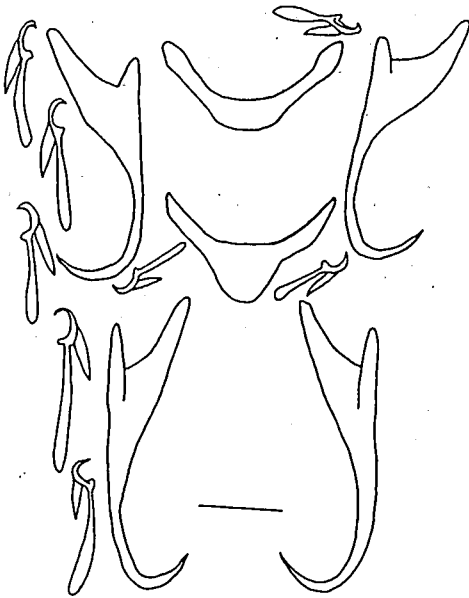
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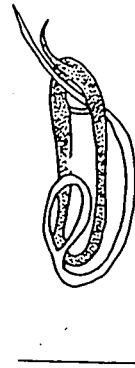
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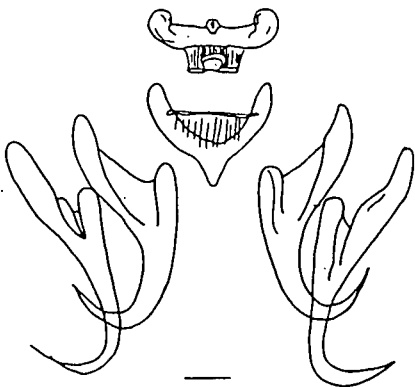
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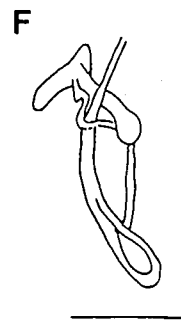
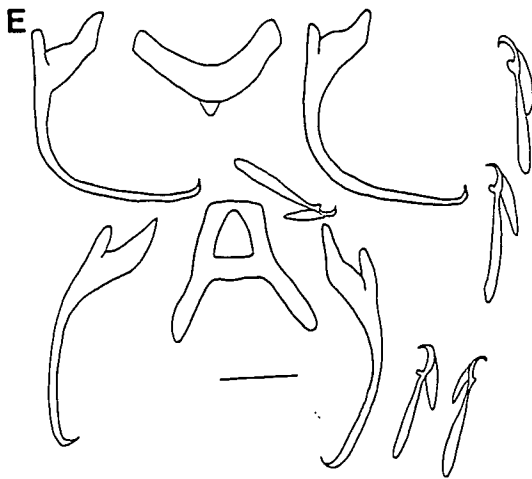
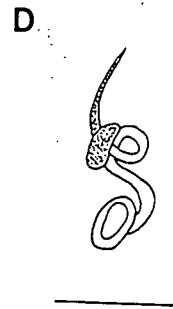
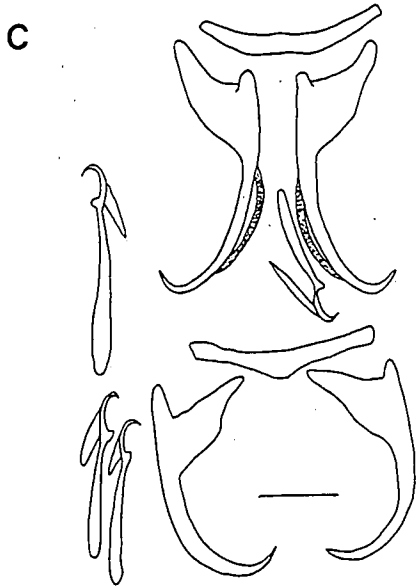
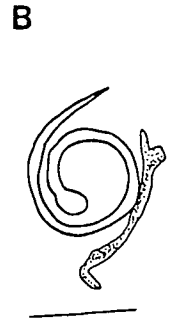
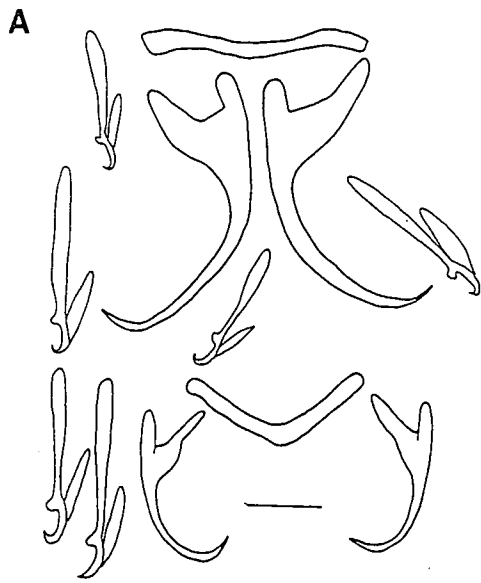




## FIGURE 4.8

- A. Diagram showing the structure of the opisthaptor armature of *Annulotrema endjami* Birgi, 1988. (redrawn from Birgi, 1988)
- B. Diagram showing the structure of the copulatory organ of *Annulotrema endjami* Birgi, 1988. (redrawn from Birgi, 1988)
- C. Diagram showing the structure of the opisthaptor armature of *Annulotrema fomenai* Birgi, 1988. (redrawn from Birgi, 1988)
- D. Diagram showing the structure of the copulatory organ of *Annulotrema fomenai* Birgi, 1988. (redrawn from Birgi, 1988)
- E. Diagram showing the structure of the opisthaptor armature of *Annulotrema gabrioni* Birgi, 1988. (redrawn from Birgi, 1988)
- F. Diagram showing the structure of the copulatory organ of *Annulotrema gabrioni* Birgi, 1988. (redrawn from Birgi, 1988)

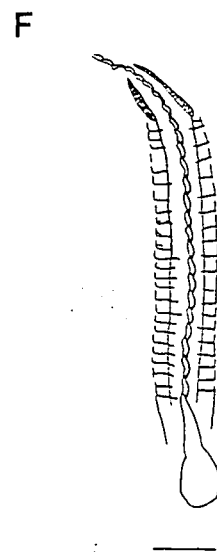
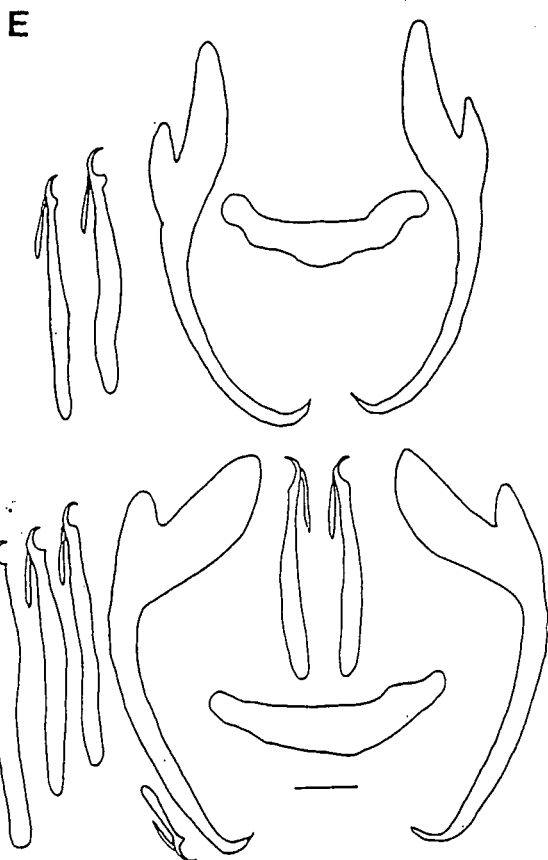
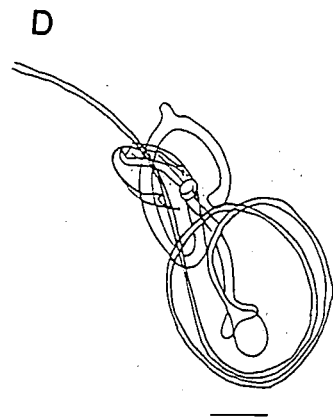
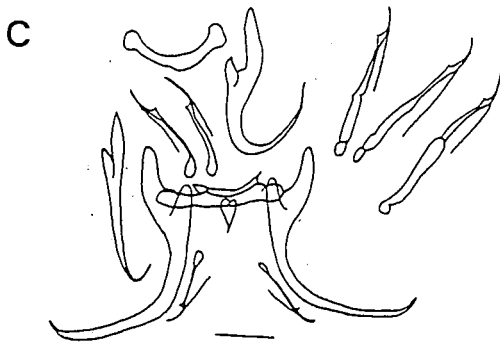
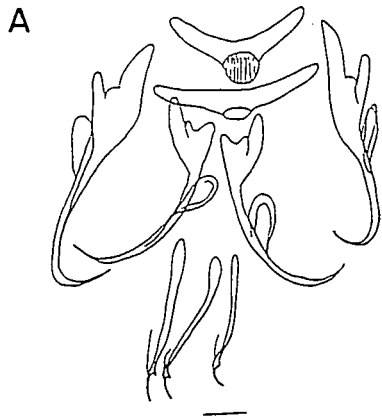
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## FIGURE 4.9

- A. Diagram showing the structure of the opisthaptoral armature of *Annulotrema gravis* Paperna & Thurston, 1969. (redrawn from Paperna & Thurston, 1969)
- B. Diagram showing the structure of the copulatory organ of *Annulotrema gravis* Paperna & Thurston, 1969. (redrawn from Paperna & Thurston, 1969)
- C. Diagram showing the structure of the opisthaptoral armature of *Annulotrema helicocirra* Paperna, 1973. (redrawn from Paperna, 1979)
- D. Diagram showing the structure of the copulatory organ of *Annulotrema helicocirra* Paperna, 1973. (redrawn from Paperna, 1979)
- E. Diagram showing the structure of the opisthaptoral armature of *Annulotrema hepseti* Paperna & Thurston, 1969. (redrawn from N'Douba, *et. al.*, 1997)
- F. Diagram showing the structure of the copulatory organ of *Annulotrema hepseti* Paperna & Thurston, 1969. (redrawn from N'Douba, *et. al.*, 1997)

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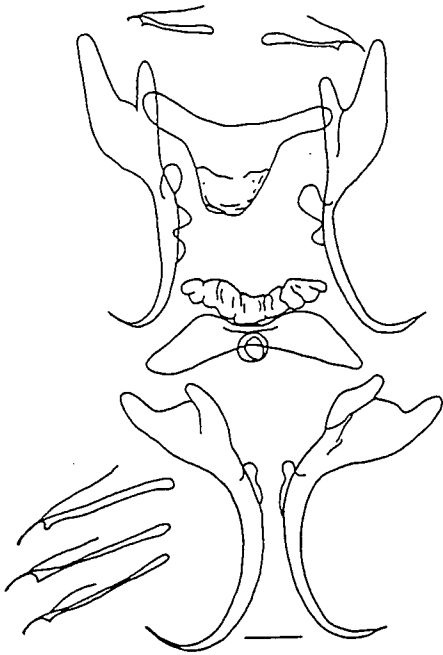


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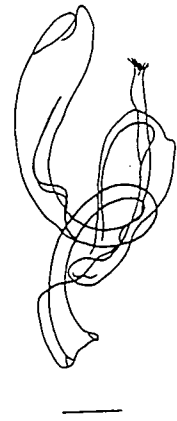
- A. Diagram showing the structure of the opisthaptor armature of *Annulotrema hydrocynusi* Paperna, 1973. (redrawn from Paperna, 1979)
- B. Diagram showing the structure of the copulatory organ of *Annulotrema hydrocynusi* Paperna, 1973. (redrawn from Paperna, 1979).
- C. Diagram showing the structure of the opisthaptor armature of *Annulotrema kribiensis* Birgi, 1988. (redrawn from Birgi, 1988)
- D. Diagram showing the structure of the copulatory organ of *Annulotrema kribiensis* Birgi, 1988. (redrawn from Birgi, 1988)
- E. Diagram showing the structure of the opisthaptor armature of *Annulotrema lamberti* Birgi, 1988. (redrawn from Birgi, 1988)
- F. Diagram showing the structure of the copulatory organ of *Annulotrema lamberti* Birgi, 1988. (redrawn from Birgi, 1988)

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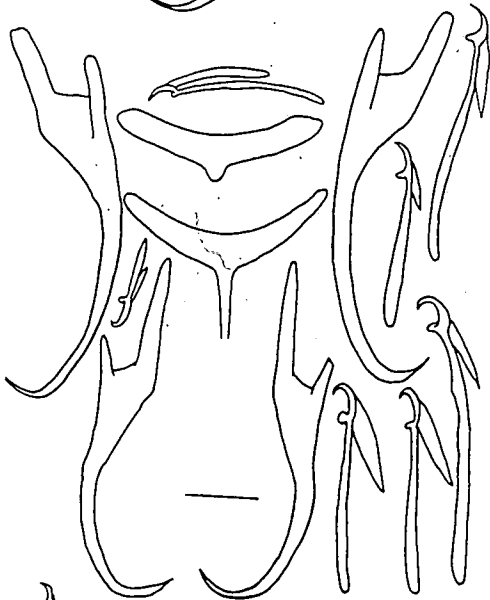
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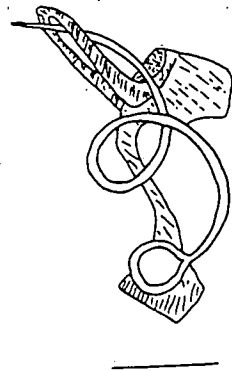
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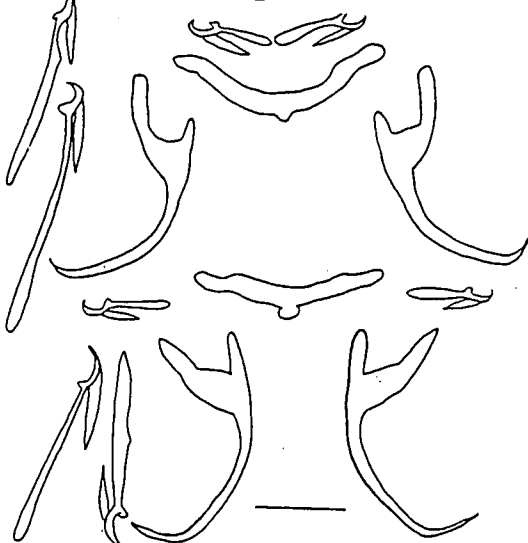
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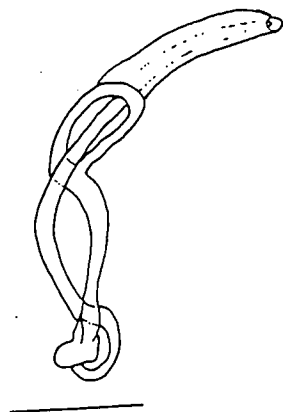
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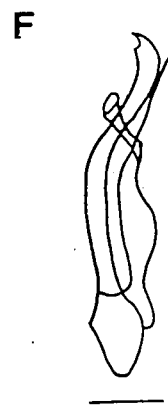
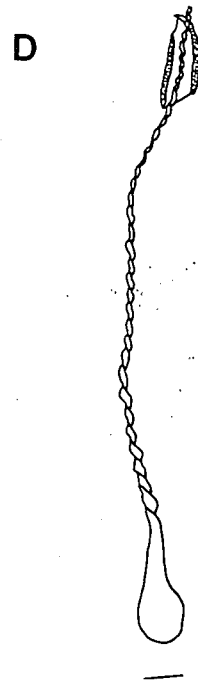
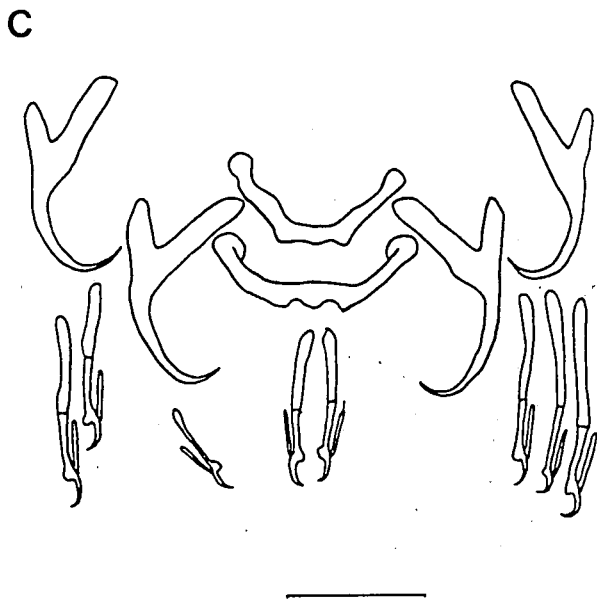
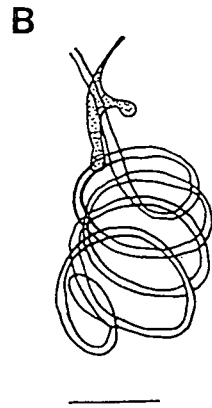
F



## FIGURE 4.11

- A. Diagram showing the structure of the opisthaptoral armature of *Annulotrema longipenis* Paperna, 1969. (redrawn from Paperna, 1969)
- B. Diagram showing the structure of the copulatory organ of *Annulotrema longipenis* Paperna, 1969. (redrawn from Paperna, 1969)
- C. Diagram showing the structure of the opisthaptoral armature of *Annulotrema macropenis* N'Douba, Pariselle & Euzet, 1997. (redrawn from N'Douba, *et. al*, 1997)
- D. Diagram showing the structure of the copulatory organ of *Annulotrema macropenis* N'Douba, Pariselle & Euzet, 1997. (redrawn from N'Douba, *et. al*, 1988)
- E. Diagram showing the structure of the opisthaptoral armature of *Annulotrema magna* Paperna, 1973. (redrawn from Paperna, 1979)
- F. Diagram showing the structure of the copulatory of *Annulotrema magna* Paperna, 1973. (redrawn from Paperna, 1979)

Scale bar: 10  $\mu$ m

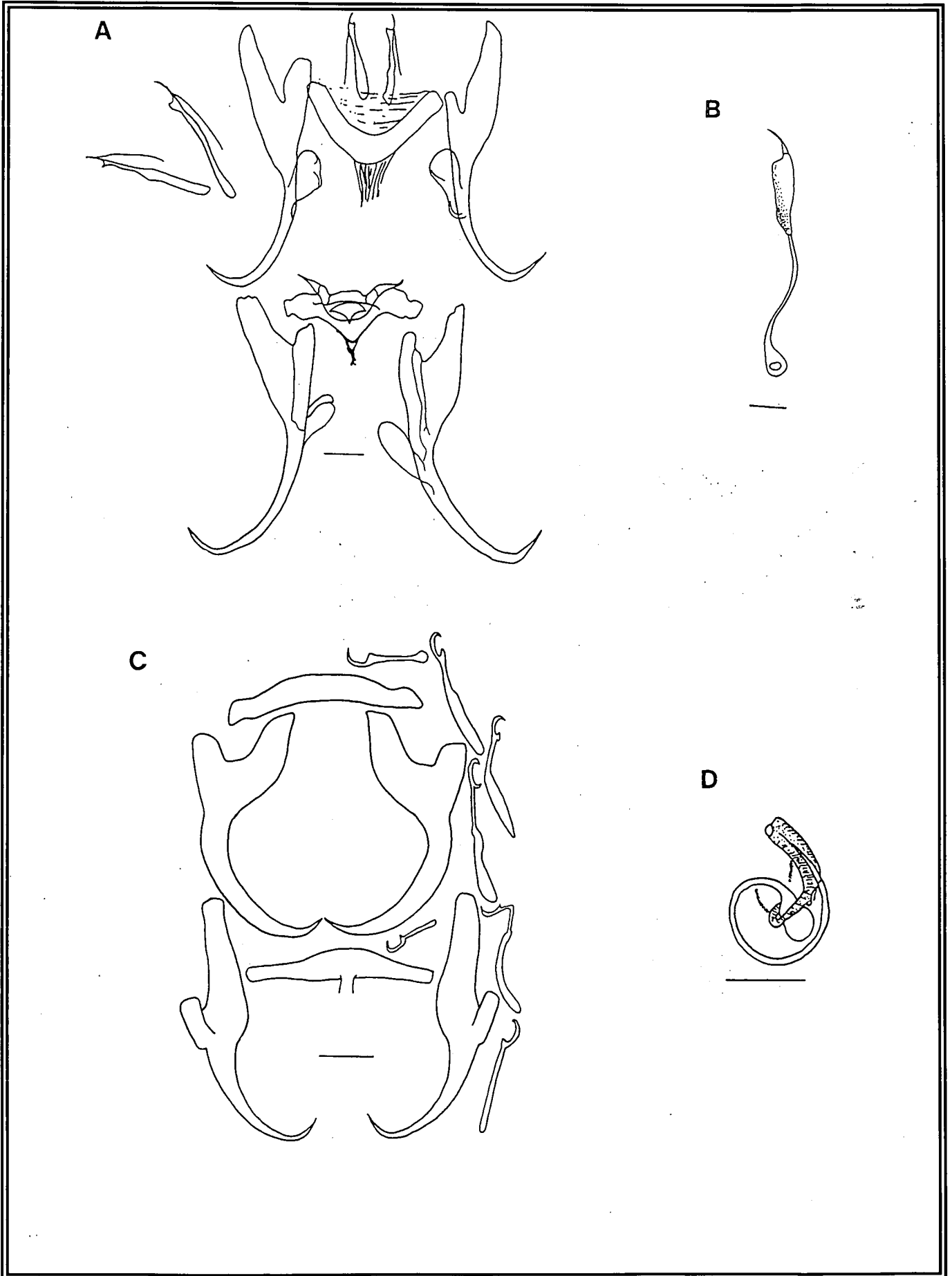




## FIGURE 4.12

- A. Diagram showing the structure of the opisthaptoral armature of *Annulotrema magnihamula* Paperna, 1973. (redrawn from Paperna, 1979)
- B. Diagram showing the structure of the copulatory organ of *Annulotrema magnihamula* Paperna, 1973. (redrawn from Paperna, 1979)
- C. Diagram showing the structure of the opisthaptoral armature of *Annulotrema maillardi* Birgi, 1988. (redrawn from Birgi, 1988)
- D. Diagram showing the structure of the copulatory organ of *Annulotrema maillardi* Birgi, 1988. (redrawn from Birgi, 1988)

Scale bar: 10  $\mu\text{m}$



## FIGURE 4.13

- A. Diagram showing the structure of the opisthaptor armature of *Annulotrema moanko* Birgi, 1988. (redrawn from Birgi, 1988)
- B. Diagram showing the structure of the copulatory organ of *Annulotrema moanko* Birgi, 1988. (redrawn from Birgi, 1988)
- C. Diagram showing the structure of the opisthaptor armature of *Annulotrema nannaethiopsis* Birgi, 1988. (redrawn from Birgi, 1988)
- D. Diagram showing the structure of the copulatory organ of *Annulotrema nannaethiopsis* Birgi, 1988. (redrawn from Birgi, 1988)

Scale bar: 10  $\mu\text{m}$

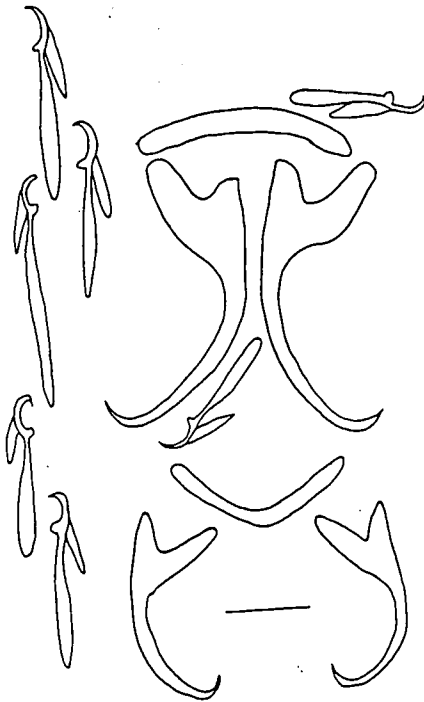
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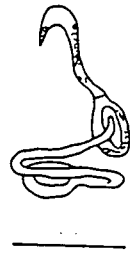
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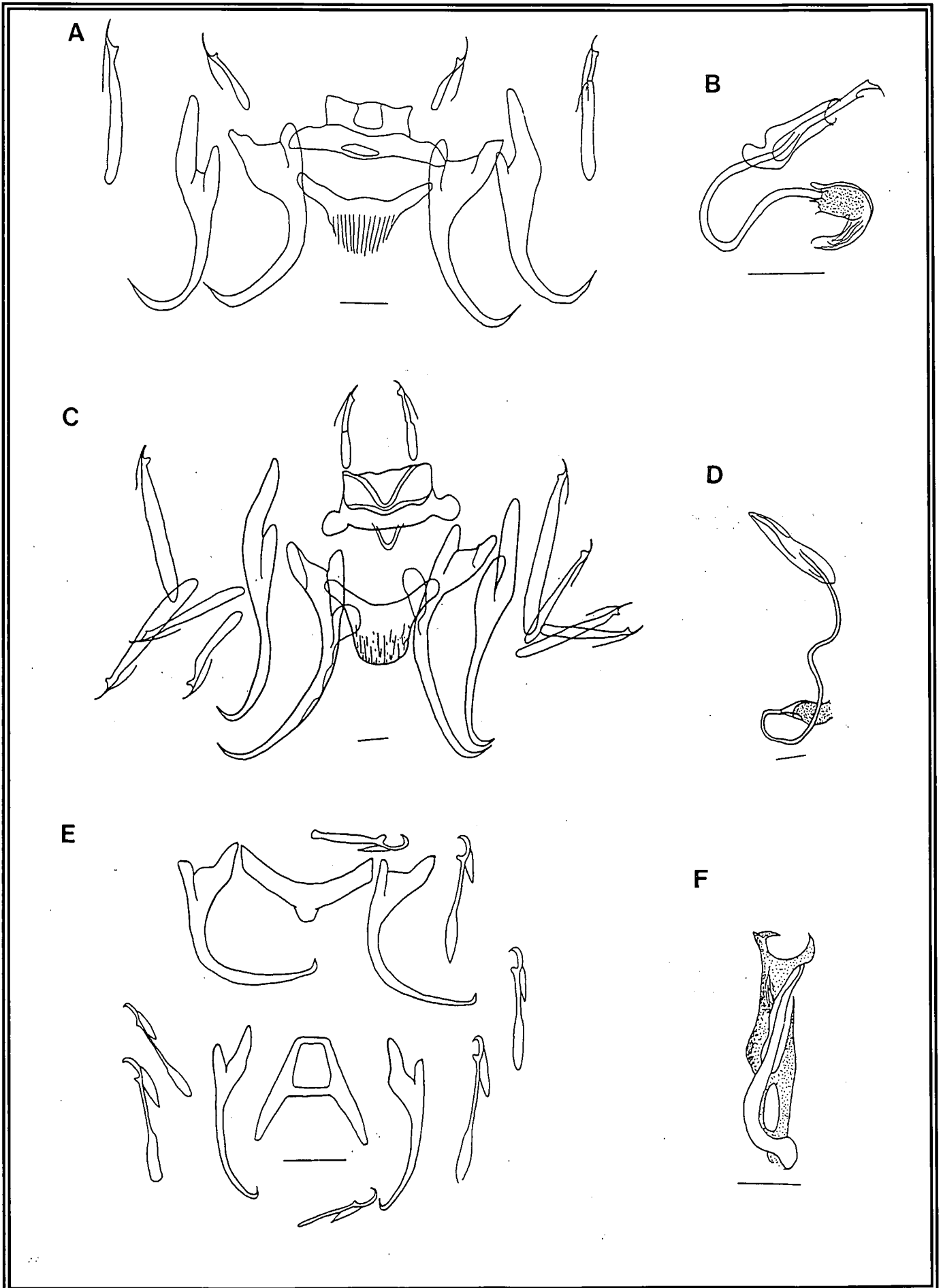
D



## FIGURE 4.14

- A. Diagram showing the structure of the opisthaptoral armature of *Annulotrema nili* Paperna, 1973. (redrawn from Paperna, 1979)
- B. Diagram showing the structure of the copulatory organ of *Annulotrema nili* Paperna, 1973. (redrawn from Paperna, 1979)
- C. Diagram showing the structure of the opisthaptoral armature of *Annulotrema nili ruahae* Paperna, 1979. (redrawn from Paperna, 1979)
- D. Diagram showing the structure of the copulatory organ of *Annulotrema nili ruahae* Paperna, 1979. (redrawn from Paperna, 1979)
- E. Diagram showing the structure of the opisthaptoral armature of *Annulotrema noyongensis* Birgi, 1988. (redrawn from Birgi, 1988)
- F. Diagram showing the structure of the copulatory organ of *Annulotrema noyongensis* Birgi, 1988. (redrawn from Birgi, 1988)

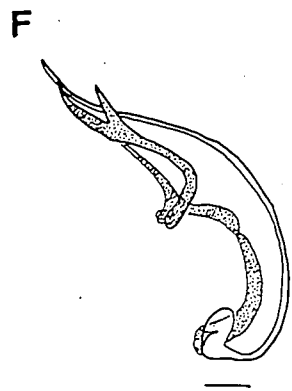
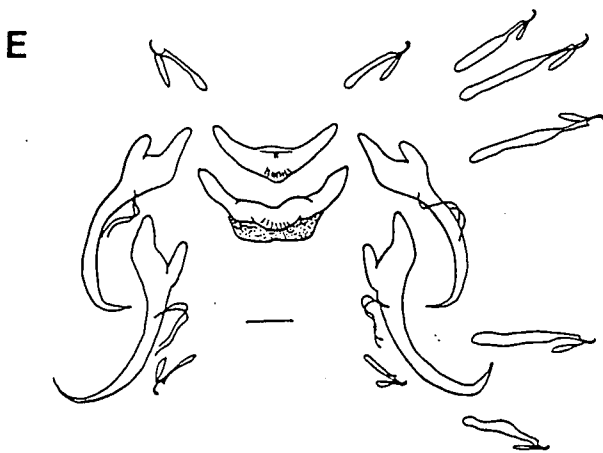
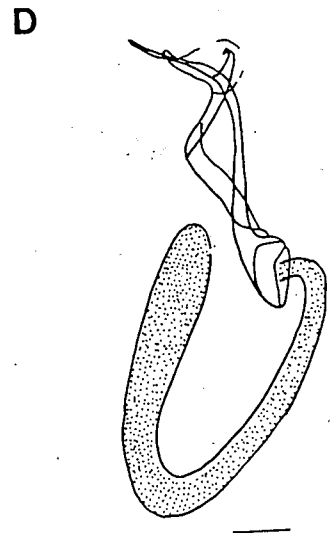
Scale bar: 10  $\mu\text{m}$



## FIGURE 4.15

- A. Diagram showing the structure of the opisthaptoral armature of *Annulotrema pikei* (Price, Peebles & Bamford, 1969). (redrawn from Paperna, 1979)
- B. Diagram showing the structure of the copulatory organ of *Annulotrema pikei* (Price, Peebles & Bamford, 1969). (redrawn from Paperna, 1979)
- C. Diagram showing the structure of the opisthaptoral armature of *Annulotrema pikei ruahae* Paperna, 1979. (redrawn from Paperna, 1979)
- D. Diagram showing the structure of the copulatory organ of *Annulotrema pikei ruahae* Paperna, 1979. (redrawn from Paperna, 1979)
- E. Diagram showing the structure of the opisthaptoral armature of *Annulotrema pikoides* Guegan, Lambert & Birgi, 1988. (redrawn from Guegan, *et. al*, 1988)
- F. Diagram showing the structure of the copulatory organ of *Annulotrema pikoides* Guegan, Lambert & Birgi, 1988. (redrawn from Guegan, *et. al*, 1988)

Scale bar: 10  $\mu$ m

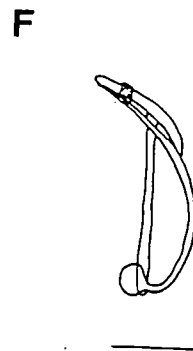
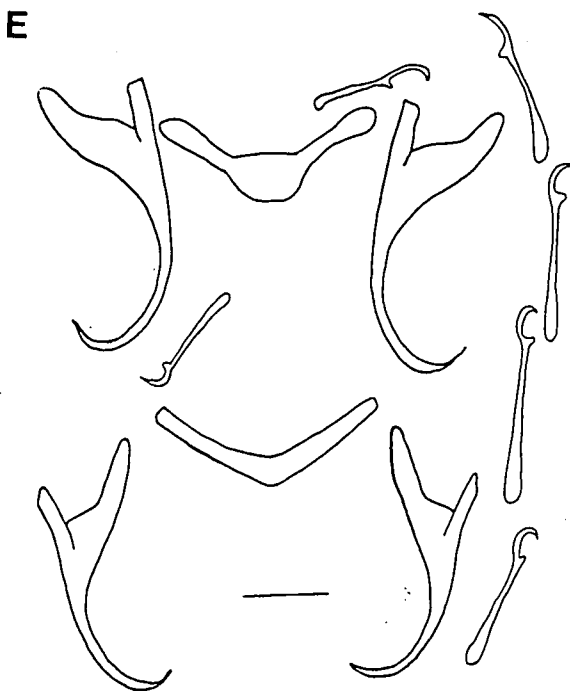
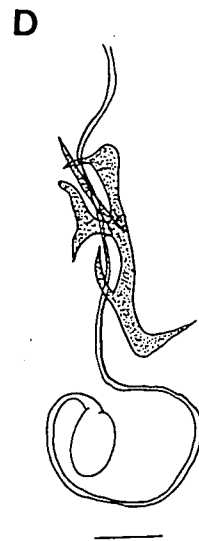
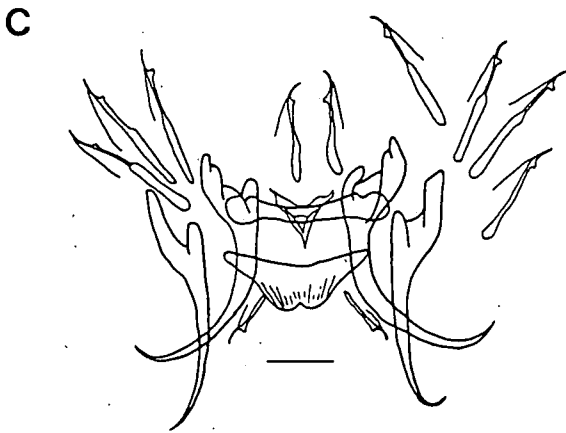
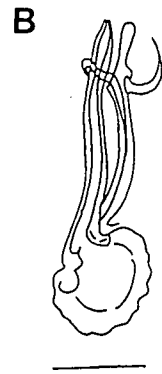




## FIGURE 4.16

- A. Diagram showing the structure of the opisthaptoral armature of *Annulotrema robusta* Paperna, 1969. (redrawn from Paperna, 1969)
- B. Diagram showing the structure of the copulatory organ of *Annulotrema robusta* Paperna, 1969. (redrawn from Paperna, 1969)
- C. Diagram showing the structure of the opisthaptoral armature of *Annulotrema ruahae* Paperna, 1973. (redrawn from Paperna, 1979)
- D. Diagram showing the structure of the copulatory organ of *Annulotrema ruahae* Paperna, 1973. (redrawn from Paperna, 1979)
- E. Diagram showing the structure of the opisthaptoral armature of *Annulotrema sangmelinensis* Birgi, 1988. (redrawn from Birgi, 1988)
- F. Diagram showing the structure of the copulatory organ of *Annulotrema sangmelinensis* Birgi, 1988. (redrawn from Birgi, 1988)

Scale bar: 10  $\mu\text{m}$

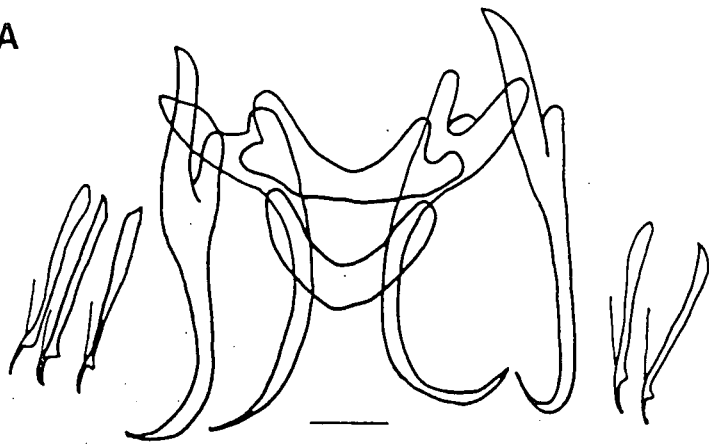


## FIGURE 4.17

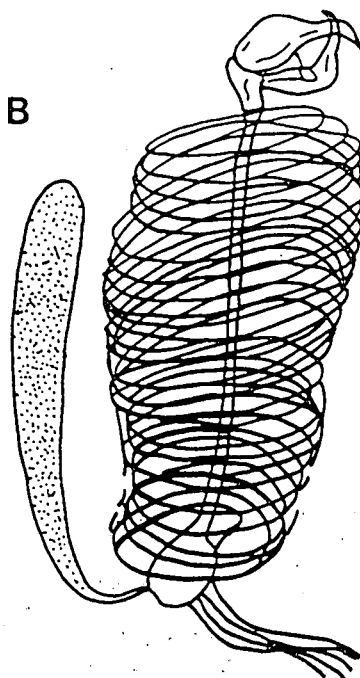
- A. Diagram showing the structure of the opisthaptoral armature of *Annulotrema spiropenis* Paperna, 1969. (redrawn from Paperna, 1969)
- B. Diagram showing the structure of the copulatory organ of *Annulotrema spiropenis* Paperna, 1969. (redrawn from Paperna, 1969)
- C. Diagram showing the structure of the opisthaptoral armature of *Annulotrema tenuicirra* Paperna, 1973. (redrawn from Paperna, 1979)
- D. Diagram showing the structure of the copulatory organ of *Annulotrema tenuicirra* Paperna, 1973. (redrawn from Paperna, 1979)

Scale bar: 10  $\mu\text{m}$

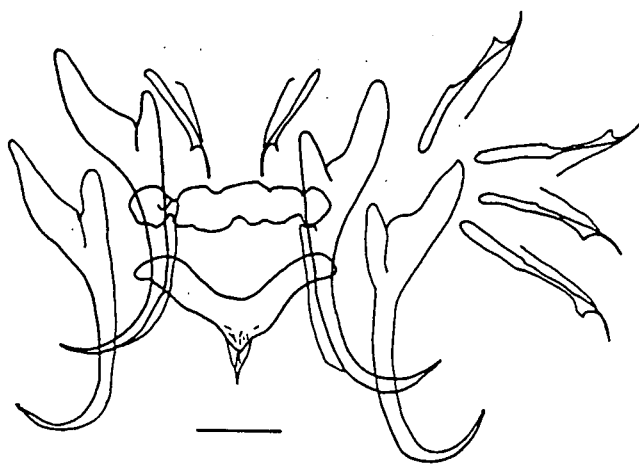
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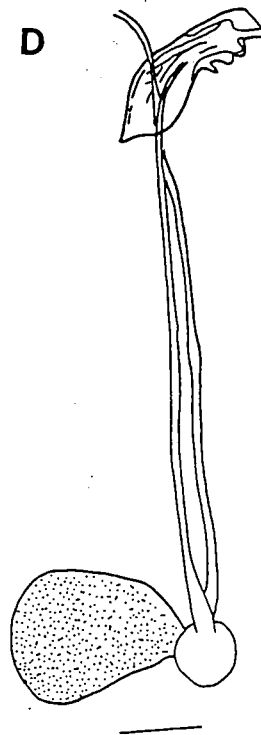
B



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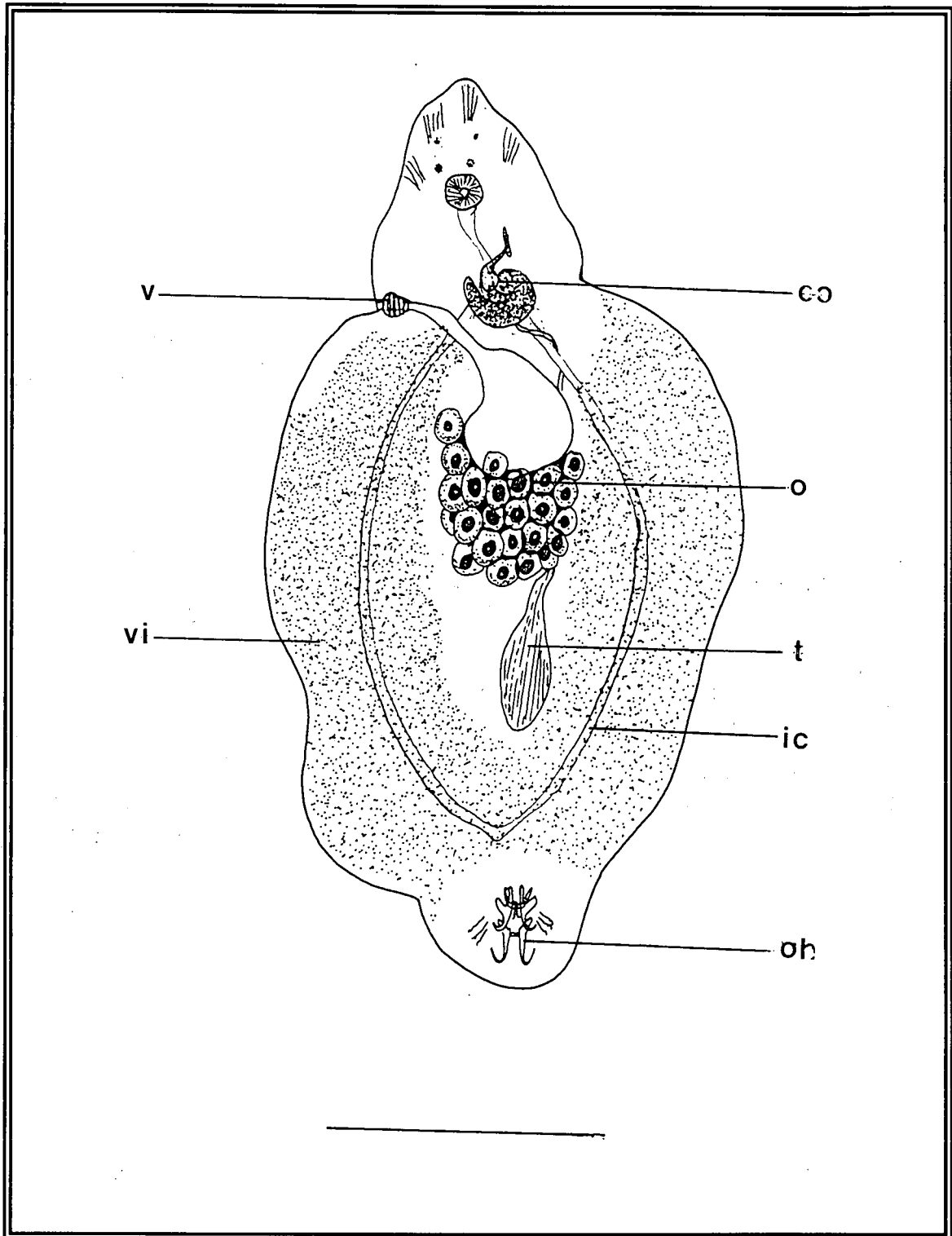


**THE GENUS *CHARACIDOTREMA* PAPERNA & THURSTON, 1968**

Species of the genus *Characidotrema*, are parasites of characiform fish in Africa. This genus is represented by 10 species, only infesting fishes of the family Characidae. *Characidotrema* shares many common characteristics with a closely related Neotropical genus, *Jainus* Mizelle, Kritsky & Crane, 1968, but is now considered as a separate genus. The similarities of this Ethiopian genus and the Neotropical genus once again indicate ancient evolutionary relationships between these two provinces.

**GENERIC DIAGNOSIS**

According to Paperna & Thurston (1968) the genus *Characidotrema* belongs to the family Dactylogyridae and sub-family Ancyrocephalinae. *Characidotrema* (Table 4.4) can be described as having a thick cuticle which is usually spinous, ciliated, papiliated or gently annulated. The cephalic region is well delimited and possesses four eyes and a muscular pharynx. The intestine consists of two caeca which do not unite posteriorly. Long muscles extend along the sides of the body from the prohaptor to the opisthaptor. The opisthaptor is fully merged with the posterior end of the body. Both the opisthaptor and the anchors are reduced in size. The outer root of the ventral anchors is much larger than the inner root. The marginal hooklets are arranged in two groups of six hooklets, one group in each of the lateral margins of the anterior most part of the opisthaptor. Another pair of small hooklets is found on the distal margin of the opisthaptor. The testis is located in a position dorso-posterior to the ovary. The vagina opens on the sinistral side of the body. A seminal receptacle is present and the vitellaria are massed on both sides of the ovary testis zone. The copulatory organ consists of a rounded funnel, a tubular cirrus and an accessory piece. Prostatic glands as well as a seminal vesicle are also present.



**FIGURE 4.18** Illustration of the morphological features of *Characidotrema* Paperna & Thurston, 1968 species. v- Vagina, vi- Vitellaria, co- copulatory organ, o- Ovaries, t- Testes, ic- Intestinal caeca, oh- Opisthaptor. Scale bar: 100  $\mu$ m

**TABLE 4.4 Summary of the taxonomic characters of representatives of the genus *Characidotrema* Paperna & Thurston, 1968**

<i>Characidotrema</i> Paperna & Thurston, 1968	
BODY	<ul style="list-style-type: none"> <li>• Cuticle usually thick, spinous, ciliated, papiliated or gently annulated</li> <li>• Long strips of muscles extend along two sides of body, from prohaptor to opisthaptor</li> </ul>
HAPTOR	<ul style="list-style-type: none"> <li>• Opisthaptor is fully merged with posterior end of body</li> <li>• Both opisthaptor and anchors reduced in size</li> <li>• Outer root of ventral anchors far larger than inner root</li> <li>• Marginal hooklets arranged in two groups of seven hooklet</li> </ul>
DIGESTIVE TRACT	<ul style="list-style-type: none"> <li>• Intestine consists of two caeca which do not unite posteriorly</li> </ul>
FEMALE REPRODUCTIVE SYSTEM	<ul style="list-style-type: none"> <li>• Vagina opens on left of body</li> <li>• Vaginal wall is muscular</li> <li>• Seminal receptacle present</li> <li>• Vitelline follicles massed on both sides of ovary-testis zone</li> </ul>
MALE REPRODUCTIVE SYSTEM	<ul style="list-style-type: none"> <li>• Testis located dorsoposterior to ovary</li> <li>• Copulatory organ consists of rounded funnel, tubular cirrus and accessory piece</li> <li>• Prostatic glands and seminal vesicle present</li> </ul>
GENERAL	<ul style="list-style-type: none"> <li>• Cephalic region and organs well delimited from rest of body</li> <li>• Four eyes present</li> <li>• Pharynx present, usually muscular</li> </ul>

## HISTORY OF THE GENUS *CHARACIDOTREMA*

The genus *Characidotrema* was created by Paperna & Thurston (1968) to accommodate *Characidotrema elongata* Paperna & Thurston, 1968, an ancyrocephaline monogenean with a reduced opisthaptor fused into the posterior end of the body and small anchors, collected from the gills of *Brycinus nurse* from Uganda. In 1969 Paperna described a new species, *Characidotrema brevipenis*, from Ghana as well as recording *C. elongata* from the same locality. According to Paperna & Thurston (1968) the specimens from Ghana differed from the type specimens in the structure of the cuticle, further reduction of the opisthaptor and morphological differences of the copulatory organ. In 1973, Ergens described *Characidotrema nursei* from *Brycinus nurse* in Egypt.

Shortly after the proposal of the genus *Characidotrema*, Paperna (1973) synonymised it with the Neotropical genus *Jaimus*. According to Kritsky, *et al.* (1987), this synonymy was not totally without merit as members of both genera exhibit characters that are similar and some-what unique. Representatives from both genera have robust bodies with poorly developed opisthaptors, modified ventral anchor-bar complexes,

overlapping gonads, strongly developed vitellaria and both taxa are restricted as parasites of characin fish (Kritsky, *et al.* 1987). Subsequently, Paperna (1973) described two new species, *Jainus longipenis* and *Jainus spinivaginus*, both from *Alestes nurse* in Uganda. The two species *Characidotrema nursei* and *Jainus longipenis* were synonymised by Kritsky, *et al.* (1987) and retained the classification of *Characidotrema nursei* as proposed by Ergens (1973).

In 1979 Paperna, described two more sub-species, *Jainus brevipenis ruahae* and *J. brevipenis nzoiae*, from Kenya and Tanzania. Both these two sub-species were later recognised as separate individual species.

Kritsky, *et al.* (1987) resurrected the genus *Characidotrema* for the Ethiopian component of the genus *Jainus*. Their reasons for this were based on information obtained from the re-examination of the type material of previously described species. According to Kritsky, *et al.* (1987) all of the Ethiopian species as well as the new ones described by them in 1987 possess relatively uniform morphology of the haptoral sclerites, which is fundamentally different from that of species in the Neotropical genus *Jainus*. Features of the internal organ systems of species of both genera are strikingly similar, but the vagina of *Jainus* is always sinistral and that of *Characidotrema* dextral. Kritsky, *et al.* (1987) also described two new species, *Characidotrema undifera* and *C. zelotes*, both from *Brycinus nurse* in Togo.

In a study of the monogenean freshwater fishes in south Cameroon, Birgi (1988), described a further two species, *Characidotrema regia* and *C. spiroopenis*, from *Brycinus kingsleyae* (Günther, 1896) and *Phenacogrammus major* Boulenger, 1903 respectively.

There are currently 10 known species of *Characidotrema*. Table 4.5 summarises these species, their locations and the hosts from where these monogeneans were described.



**TABLE 4.5 Checklist of all the currently known African species of the genus *Characidotrema* Paperna & Thurston, 1968, their hosts and distribution.**

SPECIES	SYNONYM	HOST	DISTRIB
<i>C. brevipenis</i> Paperna, 1969		<i>Alestes baremose</i> , <i>Brycinus nurse</i>	Ghana
<i>C. elongata</i> Paperna & Thurston, 1968		<i>Brycinus leuciscus</i> , <i>Brycinus nurse</i>	Ghana, Uganda
<i>C. nursei</i> Ergens, 1973	<i>Jainus longipenis</i> Paperna 1973	<i>Alestes dentex</i> , <i>Brycinus leuciscus</i> , <i>Brycinus nurse</i>	Egypt, Ghana
<i>C. nzoiae</i> (Paperna, 1979)	<i>Jainus brevipenis</i> <i>nzoiae</i> Paperna 1979	<i>Brycinus jacksoni</i>	Kenya
<i>C. regia</i> Birgi, 1988		<i>Brycinus kingsleyae</i>	Cameroon
<i>C. ruahae</i> (Paperna, 1979)	<i>Jainus brevipenis</i> <i>ruahae</i> Paperna 1979	<i>Brycinus imberi</i>	Tanzania
<i>C. spinivaginus</i> (Paperna, 1973)	<i>Jainus spinivagina</i> Paperna 1973	<i>Brycinus nurse</i>	Uganda, Ghana
<i>C. spiropenis</i> (Birgi, 1988)	<i>Jainus spiropenis</i> Birgi 1988	<i>Phenacogrammus</i> <i>major</i> , <i>Phenacogrammus</i> <i>urotaenia</i> , <i>Hemigrammopetersius</i> <i>pulcher</i>	Cameroon
<i>C. undifera</i> Kritsky, Kulo & Boeger, 1987		<i>Brycinus nurse</i>	Togo
<i>C. zelotes</i> Kritsky, Kulo & Boeger, 1987		<i>Brycinus nurse</i>	Togo

## DISTRIBUTION OF SPECIES OF THE GENUS *CHARACIDOTREMA*

The distribution of species in the genus *Characidotrema* (Figure 4.19) is very similar to that of *Annulotrema*. The differences between these two genera is that *Annulotrema* occurs as far south as the Pongola system in South Africa and *Characidotrema* has never been recorded further south than Tanzania. The geographical distribution is just as artificial as that of *Annulotrema* due to the lack of research conducted in the regions where the hosts occur.

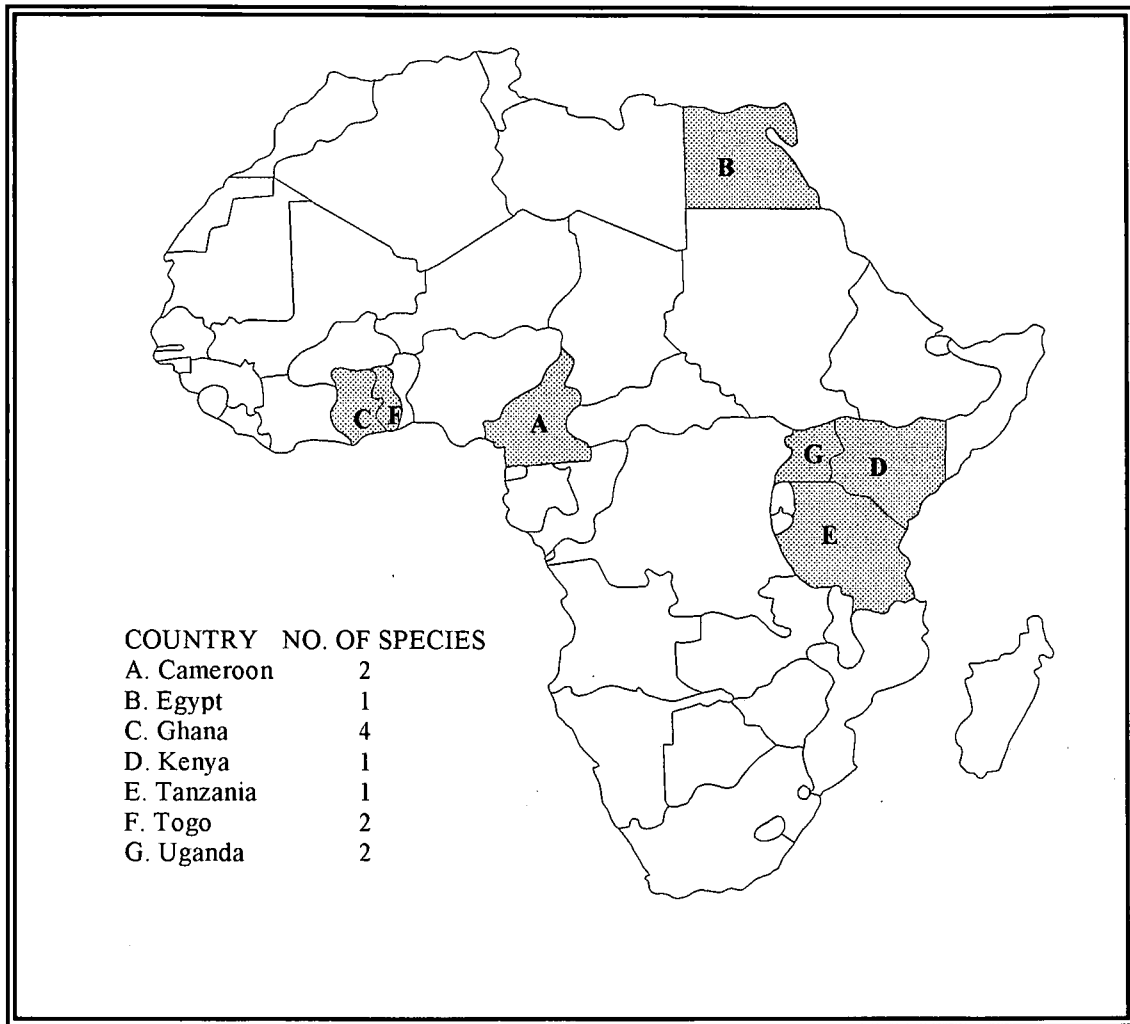
*Characidotrema* species have been recorded from 10 characin fish hosts (Table 4.6). The host species being infested by the most *Characidotrema* species is *Brycinus nurse*. This can be attributed to the widespread distribution of this *B. nurse* as well as its abundance in the water bodies where it occurs. *Brycinus nurse* is host to six of the 10 host species recorded thus far.

The species of the genus *Characidotrema* appear to exhibit varying degrees of host specificity. Four of the 10 species of *Characidotrema* have been recorded from more than one host species, however, only *Characidotrema spiropenis* has been recorded from host species of different genera. According to Birgi (1988) the remaining six species seem to exhibit a more exclusive host specificity.

**TABLE 4:6** Fish hosts of species of the genus *Characidotrema* Paperna & Thurston, 1968

	1	2	3	4	5	6	7	8	9	10
<i>C. brevipenis</i>	•						•			
<i>C. elongata</i>						•	•			
<i>C. nursei</i>		•				•	•			
<i>C. nzoiae</i>				•						
<i>C. regia</i>					•					
<i>C. ruahae</i>			•							
<i>C. spinivaginus</i>							•			
<i>C. spiropenis</i>								•	•	•
<i>C. undifera</i>							•			
<i>C. zelotes</i>							•			

1. *Alestes baremose* 2. *Alestes dentex* 3. *Brycinus imberi* 4. *Brycinus jacksoni* 5. *Brycinus kingsleyae* 6. *Brycinus leusiscus* 7. *Brycinus nurse* 8. *Hemigrammopetersius pulcher* 9. *Phenacogrammus major* 10. *Phenacogrammus urotaenia*



**FIGURE 4.19** Distribution of species of the genus *Characidotrema* Paperna & Thurston, 1968 in Africa indicating the number of species recorded from each country.

## REVIEW OF SPECIES

The reviews of the following species of the genus *Characidotrema* are based on summaries of their original descriptions. The original descriptions of the species have been summarised and edited to establish uniformity in the terminology used. All measurements are reproduced exactly as they appeared in their original form and are expressed in micrometers.

### *Characidotrema brevipenis* Paperna, 1969

**Host and Locality:** *Alestes baremose*, *Brycinus nurse*, Ghana.

**Description and Measurements:** (Kritsky, *et al.* 1987). Body foliform, total length 317 (217-425), width 91 (59-125). Tegument smooth. Cephalic margin round or truncate, lobes poorly developed or absent, cephalic glands indistinct. Four eyes, posterior pair larger than anterior pair, eye granules ovate to subspherical. Pharynx spherical, pharynx diameter 19 (13-22). Opisthaptor subhemispherical. Dorsal anchor 26 (24-27), dorsal bar 17 (16-19). Ventral anchor 19 (17-21), ventral bar (9-10) (Figure 4.20A). Cirrus 39 (38-40), accessory piece 22 (20-24) (Figure 4.20B). Testis subovate 52 (49-56) x 30 (24-36), seminal vesicle with thick muscular wall. Ovary subovate 84 (45-144) x 25 (17-32). Vagina at level of seminal vesicle.

### *Characidotrema elongata* Paperna & Thurston, 1968

**Host and Locality:** *Brycinus leuciscus*, *Brycinus nurse*, Ghana, Uganda.

**Description and Measurements:** (according to Paperna, 1969). Total length (250-300), width (50-100). Dorsal anchors 30, inner root 5-7, outer root 2-3. Dorsal bar 15. Ventral anchors 20, inner root 5, outer root 1. Ventral bar 15 (Figure 4.20C-D).

### *Characidotrema nursei* Ergens, 1973

**Host and Locality:** *Alestes dentex*, *Brycinus leuciscus*, *Brycinus nurse*, Egypt, Ghana.

**Description and Measurements:** (according to Paperna, 1979). Large worms, total length 570-740, width 140-250. Opisthaptor more reduced than other members of genus. Dorsal anchors 19-24, inner root 5-10, outer root 1-2, shaft 14-15, tip 3-5. Dorsal bar 15-17, dorsal bar width 1-2. Ventral anchors 13-17, inner root 4-6, outer root 4-7, shaft 9-12, tip 3-3. Ventral bar 9-12, ventral bar width 2-3, ventral bar arms 9-10. Marginal hooklets 7-18 (Figure 4.20E). Cirrus 70-100, very long delicate tube.

Accessory piece 17-20 sclerotised only at dextral extremity (Figure 4.20F). Vagina 45-48, sclerotised elongated tube. Vitelline zone extends from the opisthaptor to pharynx.

*Characidotrema nzoiae* (Paperna, 1973)

**Host and Locality:** *Brycinus jacksoni*, Kenya

**Description and Measurements:** (according to Paperna, 1979). Total length 300-440. Prohaptor length 120-160, prohaptor width 40-60. Dorsal anchors 13-17, inner root 6-6, outer root 1-3, shaft 10-13, tip 3-4. Dorsal bar 22. Ventral anchor 10-14, inner root 4-6, outer root 3-6, shaft 6-9, tip 2-3. Ventral bar 9-11. Marginal hooklets 9-10 (Figure 4.21A). Cirrus 15-20 (Figure 4.21B).

*Characidotrema regia* Birgi, 1988

**Host and Locality:** *Brycinus kingsleyae*, Ebogo, Cameroon.

**Description and Measurements:** (according to Birgi, 1988). Total length 250-450. Dorsal anchors 20-22, inner root 6-8, outer root 1-2, shaft 15-18, tip 7-9. Dorsal bar 20, dorsal bar width 2. Ventral anchors 18-22, inner root 7-9, outer root 5-7, shaft 10-15, tip 2. Ventral bar 10, ventral bar width 10-13, ventral bar arms 2-5. Marginal hooklets; III-IV= 13-17, V-VI-VII= 15-17 (Figure 4.21C). Cirrus 35-45 (Figure 4.21D). Vagina sclerotised 15-20.

*Characidotrema ruahae* (Paperna, 1979)

**Host and Locality:** *Brycinus imberi*, Tanzania.

**Description and Measurements:** (according to Paperna, 1979). Total length 350-400. Prohaptor length 80-90, prohaptor width 50-50. Dorsal anchors 19-21, inner root 5-8, outer root vestigial, shaft 15-17, tip 4-8. Dorsal bar 15-16. Ventral anchor 12-14, inner root 6-7, outer root 4-6, shaft 9-10. Ventral bar 9-14. Marginal hooklets 11-12 (Figure 4.21E). Cirrus 34-46 (Figure 4.21F).

*Characidotrema spinivaginus* (Paperna, 1973)

**Host and Locality:** *Brycinus nurse*, Volta Lake, Ghana, Lake Albert, Uganda.

**Description and Measurements:** (according to Paperna, 1979). Medium size worms, total length 400-470, width 70-120. Dorsal anchors 20-29, inner root 6-13, outer root 1-1, shaft 15-18, tip 3-5. Dorsal bar 17-20, dorsal bar width 1-1. Ventral anchors 12-17, inner root 5-6, outer root 4-5, shaft 8-9, tip 3-4. Ventral bar 9-10, ventral bar width 3-4, ventral bar arms 14-15. Marginal hooklets 14-15 (Figure 4.22A). Cirrus 63-80, accessory piece 5-5 (Figure 4.22B). Vaginal prop 10-15 x 9-10, triangular armed with large strong spines or dents

*Characidotrema spiropenis* (Birgi, 1988)

**Host and Locality:** *Phenacogrammus major*, *Phenacogrammus urotaenia*, *Hemigrammopetersius pulcher*, Yaoundé, Sangmélina.

**Description and Measurements:** (according to Birgi, 1988). Total length 350-750, width 40-120. Dorsal anchors 20-22, inner root 6-8, outer root 1-2, shaft 15-16, tip 6-8. Ventral anchors 16-18, inner root 5-6, outer root 6-8, shaft 10-11, tip 2. Ventral bar 8-10, ventral bar width 2. Marginal hooklets; I-II= 10-14, III-IV= 13-15, V-VI-VII= 15-18 (Figure 4.22C). Cirrus forms up to 5 spirals, 10 long and 8 wide. Accessory piece 15, accessory piece width 2 (Figure 4.22D).

*Characidotrema undifera* Kritsky, Kulo & Boeger, 1987

**Host and Locality:** *Brycinus nurse*, Mono River, Kolokopé, Togo.

**Description and Measurements:** (according to Kritsky, *et al.*, 1987). Body spindle shaped, total length 401 (303-499), width 163 (140-238). Cephalic region with two terminal, poorly developed cephalic lobes. Pharynx spherical, pharynx diameter 34 (27-41). Opisthaptor indistinct, extension of body trunk. Dorsal anchor 30 (28-31), base width 10 (9-12). Dorsal bar 15 (14-16). Ventral anchor 26 (23-29), base width 13 (11-14). Ventral bar 15-16, bilateral arms elongate, well developed. Marginal hooklet 18 (14-20) (Figure 4.23A). Cirrus 34 (33-35), curved shaft with subterminal angular bend. Accessory piece 15 (13-18), long, curved (Figure 4.23B). Gonads subovate, testis 72 (53-85) x 38 (27-39). Ovary 123 (75-150) x 39 (28-45). Vagina opening dextroventral, delicate sclerotised tube slight distal enlargement. Vitellaria comprising large cellular masses.

*Characidotrema zelotes* Kritsky, Kulo & Boeger, 1987

**Host and Locality:** *Brycinus nurse*, Mono River, Kolokopé, Togo.

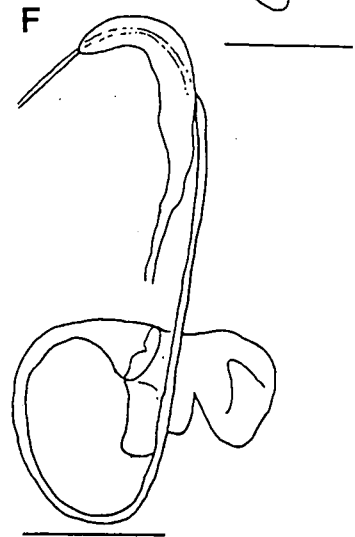
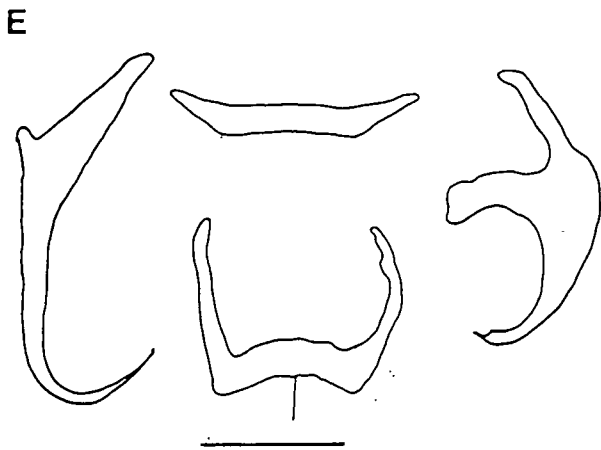
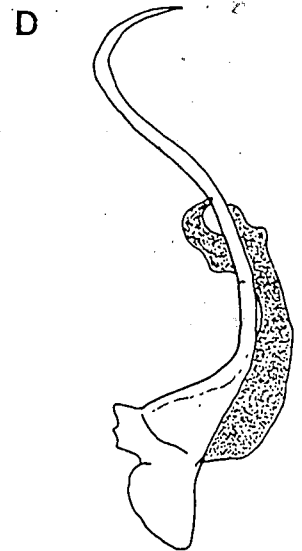
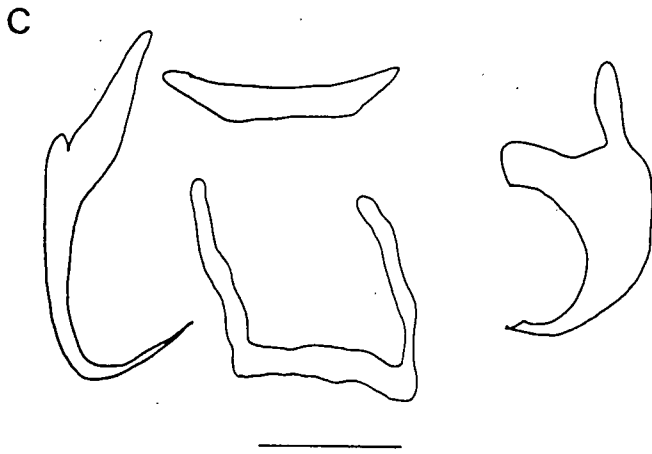
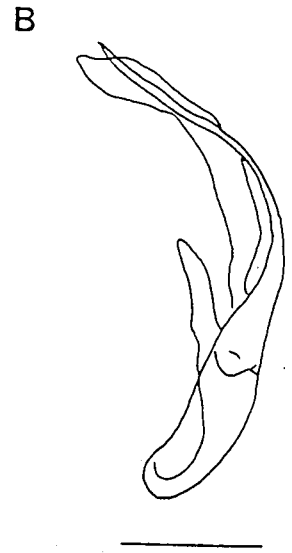
**Description and Measurements:** (according to Kritsky, *et al.*, 1987). Body foliiform, total length 216 (169-250), width 111 (92-136). Cephalic margin rounded or with two poorly developed lobes. Pharynx spherical, pharynx diameter 13-14. Opisthaptor extension of trunk. Dorsal anchor 22 (20-23), base width 8 (7-9). Dorsal bar 15 (14-17). Ventral anchor 16 (13-18), base width 9 (7-10). Ventral bar 10 (9-11), bilateral arms delicate (Figure 4.23C). Cirrus 28-29. Accessory piece 13 (11-14) (Figure 4.23D). Gonads overlapping, ovate to pyriform. Testis 49 (45-53) x 33 (25-40). Ovary 72 (64-79) x 34 (29-38). Seminal vesicle bulbous. Vagina unsclerotised opening dextroventrally. Vitellaria well developed, absent from cephalic and haptoral regions.

## FIGURE 4.20

- A. Diagram showing the structure of the opisthaptor armature of *Characidotrema brevipenis* Paperna, 1969. (redrawn from Kritsky, *et. al*, 1987)
- B. Diagram showing the structure of the copulatory organ of *Characidotrema brevipenis* Paperna, 1969. (redrawn from Kritsky, *et. al*, 1987)
- C. Diagram showing the structure of the opisthaptor armature of *Characidotrema elongata* Paperna & Thurston, 1968. (redrawn from Kritsky, *et. al*, 1987)
- D. Diagram showing the structure of the copulatory organ of *Characidotrema elongata* Paperna & Thurston, 1968. (redrawn from Kritsky, *et. al*, 1987)
- E. Diagram showing the structure of the opisthaptor armature of *Characidotrema nursei* Ergens, 1973. (redrawn from Kritsky, *et. al*, 1987)
- F. Diagram showing the structure of the copulatory organ of *Characidotrema nursei* Ergens, 1973. (redrawn from Kritsky, *et. al*, 1987)

Scale bar: 10  $\mu$ m



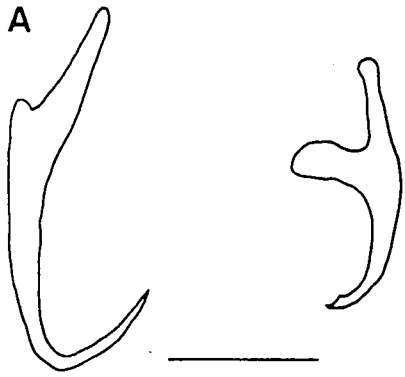


## FIGURE 4.21

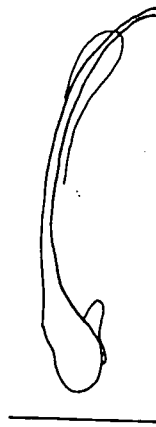
- A. Diagram showing the structure of the opisthaptoral armature of *Characidotrema nzoiae* (Paperna, 1979). (redrawn from Kritsky, *et. al*, 1987)
- B. Diagram showing the structure of the copulatory organ of *Characidotrema nzoiae* (Paperna, 1979). (redrawn from Kritsky, *et. al*, 1987)
- C. Diagram showing the structure of the opisthaptoral armature of *Characidotrema regia* Birgi, 1988. (redrawn from Birgi, 1988)
- D. Diagram showing the structure of the copulatory organ of *Characidotrema regia* Birgi, 1988. (redrawn from Birgi, 1988)
- E. Diagram showing the structure of the opisthaptoral armature of *Characidotrema ruahae* (Paperna, 1979). (redrawn from Kritsky, *et. al*, 1987)
- F. Diagram showing the structure of the copulatory organ of *Characidotrema ruahae* (Paperna, 1979). (redrawn from Kritsky, *et. al*, 1987)

Scale bar: 10  $\mu$ m

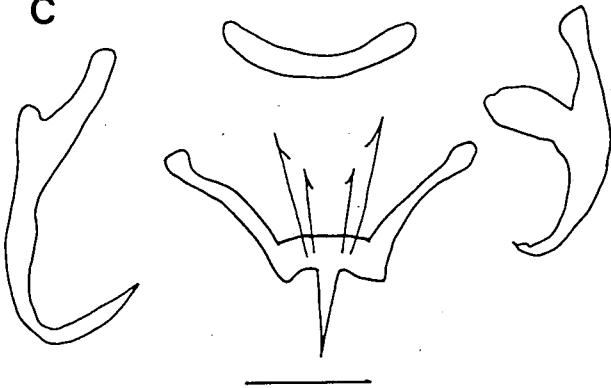
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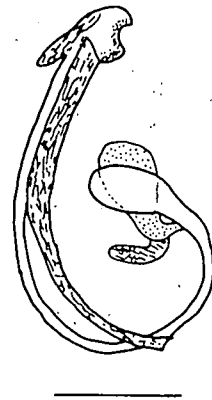
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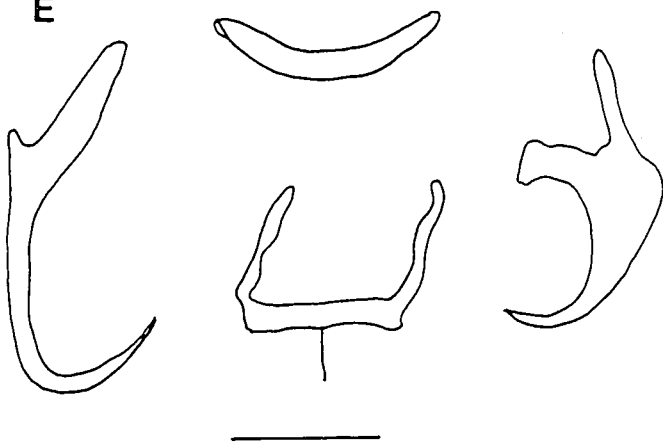
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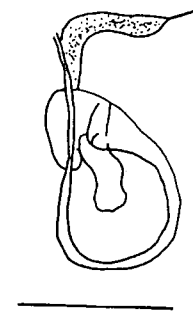
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E



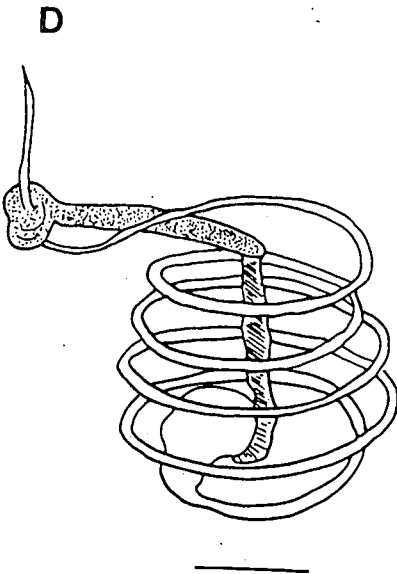
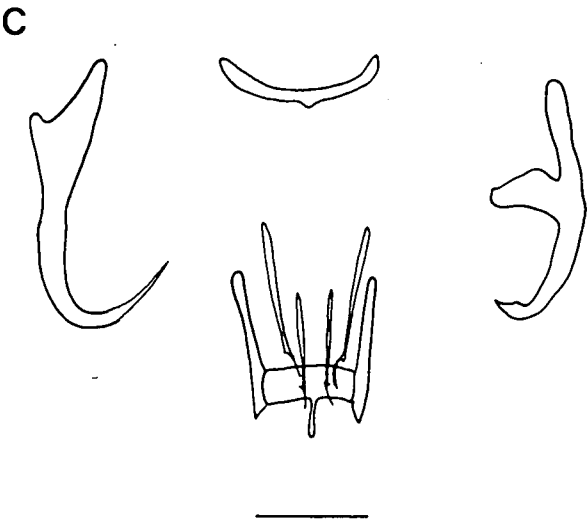
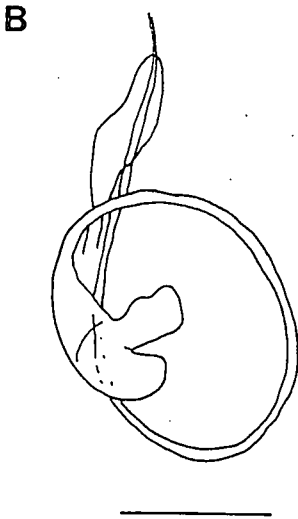
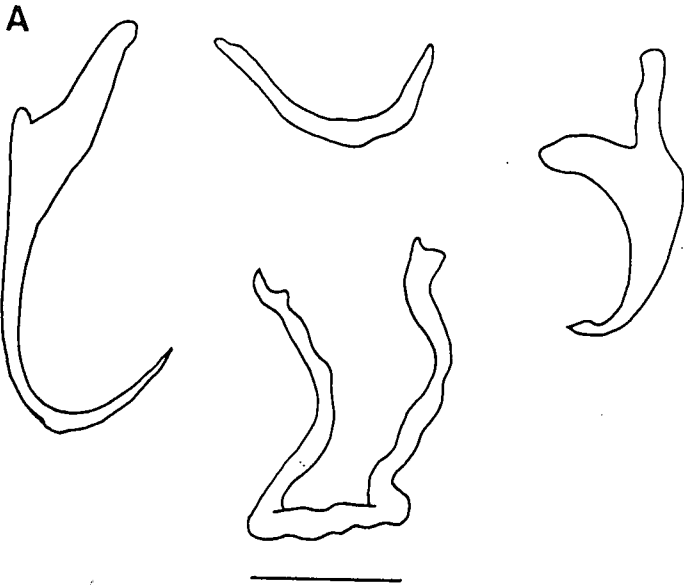
F



## FIGURE 4.22

- A. Diagram showing the structure of the opisthaptoral armature of *Characidotrema spinivaginus* (Paperna, 1973). (redrawn from Kritsky, *et. al*, 1987)
- B. Diagram showing the structure of the copulatory organ of *Characidotrema spinivaginus* (Paperna, 1973). (redrawn from Kritsky, *et. al*, 1987)
- C. Diagram showing the structure of the opisthaptoral armature of *Characidotrema spiopenis* Birgi, 1988. (redrawn from Birgi, 1988)
- D. Diagram showing the structure of the copulatory organ of *Characidotrema spiopenis* Birgi, 1988. (redrawn from Birgi, 1988)

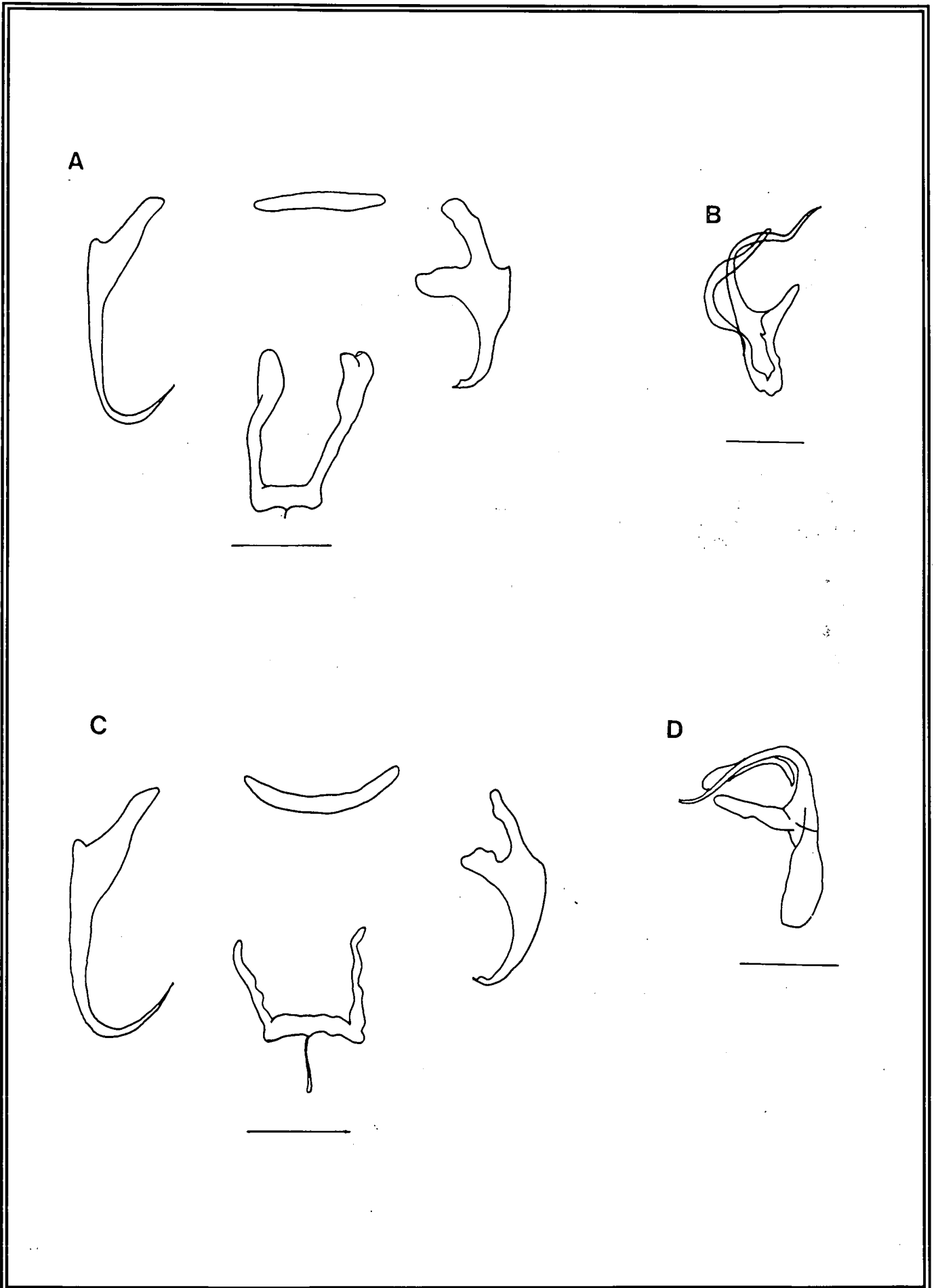
Scale bar: 10  $\mu$ m



## FIGURE 4.23

- A. Diagram showing the structure of the opisthaptoral armature of *Characidotrema undifera* Kritsky, Kulo & Boeger, 1987. (redrawn from Kritsky, *et. al*, 1987)
- B. Diagram showing the structure of the copulatory organ of *Characidotrema undifera* Kritsky, Kulo & Boeger, 1987. (redrawn from Kritsky, *et. al*, 1987)
- C. Diagram showing the structure of the opisthaptoral armature of *Characidotrema zelotes* Kritsky, Kulo & Boeger, 1987. (redrawn from Kritsky, *et. al*, 1987)
- D. Diagram showing the structure of the copulatory organ of *Characidotrema zelotes* Kritsky, Kulo & Boeger, 1987. (redrawn from Kritsky, *et. al*, 1987)

Scale bar: 10  $\mu\text{m}$



# CHAPTER 5





# BRANCHIAL MONOGENEANS OF OKAVANGO CHARACINS

Five species of the genus *Annulotrema* and one species of the genus *Characidotrema* were collected from Okavango characiform fish. Of the five *Annulotrema* species collected, three are known species and the other two, new species, which are described later in this chapter. A species belonging to the genus *Characidotrema* was also collected, this is a known species, previously recorded from northern Africa. The monogeneans collected here all represent new ranges in the geographical distributions, not only of the species but also of the genera.

*Annulotrema* species are characterised by their annulated tegument. These tegumental annulations cover the posterior half of the body trunk and are distinct in most cases. These monogeneans possess a conspicuous opisthaptor bearing two pairs of large anchors and 14 marginal hooklets. Both pairs of anchors were prominent and were supported by two transverse bars, which varied in shape and size from species to species. Another notable feature of these monogeneans is the copulatory organ, which consists of an elongated tubular cirrus and a sclerotised accessory piece, which differs from species to species. The shape and size of the copulatory organs usually a good criterion to use for specific diagnosis as this structure genetically isolates other similar monogeneans which are not suited to accommodate this structure. It is however important to note that similarity in the shape and size of the copulatory organ alone does not necessarily constitute a specific diagnosis, but other criteria are also important in speciation.

Specimens of the genus *Characidotrema* are characterised by a sub-terminal opisthaptor of which the ventral hooks are reduced. As opposed to *Annulotrema* species for example, the opisthaptor of *Characidotrema* species is not prominent. Other characteristics of species in the genus *Characidotrema* is the terminal mouth and the cephalic region, which is clearly distinct from the body trunk.

***Annulotrema curvipenis* Paperna, 1969****HOST:** *Brycinus lateralis* (Boulenger, 1900)**LOCATION ON HOST:** Gills**LOCALITY:** Mainstream (Xaro) (18°25'23.6"S; 21°56'18.2"E), Lagoon (Xaro) & Guma Lagoon (18°57'44.9"S; 22°22'26.7"E).**REFERENCE MATERIAL:** 98 / 07 / 03 - 01**MATERIAL:** Measurements from 10 specimens mounted in Ammonium picrate.

**DESCRIPTION AND MEASUREMENTS:** Small worms, total length  $221 \pm 25.0$  (170-250), width  $77 \pm 10.6$  (70-100) (Figure 5.1A, 5.2A, 5.3A). Tegument smooth, annulated in posterior half, annulations overlapping with wavy edges, annulations not too distinct (Figure 5.3B). Prohaptor (Figure 5.3D) consists of four clearly defined cephalic lobes, sensory setae present on prohaptor, especially on cephalic lobes, prohaptor contains oral opening. Opisthaptor (Figure 5.1B, 5.2B, 5.3C) clearly separated from body trunk, dorsal anchors  $37 \pm 5.1$  (31-45), inner root  $8 \pm 2.6$  (5-12), outer root  $4 \pm 1.2$  (3-6), shaft  $29 \pm 3.4$  (22-32), tip  $3 \pm 1.2$  (2-5) (Figure 5.1B, 5.2C). Dorsal bar length  $23 \pm 4.8$  (18-32), dorsal bar width  $3 \pm 1.5$  (2-6) (Figure 5.1B, 5.2E). Ventral anchors  $39 \pm 5.7$  (32-48), inner root  $8 \pm 2.5$  (4-10), outer root  $3 \pm 0.9$  (2-5), shaft  $32 \pm 6.6$  (25-44), tip  $3 \pm 0.7$  (2-4) (Figure 5.1B, 5.2D). Ventral bar length  $25 \pm 4.1$  (19-28), ventral bar width  $5 \pm 1.0$  (4-6) (Figure 5.1B, 5.2F). Marginal hooklets; I=  $12 \pm 3.5$  (8-17), II=  $22 \pm 5.6$  (12-26), III=  $24 \pm 6.2$  (16-31), IV=  $22 \pm 4.3$  (16-27), V=  $20 \pm 5.1$  (13-29), VI=  $19 \pm 4.7$  (13-26), VII=  $15 \pm 5.7$  (8-25) (Figure 5.1B, 5.2G). Copulatory organ opens ventrally, posterior to oral opening (Figure 5.1C, 5.3E), consists of curved cirrus and distally forked accessory piece (Figure 5.1C, 5.2H), cirrus  $39 \pm 14.0$  (26-65), accessory piece  $15 \pm 2.1$  (12-18). Vagina not sclerotised opening sinistral (Figure 5.3F).

**REMARKS:** When comparing the Okavango population of *Annulotrema curvipenis* with the type population from Uganda, the most obvious difference is in body size. As can be seen from Table 5.1, the Okavango specimens appear to be much smaller than those from Uganda. The sclerotised parts of the two populations, however, show a marked resemblance in shape and size. The ventral transverse bar of the Okavango

material differs slightly from that of the Uganda population in lacking the two anterio-lateral processes indicated by Paperna (1969).

The other marked difference between the populations from the Okavango System and Uganda is the fish host from where these parasites were collected. To date, *Annulotrema curvipenis* has been recorded from *Alestes baremose* and *Hydrocynus forskalii*. The Okavango specimens were recovered from the gills of *Brycinus lateralis*, which represents the first record of these parasites from this host.

**TABLE 5.1** Table comparing the Okavango population of *Annulotrema curvipenis* Paperna, 1969 to the populations from Uganda.

	<b>OKAVANGO</b>	<b>UGANDA</b>
Fish host	<i>Brycinus lateralis</i>	<i>Alestes baremose</i>
Total length	170-250	300-400
Ventral anchor	32-48	40-50
Dorsal anchor	31-45	40-50
Largest marginal hooklet	16-27	18-22
Cirrus	26-65	40-50
Vagina	Not sclerotised	Sclerotised
Annulation	Not too distinct	Not too distinct

## FIGURE 5.1

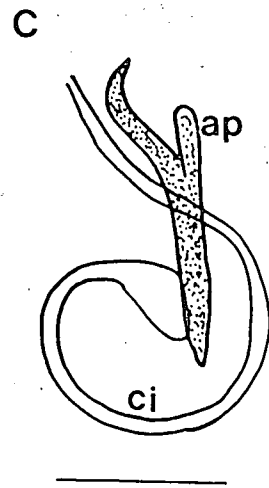
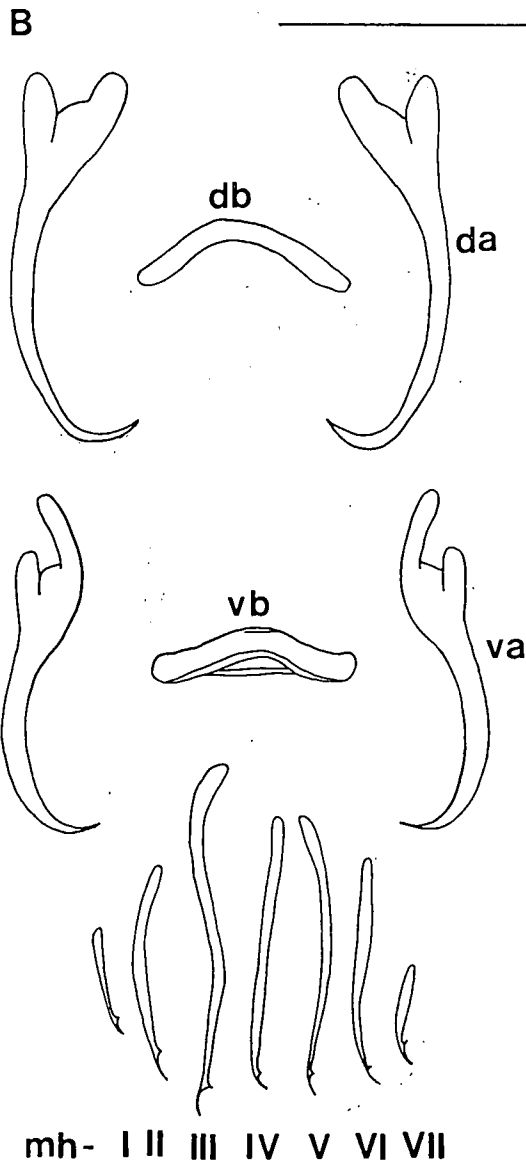
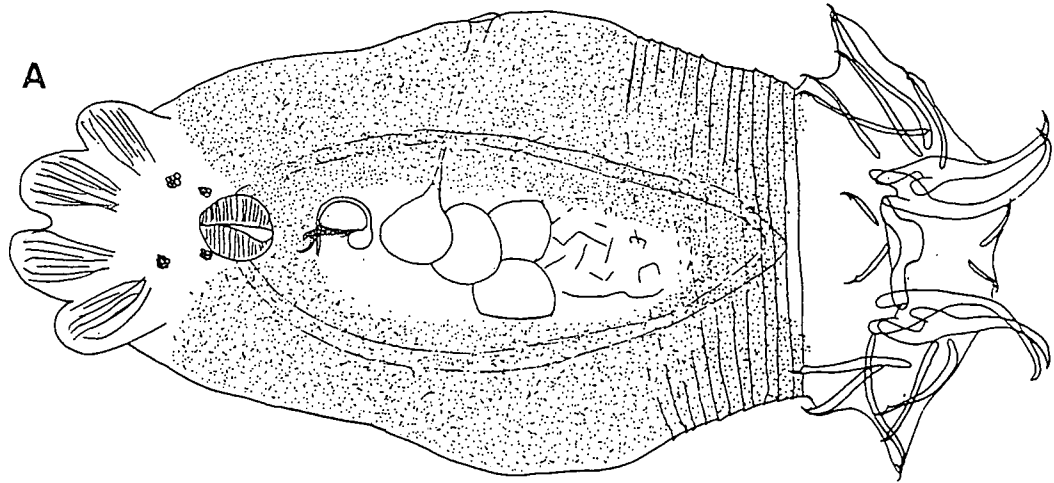
Microscope projection drawings of *Annulotrema curvipenis* Paperna, 1969, occurring on the gill filaments of *Brycinus lateralis* (Boulenger, 1900).

A. Whole mount

B. Opisthaptor sclerites (db-dorsal bar, vb- ventral bar, da- dorsal anchor, va- ventral anchor, mh- marginal hooklets)

C. Copulatory organ (ap- accessory piece, ci- cirrus)

Scale bar: A- 100  $\mu\text{m}$ . B&C- 10  $\mu\text{m}$ .



## FIGURE 5.2

Light micrographs of *Annulotrema curvipenis* Paperna, 1969, occurring on the gill filaments of *Brycinus lateralis* (Boulenger, 1900).

A. Whole mount

B. Opisthaptor

C. Dorsal anchor

D. Ventral anchor

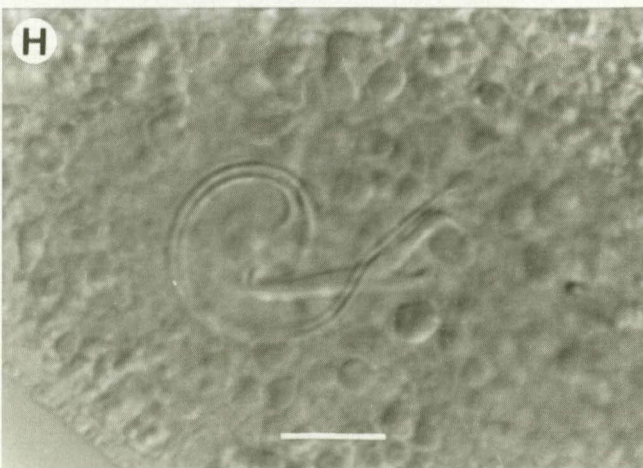
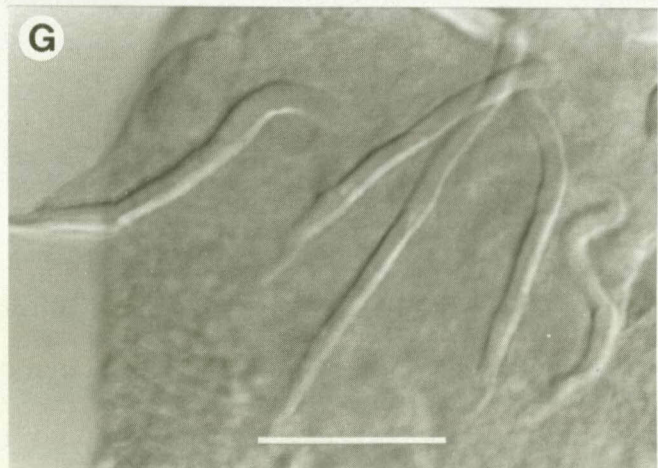
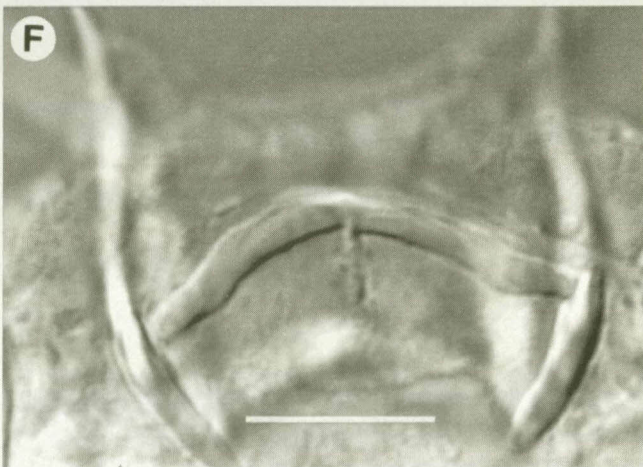
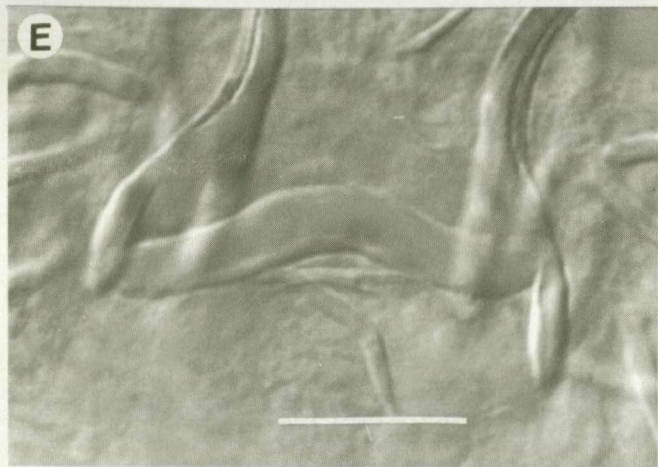
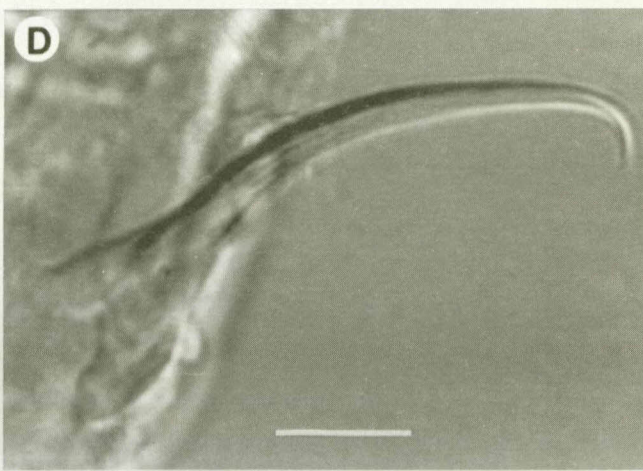
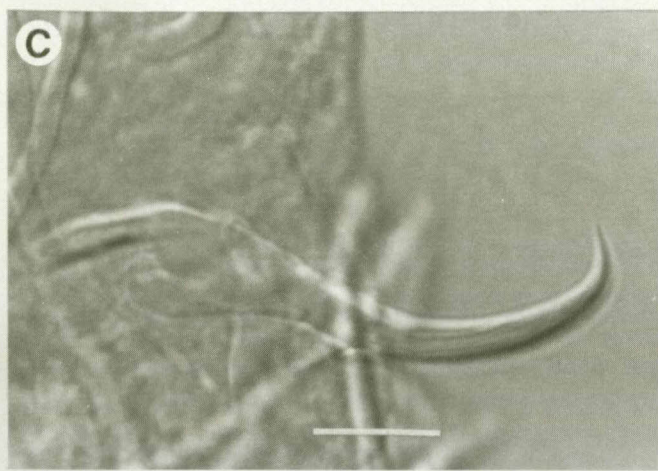
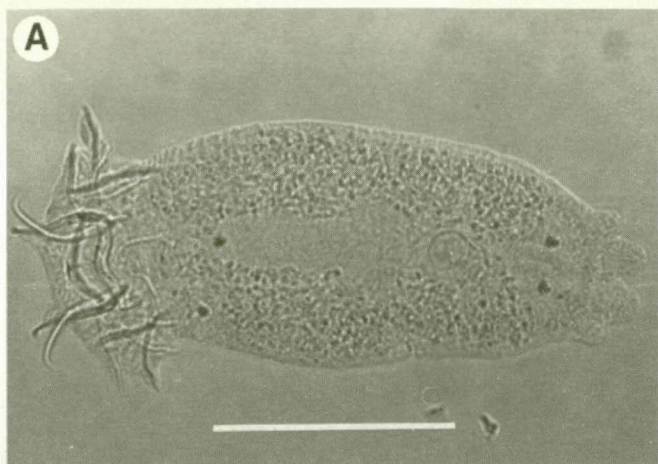
E. Dorsal bar

F. Ventral bar

G. Marginal hooklets

H. Copulatory organ

Scale bar: A- 100  $\mu\text{m}$  B-H- 10  $\mu\text{m}$



## FIGURE 5.3

Scanning electron micrographs of *Annulotrema curvipenis* Paperna, 1969, occurring on the gill filaments of *Brycinus lateralis* (Boulenger, 1900).

A. Whole mount

B. Tegumental annulations

C. Opisthaptor

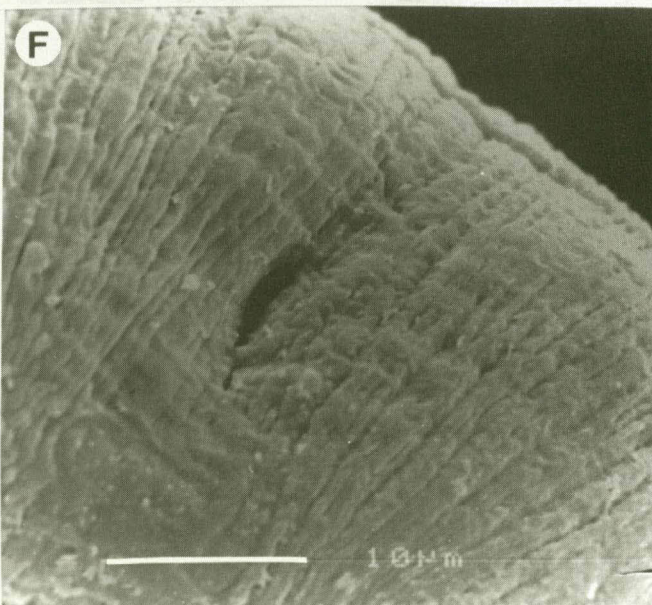
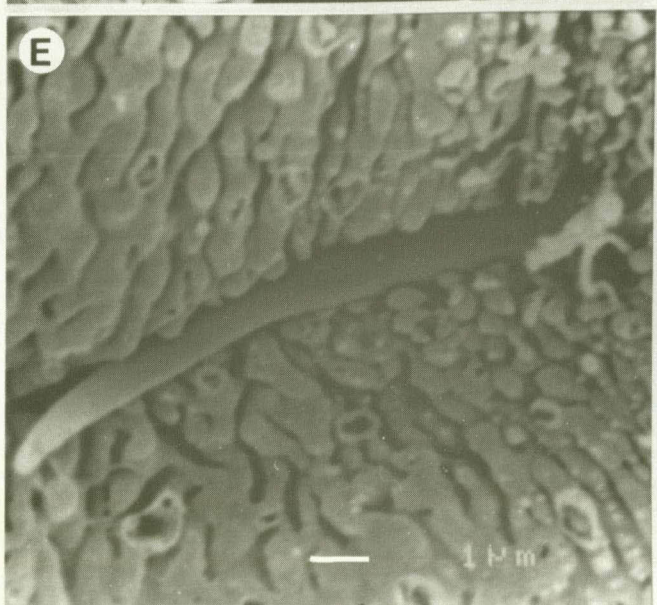
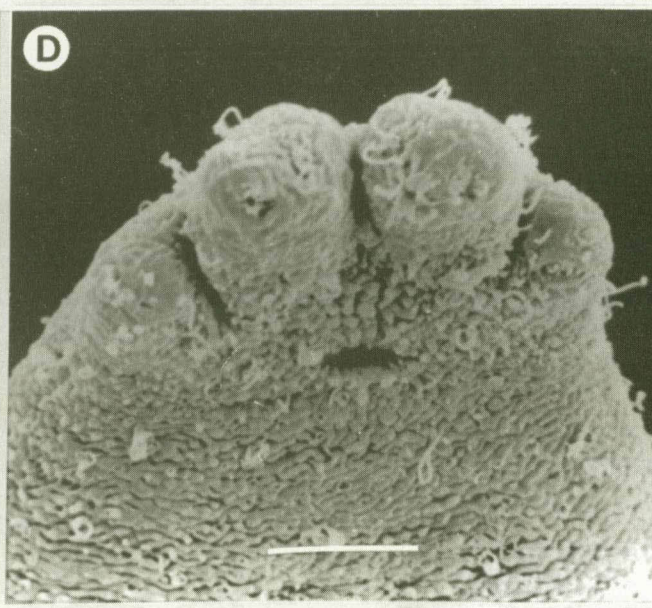
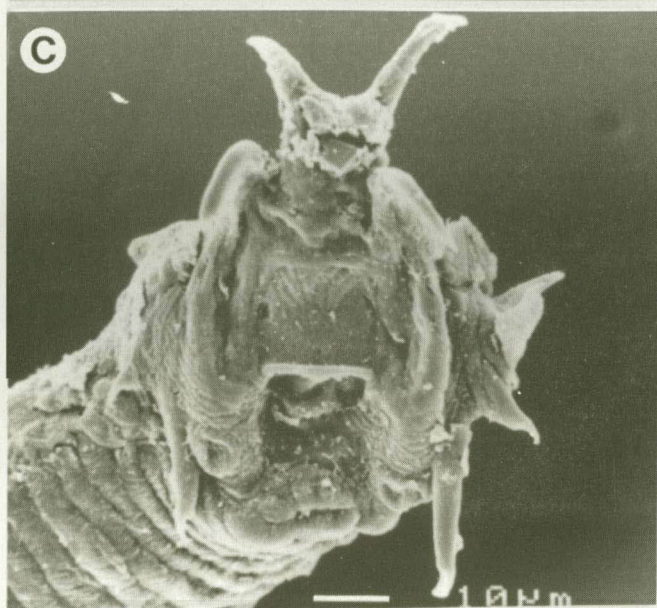
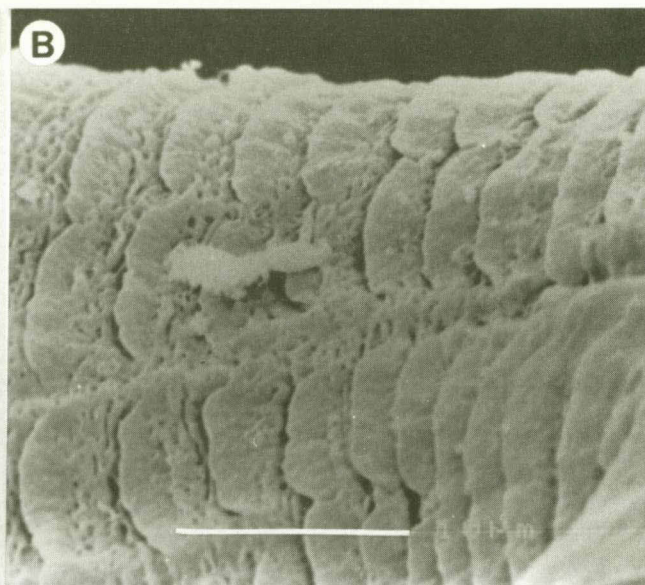
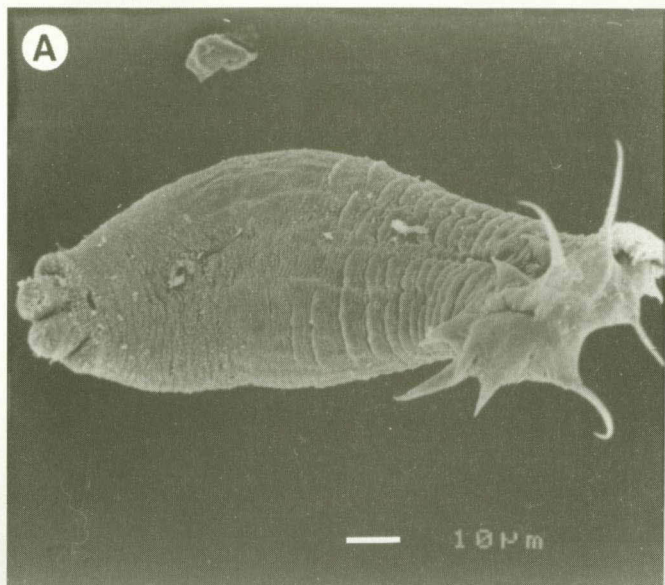
D. Prohaptor

E. Cirrus opening

F. Vaginal opening

Scale bar: A- 100  $\mu\text{m}$  B-F- 10  $\mu\text{m}$





***Annulotrema hepseti* Paperna & Thurston, 1969****HOST:** *Hepsetus odoe* (Bloch, 1794)**LOCATION ON HOST:** Gills**LOCALITY:** Xaro Backwaters, Lagoon (Xaro) (18°25'23.6"S; 21°56'18.2"), Kalatog Channel, Kalatog Lagoon, Mainstream (Drotsky), Lagoon (Drotsky) and Guma Lagoon (18°57'44.9"S; 22°22'26.7"E).**REFERENCE MATERIAL:** 97 / 10 / 21 - 05; 98 / 06 / 17 - 07**MATERIAL:** Measurements from 20 specimens mounted in Ammonium picrate.**DESCRIPTION AND MEASUREMENTS:** Medium to large worms, total length  $462 \pm 64.9$  (310-560), width at level of copulatory organ  $168 \pm 37.1$  (130-250) (Figure 5.4 A, 5.5A, 5.6A). Tegument smooth, posterior half, annulated annulations distinct (Figure 5.6B) Prohaptor consists of four indistinct cephalic lobes, contains oral opening, prohaptoral tegument contains sensory pits and setae (Figure 5.6D). Oral opening sub-terminal. Pharynx  $27 \pm 3.5$  (18-33). Opisthaptor triangular in shape with large anchors and marginal hooklets (Figure 5.4B, 5.5B, 5.6C). Dorsal anchors  $65 \pm 5.8$  (58-83), inner root  $23 \pm 1.9$  (20-28), outer root  $8 \pm 1.6$  (5-11), shaft  $47 \pm 6.7$  (36-60), tip  $6 \pm 2.8$  (2-12) (Figure 5.4B, 5.5C). Dorsal bar slightly concave, length  $35 \pm 3.0$  (31-43), dorsal bar width  $6 \pm 0.9$  (4-7) (Figure 5.4B, 5.5E). Ventral anchors  $67 \pm 5.3$  (61-77), inner root  $23 \pm 2.9$  (17-28), outer root  $7 \pm 2.1$  (4-14), shaft  $49 \pm 3.8$  (43-57), tip  $4 \pm 1.3$  (3-7) (Figure 5.4B, 5.5D). Ventral bar length  $38 \pm 3.8$  (30-44), ventral bar width  $6 \pm 1.1$  (4-8) (Figure 5.4B, 5.5F). Marginal hooklets; I=  $15 \pm 1.1$  (13-17), II=  $46 \pm 5.2$  (33-55), III=  $43 \pm 6.4$  (27-54), IV=  $42 \pm 4.5$  (32-46), V=  $43 \pm 5.4$  (27-52), VI=  $41 \pm 3.6$  (37-51), VII=  $36 \pm 4.4$  (26-44) (Figure 5.4B, 5.5G). Copulatory organ opens ventrally, posterior to oral opening (Figure 5.4C, 5.6E), consists of long spiralled cirrus in thick muscular sheath or accessory piece, number of turns averages 25 and ranges from 21-29, cirrus length  $58 \pm 8.2$  (43-78) (Figure 5.4C, 5.5H). Vagina not sclerotised, vaginal opening dextral (Figure 5.6F).**REMARKS:** *Annulotrema hepseti* shares many common characteristics with *A. biaensis* and *A. macropenis*, which have been described from the same host from the Ivory Coast. According to N'Douba, *et al.* (1997) *A. hepseti* differs from *A. macropenis*

by the form and size of the sclerotised parts of the opisthaptor and particularly the size of the cirrus. *Annulotrema biaensis* on the other hand is clearly distinguished from *A. macropenis* in the size of the cirrus but is more close to *A. hepseti*. *Annulotrema biaensis* and *A. hepseti* are separated according to N'Douba, *et al.* (1997) by the size of the opisthaptoral hooks especially the size of the third and seventh marginal hooklets.

As can be seen from Table 5.2, the three populations of *A. hepseti* recorded from Ghana (Paperna & Thurston, 1969), Ivory Coast (N'Douba, *et al.*, 1997) and the Okavango System differ quite considerably in the measurements of the various specimens. The Ivory Coast population seems to be represented by specimens, far larger than the other two populations. The population from Ghana on the other hand, is represented by very small specimens with the Okavango specimens being about in the middle when taking size into consideration. The major difference between the three populations is the morphology and location of the vagina. According to Paperna & Thurston (1969) the specimens from Ghana have a vagina that opens sinistrally. No comment was made about whether or not the vagina was sclerotised. N'Douba, *et al.* (1997) noted that the vagina of the Ivory Coast specimens open laterally and that the vaginas of these specimens are sclerotised. No sclerotisation of the vagina was noticeable in the Okavango specimens and with the aid of scanning electron microscopy as well as light microscopy, it was determined that the vagina of the Okavango specimens open dextrally (Figure 5.6A, 5.6F). A possible explanation for this contradiction could be due to the confusion of the dorsal ventral axis when using light microscopy hence confusing the dextral sinistral axis.

**TABLE 5:2** Table comparing the Okavango population of *Annulotrema hepseti* Paperna & Thurston, 1969 To Populations from other areas of its distribution.

	<b>Okavango</b>	<b>Ghana</b>	<b>Ivory Coast</b>
Total Length	310-560	200-300	418-777
Dorsal Anchors	58-83	70-100	45-66
Ventral Anchors	61-77	60-75	55-74
Largest Marginal Hooklets	33-55	40-60	46-58
Annulation	Distinct	Distinct	Distinct
Cirrus	43-78		65-82
Vagina	Dextral	Sinistral	Lateral

## FIGURE 5.4

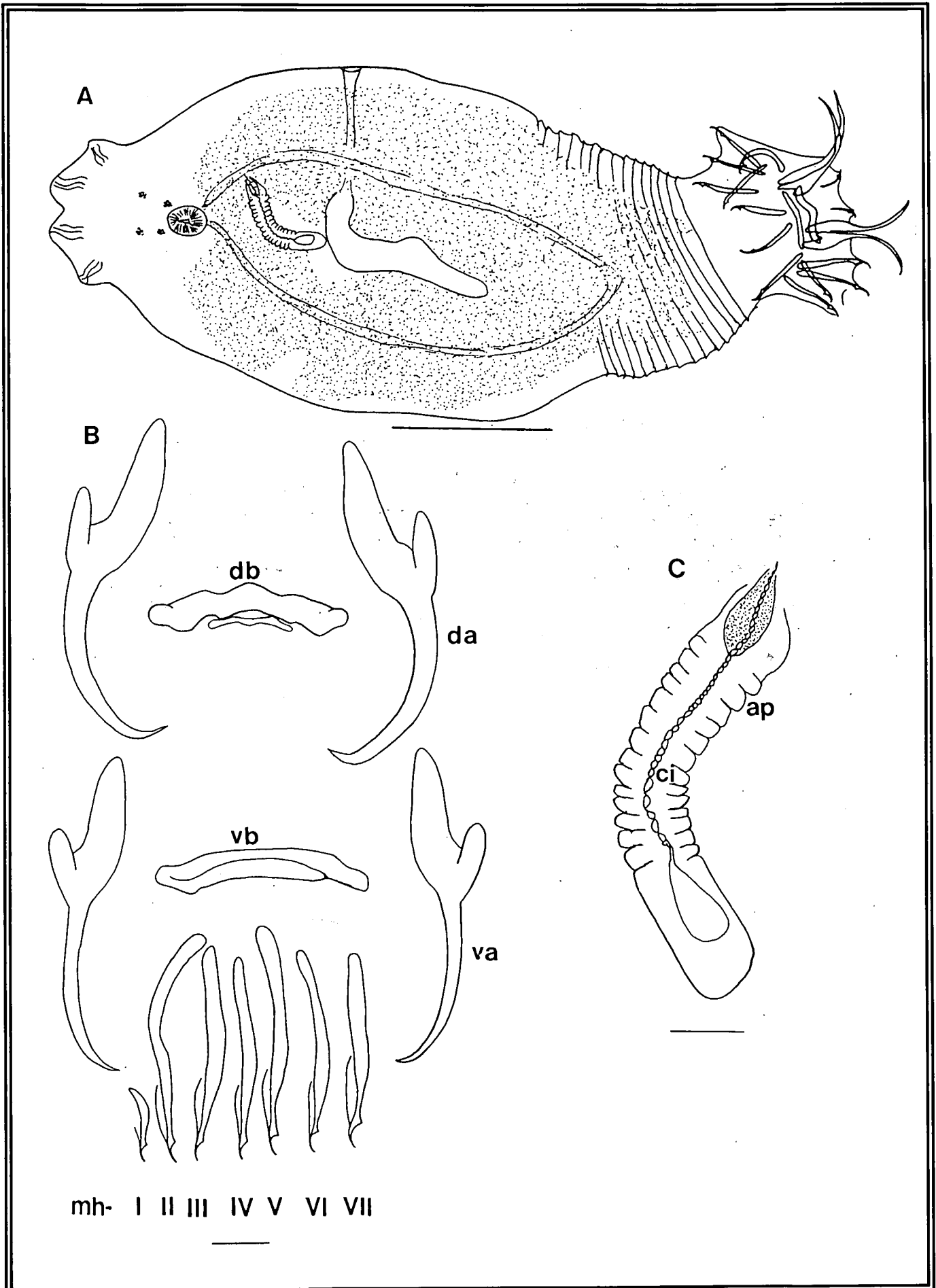
Microscope projection drawings of *Annulotrema hepseti* Paperna & Thurston, 1969, occurring on the gills of *Hepsetus odoe* (Bloch, 1794).

A. Whole mount

B. Opisthaptor sclerites (db-dorsal bar, vb- ventral bar, da- dorsal anchor, va- ventral anchor, mh- marginal hooklets)

C. Copulatory organ (ap- accessory piece, ci- cirrus)

Scale bar: A- 100  $\mu\text{m}$  B&C- 10 $\mu\text{m}$



## FIGURE 5.5

Light micrographs of *Annulotrema hepseti* Paperna & Thurston, 1969, occurring on the gill filaments of *Hepsetus odoe* (Bloch, 1794).

A. Whole mount

B. Opisthaptor

C. Dorsal anchor

D. Ventral anchor

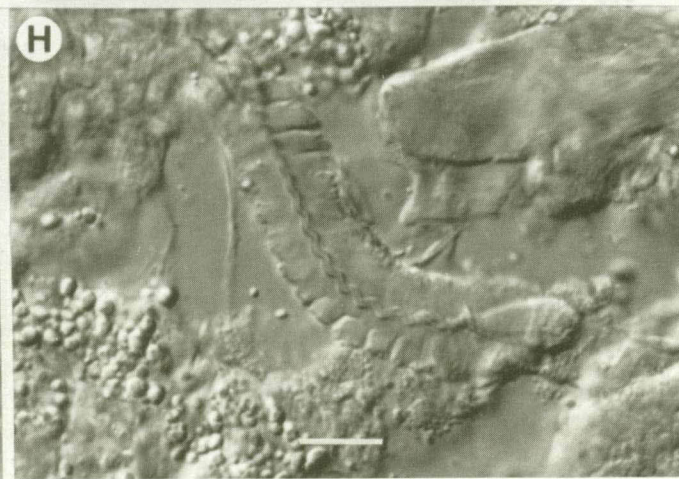
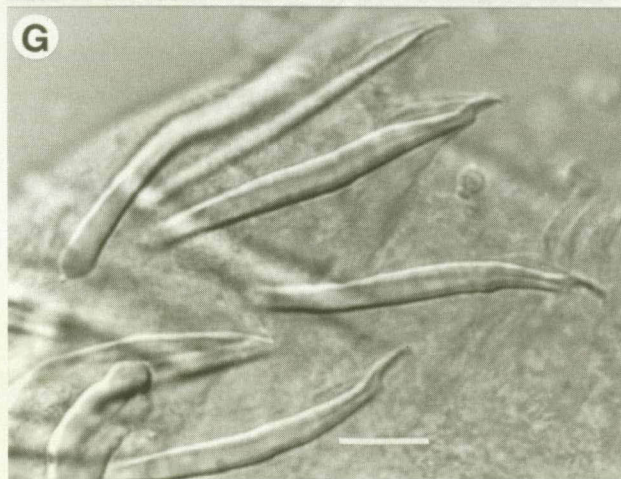
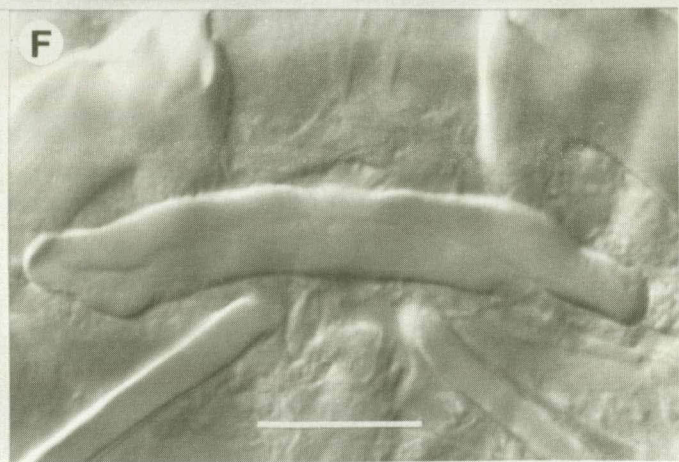
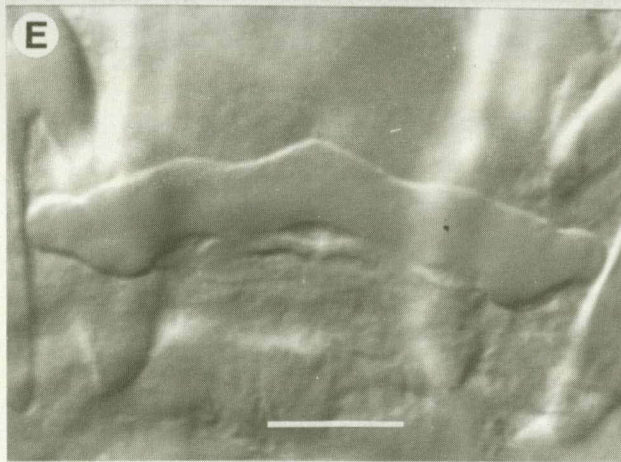
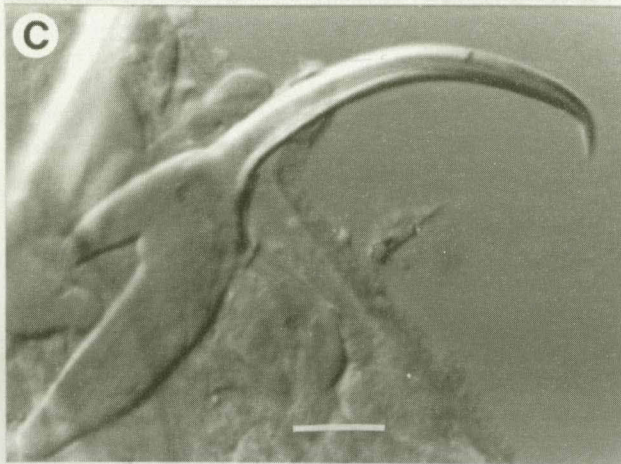
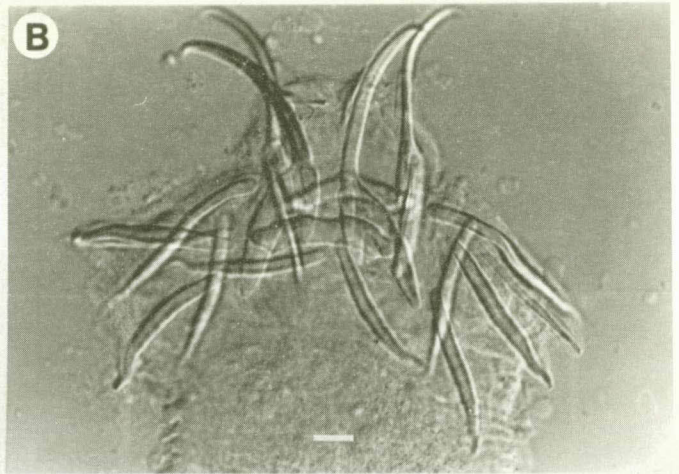
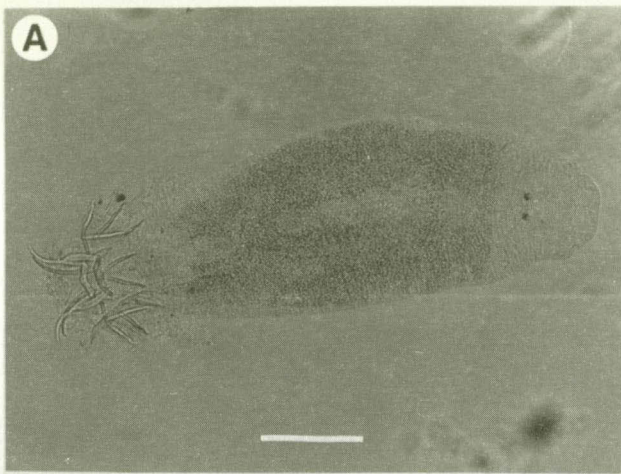
E. Dorsal bar

F. Ventral bar

G. Marginal hooklets

H. Copulatory organ

Scale bar: A- 100  $\mu\text{m}$  B-H- 10  $\mu\text{m}$





## FIGURE 5.6

Scanning electron micrographs of *Annulotrema hepseti* Paperna & Thurston, 1969, occurring on the gill filaments of *Hepsetus odoe* (Bloch, 1794).

A. Whole mount

B. Tegumental annulations

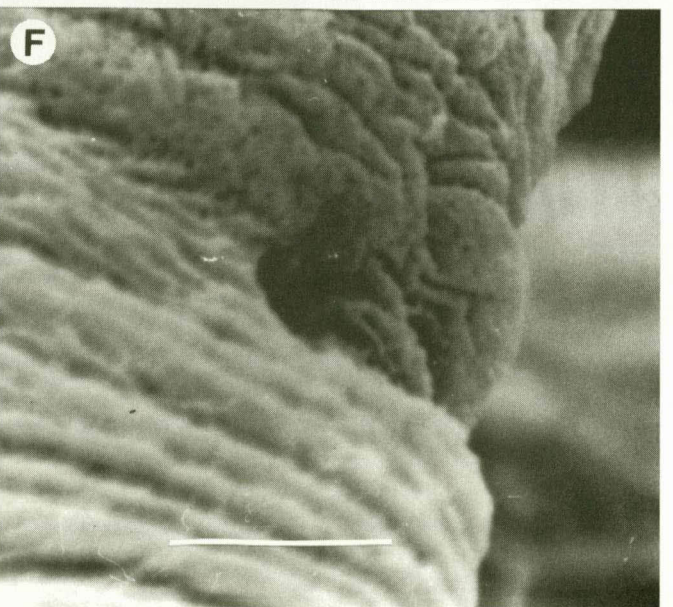
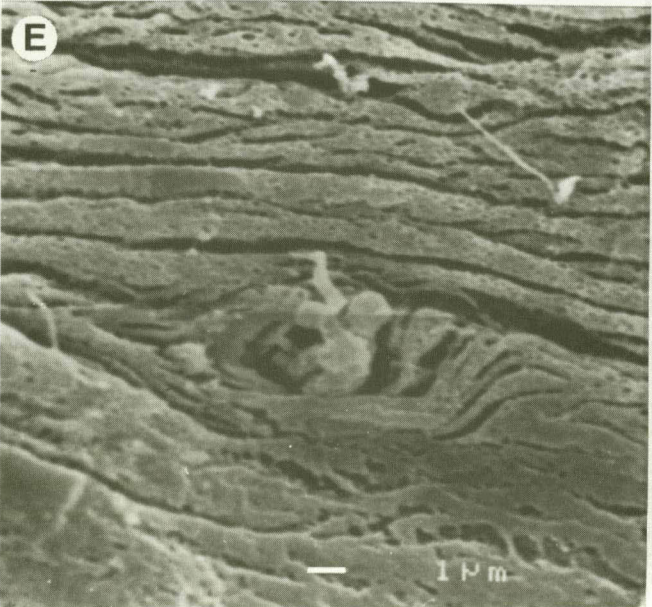
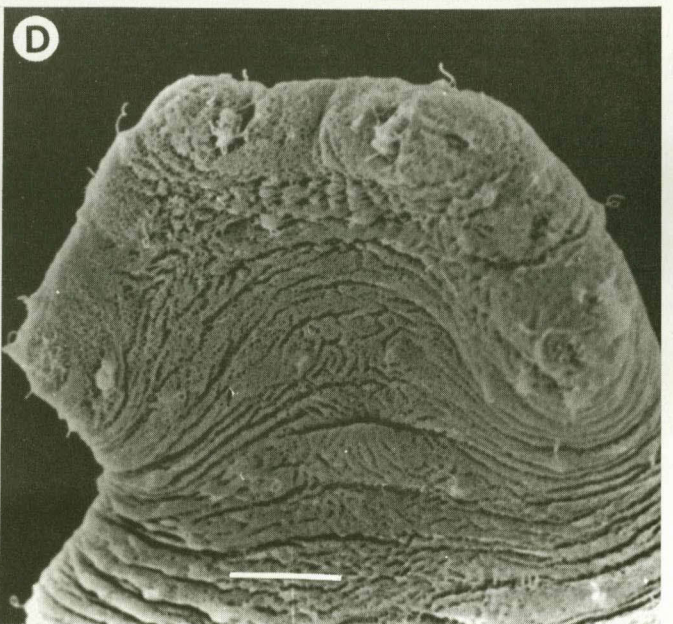
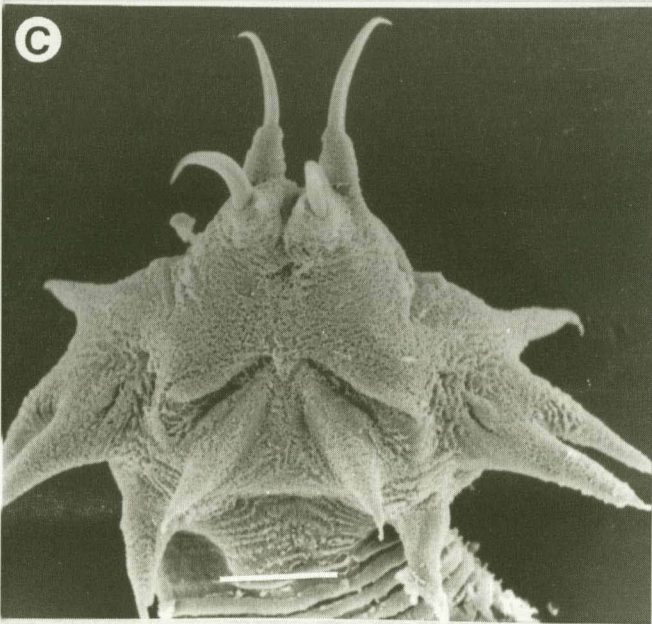
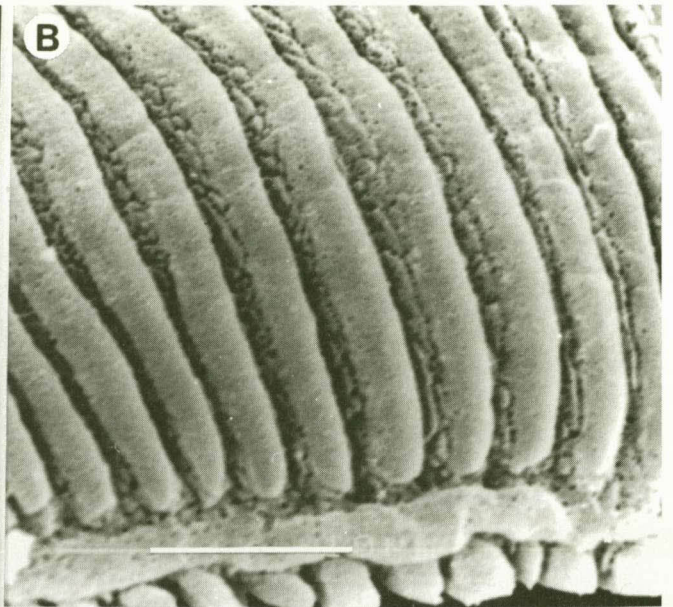
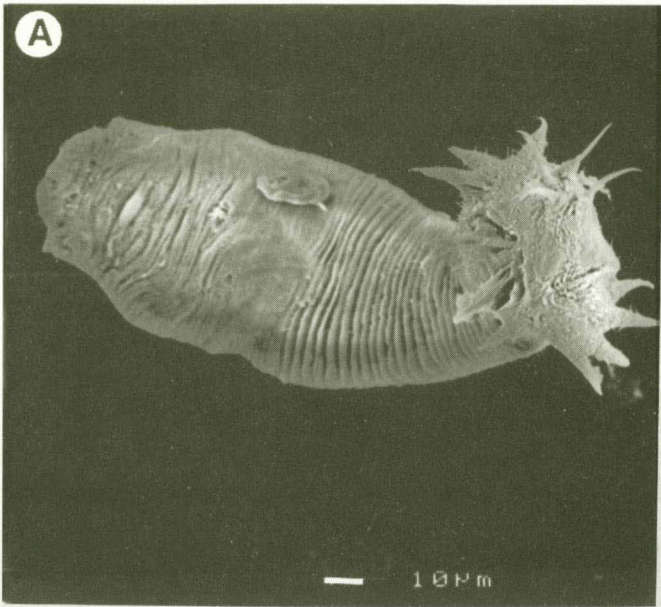
C. Opisthaptor

D. Prohaptor

E. Cirrus opening

F. Vaginal opening

Scale bar: A- 100  $\mu\text{m}$  B-F- 10  $\mu\text{m}$



***Annulotrema pikei* (Price, Peebles & Bamford, 1969)**

**HOST:** *Hydrocynus vittatus* Castelnau, 1861

**LOCATION ON HOST:** Gills

**LOCALITY:** Mainstream (Xaro) (18°25'23.6"S; 21°56'18.2"E), Kalatog Channel, Mainstream (Drotsky), Lagoon (Drotsky) and Philipo Channel.

**REFERENCE MATERIAL:** 98 / 08 / 08 - 03; 97 / 10 / 27 - 03

**MATERIAL:** Measurements from 20 specimens mounted in Ammonium picrate.

**DESCRIPTION AND MEASUREMENTS:** Medium to large worms, total length  $462 \pm 68.86$  (350-580), total width at level of cirrus  $105 \pm 24.23$  (70-170) (Figure 5.7A, 5.8A, 5.9A). Tegument smooth, posterior half annulated, annulations distinct (Figure 5.9B). Prohaptor, four well defined cephalic lobes with sensory pits and setae, oral opening ventral. Pharynx  $21 \pm 7.69$  (9-29), intestinal caeca fused posteriorly. Opisthaptor (Figure 5.7B, 5.8B, 5.9 C) with large anchors, dorsal anchor  $52 \pm 3.99$  (44-58), inner root  $13 \pm 3.25$  (8-18), outer root  $5 \pm 1.63$  (2-9), shaft  $40 \pm 4.06$  (33-50), tip  $6 \pm 1.73$  (3-9) (Figure 5.7B, 5.8C). Dorsal bar length  $39 \pm 8.02$  (22-53), dorsal bar width  $9 \pm 2.13$  (5-14) (Figure 5.7B, 5.8E). Ventral anchor  $53 \pm 4.63$  (44-62), inner root  $14 \pm 4.24$  (6-21), outer root  $5 \pm 1.66$  (3-9), shaft  $40 \pm 3.72$  (34-48), tip  $6 \pm 1.49$  (4-10) (Figure 5.7B, 5.8D). Ventral bar length  $38 \pm 4.59$  (28-46), ventral bar width  $7 \pm 1.73$  (5-12) (Figure 5.7B, 5.8F). Marginal hooklets I=  $15 \pm 4.21$  (9-22), II=  $29 \pm 4.54$  (21-36), III=  $29 \pm 5.14$  (21-38), IV=  $29 \pm 8.26$  (16-43), V=  $29 \pm 6.58$  (20-43), VI=  $26 \pm 3.95$  (21-33), VII=  $20 \pm 3.13$  (16-25) (Figure 5.7B, 5.8G). Copulatory organ opens ventrally, posterior to oral opening (Figure 5.7C, 5.9E), consists of elongated cirrus entwined with the accessory piece, cirrus  $84 \pm 25.43$  (29-120), accessory piece  $83 \pm 17.96$  (31-102). Vagina opens sinistrally (Figure 5.9F) and is not sclerotised, vitellaria are massed on both sides of the reproductive organs, not extending into opisthaptor (Figure 5.7A, 5.8A).

**REMARKS:** The specimens of *Annulotrema pikei* collected from *Hydrocynus vittatus* from the Okavango System have close affinities with *Annulotrema pikei ruahae* and *A. pikoides* as described by Paperna (1979) and Guegan, *et al.* (1988) respectively. As these three species have very similar opisthaptor hook arrangements and morphology,

differential diagnosis depends on the morphology of the copulatory organ. The copulatory organ of *A. pikei* consists of an elongated tubular cirrus extending from the seminal vesicle intertwined with the accessory piece which is almost as long as the cirrus.

As can be seen from Table 5.3, the Okavango population of *Annulotrema pikei* is comparable to the populations from Ghana, South Africa, Tanzania and Uganda respectively. The size range of the Okavango specimens fits well within the size ranges of the other populations. The anchors, both dorsal and ventral, seem to be slightly larger than those of the other four populations. The population of *A. pikei* from the Okavango seems to be more closely associated with the population from The Volta Lake, Ghana, as these specimens are very similar in size and both exhibit distinct cuticular annulation. The other three populations on the other hand are generally slightly smaller and do not have distinct cuticular annulation.

**TABLE 5.3** Table comparing the Okavango population of *Annulotrema pikei* (Price, Peebles & Bamford, 1969) to populations from other areas of its distribution.

	OKAVANGO	GHANA	PONGOLA	TANZANIA	UGANDA
Fish host	<i>H. vittatus</i>	<i>Hydrocynus</i> <i>s sp.</i>	<i>H. vittatus</i>	<i>H. vittatus</i>	<i>H.</i> <i>forskalii</i>
Total length	350-580	300-700	197-332	310-490	360-490
Ventral anchor	44-62	40-42	36-43	42-43	38-42
Dorsal anchor	44-58	43-47	35-43	43-47	37-40
Largest marginal hooklet	20-43	30	26-29	34	25
Cirrus		40	40-52	52-57	57
Annulation	Distinct	Distinct	Not Distinct	Not Distinct	Not Distinct

## FIGURE 5.7

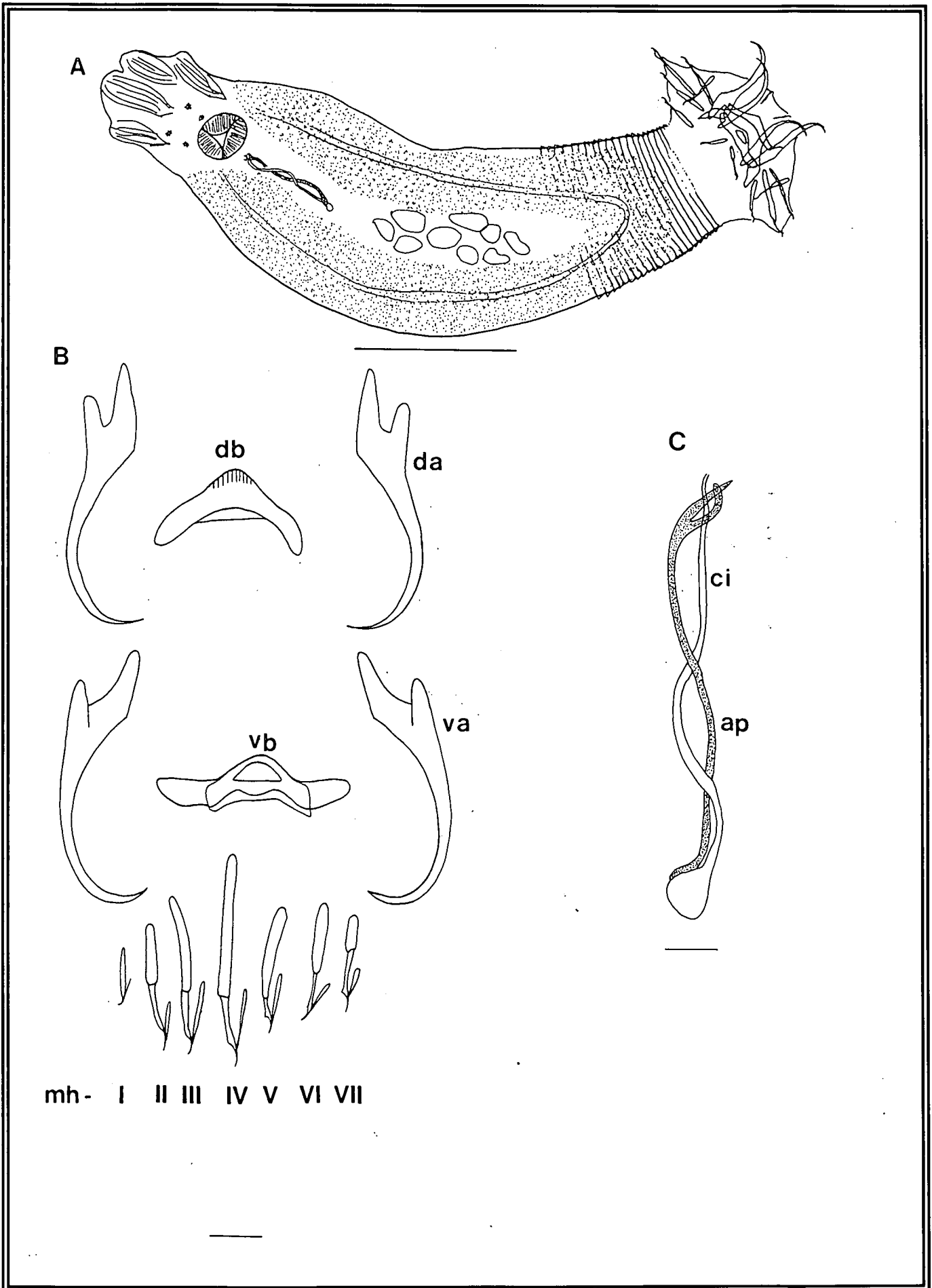
Microscope projection drawings of *Annulotrema pikei* (Price, Peebles & Bamford, 1969), occurring on the gill filaments of *Hydrocynus vittatus* Castelnau, 1861.

A. Whole mount

B. Opisthaptor sclerites (db-dorsal bar, vb- ventral bar, da- dorsal anchor, va- ventral anchor, mh- marginal hooklets).

C. Copulatory organ (ap- accessory piece, ci- cirrus)

Scale bar: A- 100  $\mu\text{m}$  B&C- 10  $\mu\text{m}$



## FIGURE 5.8

Light micrographs of *Annulotrema pikei* (Price, Peebles & Bamford, 1969), occurring on the gill filaments of *Hydrocynus vittatus* Castelnau, 1861.

A. Whole mount

B. Opisthaptor

C. Dorsal anchor

D. Ventral anchor

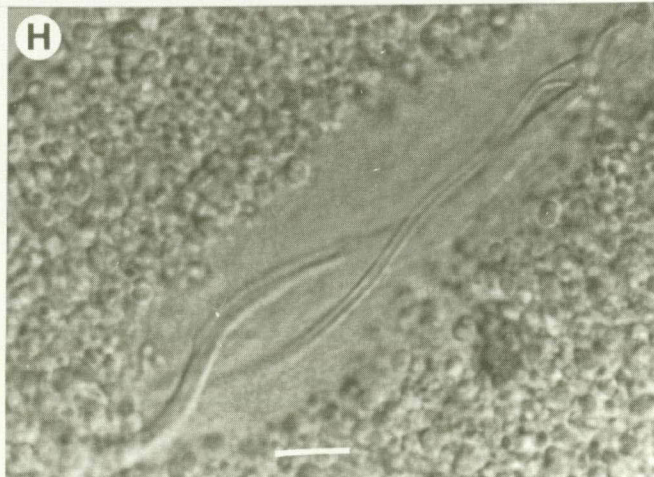
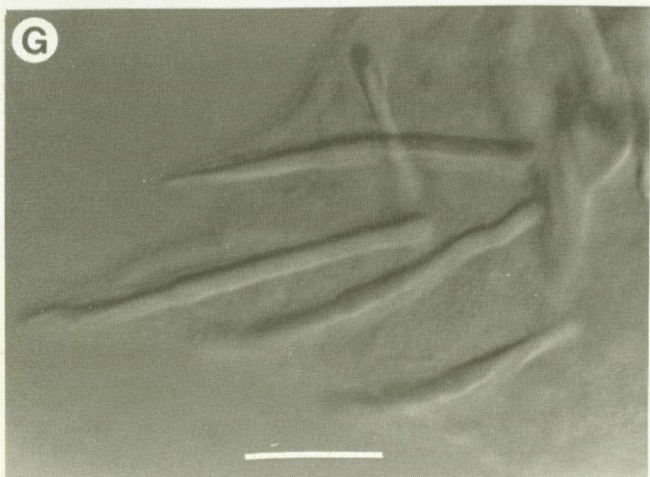
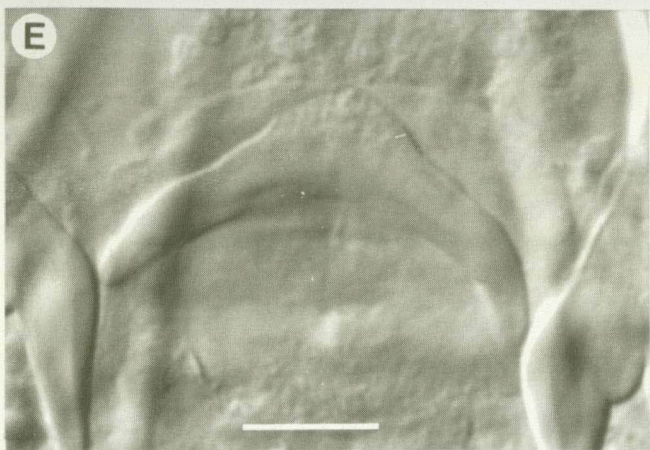
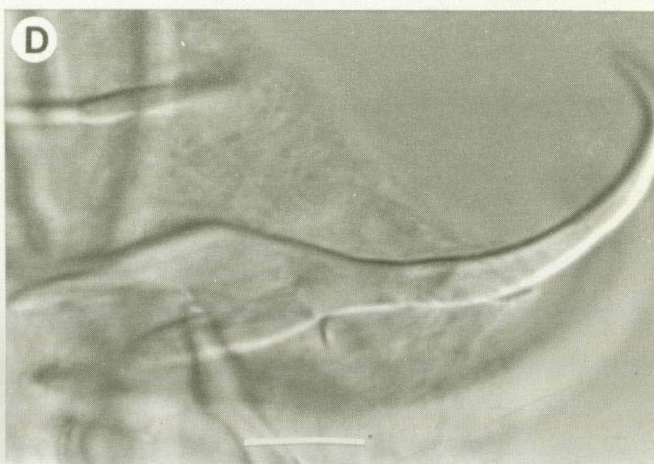
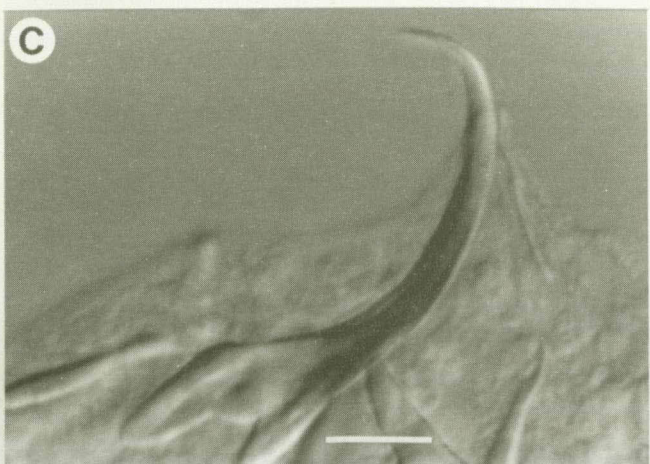
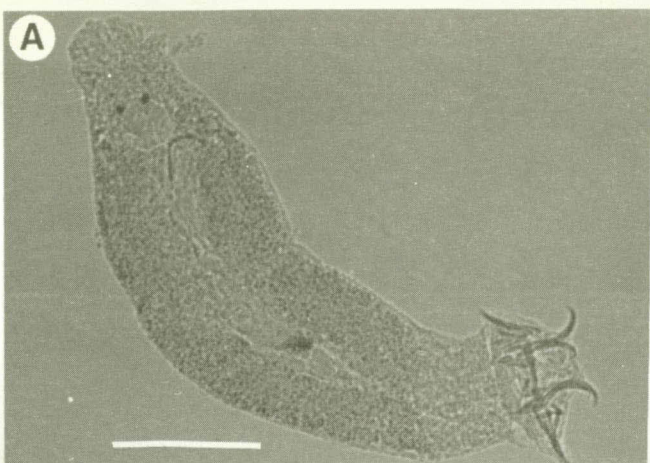
E. Dorsal bar

F. Ventral bar

G. Marginal hooklets

H. Copulatory organ

Scale bar: A- 100  $\mu$ m B-H- 10  $\mu$ m





## FIGURE 5.9

Scanning electron micrographs of *Annulotrema pikei* (Price, Peebles & Bamford, 1969), occurring on the gills of *Hydrocynus vittatus* Castelnau, 1861.

A. Whole mount

B. Tegumental annulations

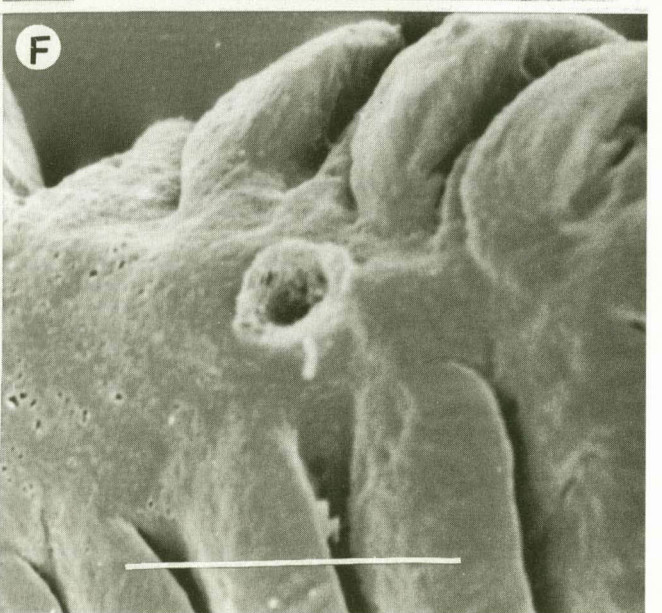
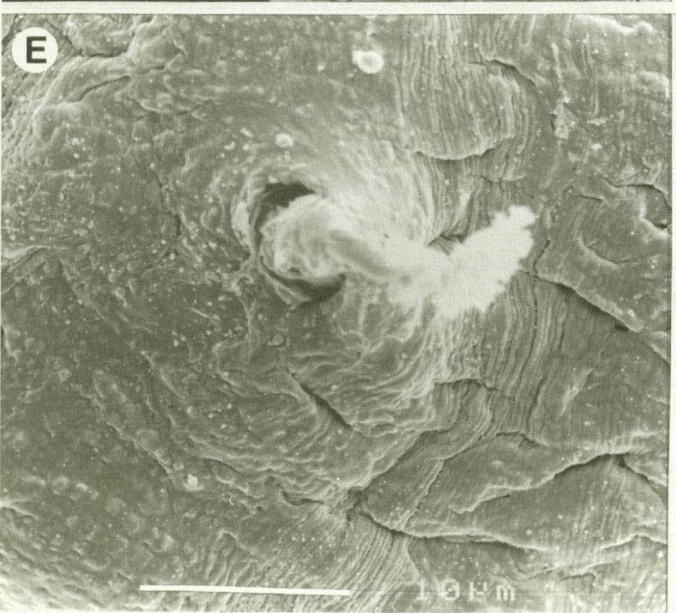
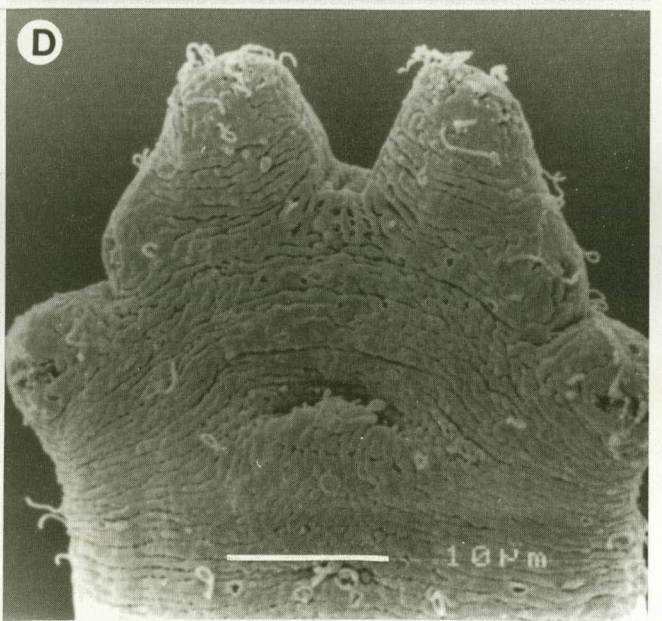
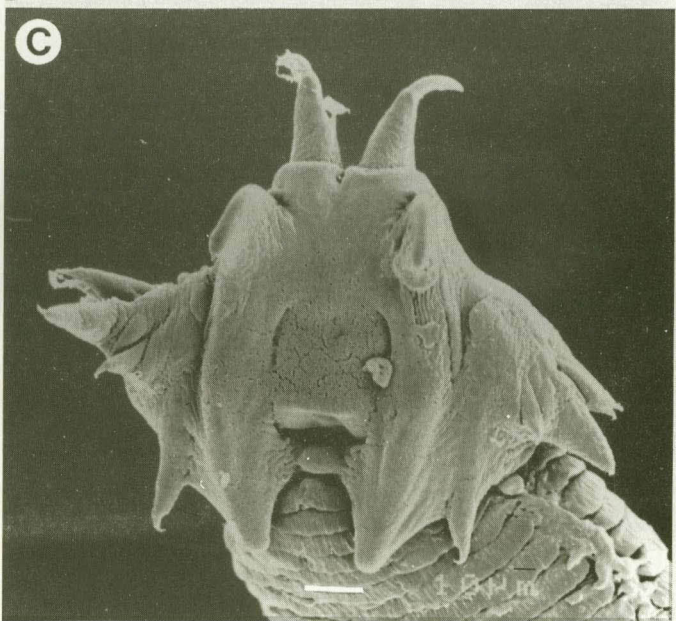
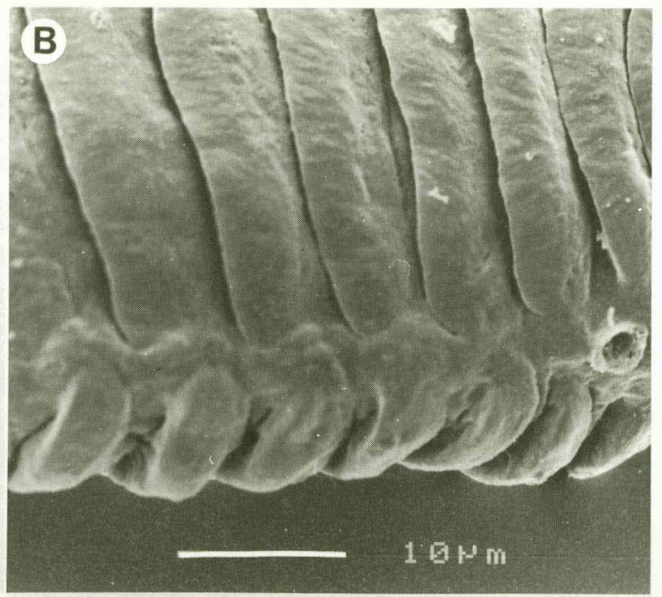
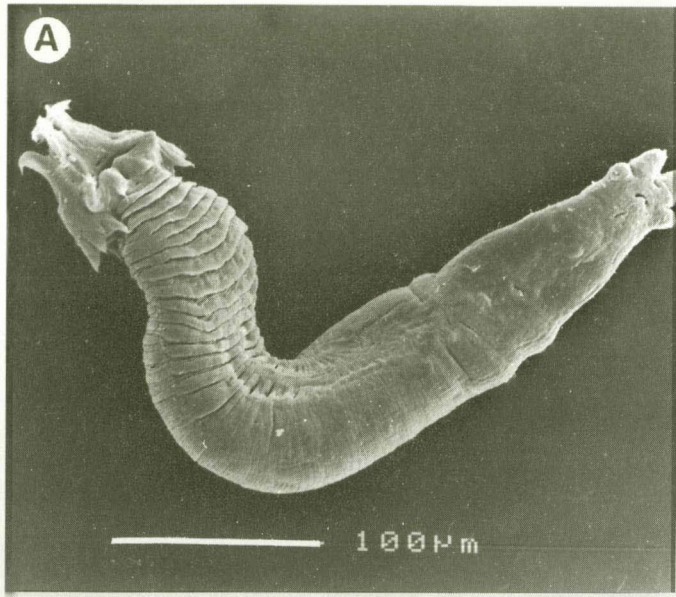
C. Opisthaptor

D. Prohaptor

E. Cirrus opening

F. Vaginal opening

Scale bar: A- 100  $\mu\text{m}$  B-F- 10  $\mu\text{m}$



***Annulotrema micralesti* sp. n.****TYPE HOST:** *Micralestes acutidens* (Peters, 1852)**LOCATION ON HOST:** Gills**TYPE LOCALITY:** Mainstream (Xaro) (18°25'23.6"S; 21°56'18.2"E)**TYPE MATERIAL:** Holotype: 98 / 06 / 24 – 03; NMBP219

Paratypes: 98 / 06 / 24 – 04; NMBP220 &amp; NMB221

**MATERIAL:** Measurements from 10 specimens mounted in Ammonium picrate.**ETYMOLOGY:** Name derived from the host fish, *Micralestes acutidens*, from where these parasites were found.**DESCRIPTION AND MEASUREMENTS:** Small to medium sized worms, total length  $299 \pm 41.4$  (240-350), width  $94 \pm 18.0$  (60-120) (Figure 5.10A, 5.11A). Tegument smooth, posterior half annulated, annulations not too distinct. Prohaptor consists of four well defined cephalic lobes. Oral opening, sub-terminal opening ventrally, pharynx  $23 \pm 3.9$  (18-26), intestinal caeca fused posteriorly. Opisthaptor terminal (Figure 5.10B, 5.11B), dorsal anchors  $28 \pm 1.4$  (25-30), inner root  $9 \pm 0.9$  (7-10), outer root  $5 \pm 1.4$  (3-7), shaft  $19 \pm 1.2$  (18-22), tip  $4 \pm 0.8$  (2-4) (Figure 5.10B, 5.11C). Dorsal bar length  $26 \pm 1.7$  (24-29), dorsal bar width  $5 \pm 1.6$  (3-7) (Figure 5.10B 5.11E). Ventral anchors  $34 \pm 2.7$  (32-39), inner root  $8 \pm 0.3$  (4-14), outer root  $6 \pm 2.3$  (4-10), shaft  $27 \pm 1.9$  (24-28), tip  $3 \pm 0.7$  (3-5) (Figure 5.10B, 5.11D). Ventral bar length  $25 \pm 3.2$  (20-29), ventral bar width  $9 \pm 1.6$  (7-12) (Figure 5.10B, 5.11F). Marginal hooklets; I=  $7 \pm 1.6$  (5-8), II=  $15 \pm 4.0$  (8-21), III=  $20 \pm 5.0$  (14-26), IV=  $18 \pm 3.9$  (13-24), V=  $15 \pm 2.7$  (11-19), VI=  $11 \pm 3.5$  (6-16), VII=  $12 \pm 2.2$  (8-14) (Figure 5.10B, 5.11G). Copulatory organ opening ventrally posterior to oral opening, consists of curved tubular cirrus with distally bifurcated accessory piece, cirrus  $54 \pm 13.1$  (30-65). Accessory piece  $23 \pm 1.0$  (22-24) (Figure 5.10C). Vagina opens sinistrally, not sclerotised, Vitellaria massed on either side of reproductive organs, not extending into opisthaptor.

**REMARKS:** *Annulotrema micralesti* can be distinguished from the *Annulotrema* species collected in the Okavango in being a small monogenean and only being recorded from *Micralestes acutidens*. The anchors of this monogenean are prominent with the dorsal and ventral anchors being similar in shape. The dorsal bar is narrow and elongated with a hole in the middle and the ventral bar is A- shaped and does not resemble any of the other species.. The marginal hooklets of *A. micralesti* are also comparatively small. The copulatory organ consists of an elongated, curved cirrus, which is associated with the accessory piece both distally and proximally. The accessory piece makes a smaller curve parallel to the cirrus. The accessory piece is trifold distally and is similar to that of *A. curvipenis*, which is bifid. The distal ends of the accessory piece curve away from each other whereas that of *A. curvipenis* curve toward each other. The copulatory of *A. micralesti* is also much larger than that of *A. curvipenis* from Uganda and the Okavango.

## FIGURE 5.10

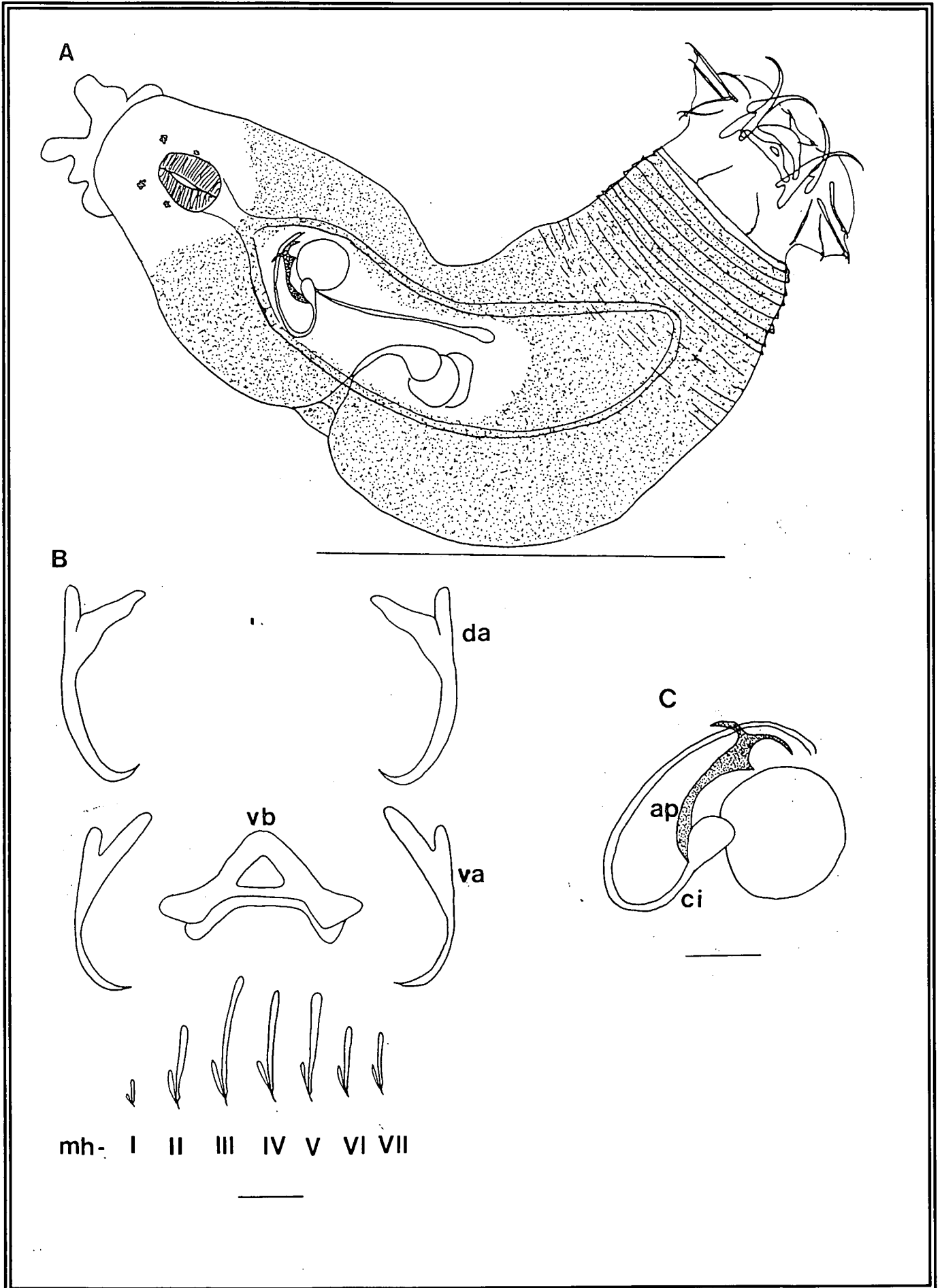
Microscope projection drawings of *Annulotrema micralesti* sp. n., occurring on the gill filaments of *Micralestes acutidens* (Peters, 1852).

A. Whole mount

B. Opisthaptor sclerites (db-dorsal bar, vb- ventral bar, da- dorsal anchor, va- ventral anchor, mh- marginal hooklets)

C. Copulatory organ (ap- accessory piece, ci cirrus)

Scale bar: A- 100  $\mu$ m B&C- 10  $\mu$ m



## FIGURE 5.11

Light micrographs of *Annulotrema micralesti* sp. n., occurring on the gill filaments of *Micralestes acutidens* (Peters, 1852).

A. Whole mount

B. Opisthaptor

C. Dorsal anchor

D. Ventral anchor

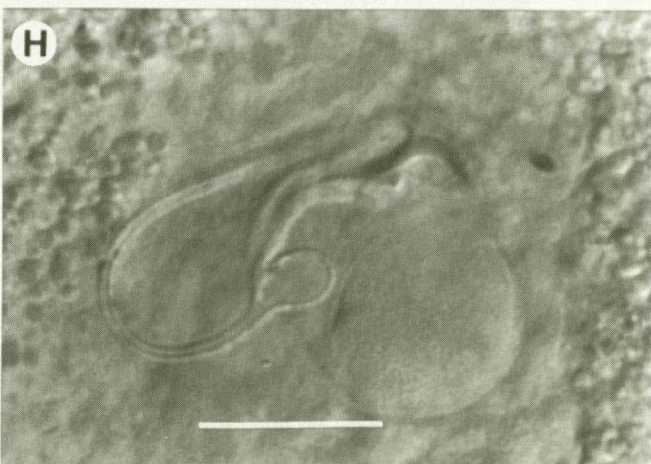
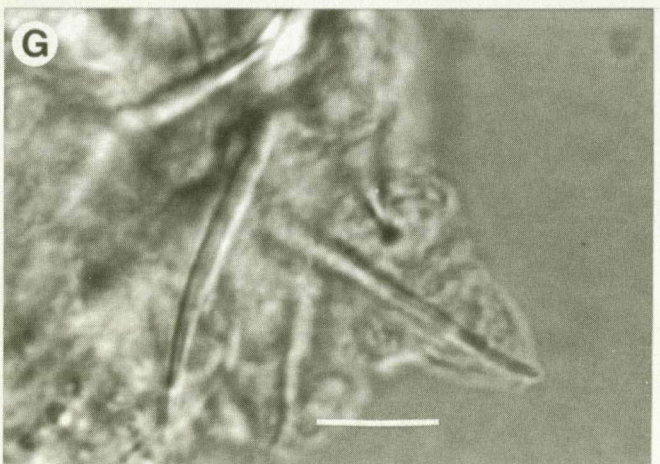
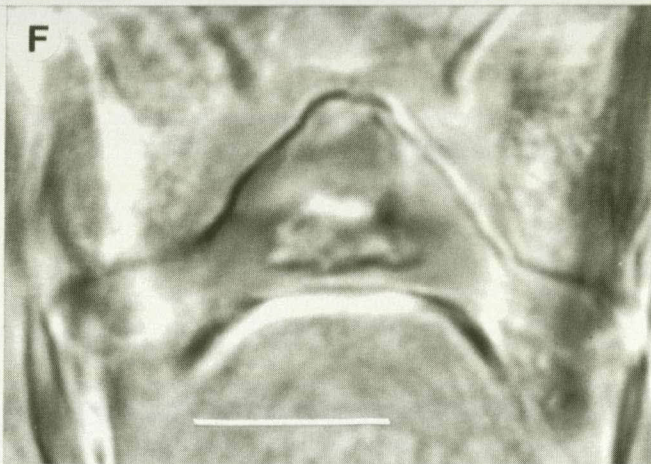
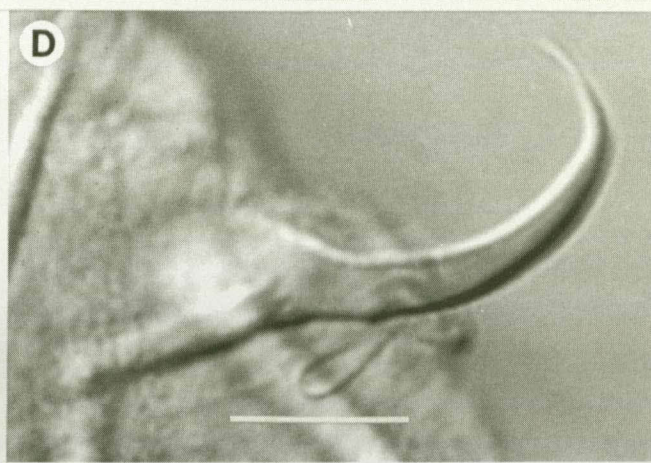
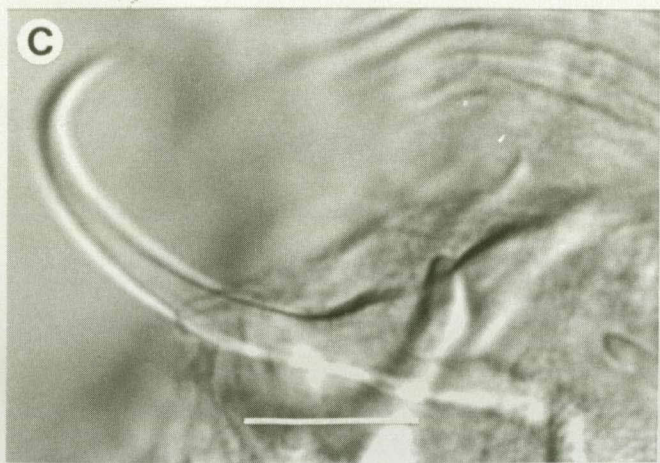
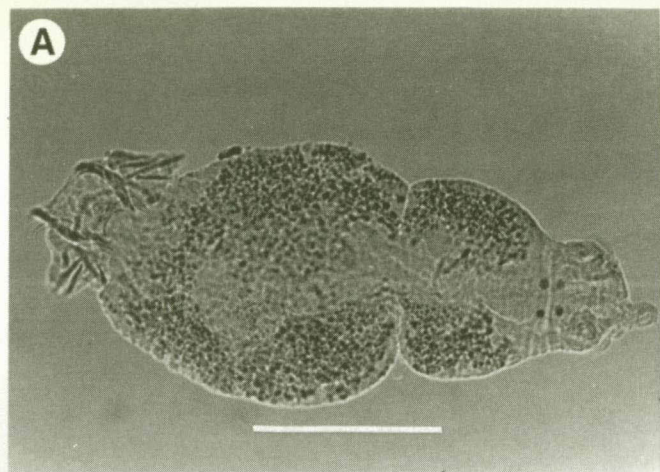
E. Dorsal bar

F. Ventral bar

G. Marginal hooklets

H. Copulatory organ

Scale bar: A- 100  $\mu$ m B-H- 10  $\mu$ m





***Annulotrema rhabdalesti* sp. n.****TYPE HOST:** *Rhabdalestes maunensis* (Fowler, 1935)**LOCATION ON HOST:** Gills**TYPE LOCALITY:** Mainstream (Xaro) (18°25'23.6"S; 21°56'18.2"E)**TYPE MATERIAL:** Holotype: 98 / 06 / 23 -06; NMBP216

Paratypes: 98 / 06/ 23- 07; NMBP217 &amp; NMBP218

**MATERIAL:** Measurements from 10 specimens mounted in Ammonium picrate.**ETYMOLOGY:** Name derived from the host fish, *Rhabdalestes maunensis*, from where these parasites were found.**DESCRIPTION AND MEASUREMENTS:** Medium sized worms, total length  $305 \pm 48.6$  (240-360), width  $94 \pm 19.6$  (70-130) (Figure 5.12A, 5.13A, 5.14A). Tegument annulated, annulations distinct (Figure 5.14B). Prohaptor consists of four clearly defined cephalic lobes, oral opening ventral, sub-terminal. Pharynx  $23 \pm 3.6$  (17-26), intestinal caeca fuse posteriorly. Opisthaptor terminal (Figure 5.12B, 5.13B, 5.14C), clearly separated from body trunk, dorsal anchors  $32 \pm 4.0$  (26-38), inner root  $11 \pm 3.0$  (8-17), outer root  $6 \pm 1.8$  (2-8), shaft  $22 \pm 3.0$  (19-28), tip  $4 \pm 0.9$  (3-6) (Figure 5.13B, 5.13C). Dorsal bar length  $26 \pm 2.7$  (22-30), dorsal bar width  $5 \pm 1.3$  (3-7) (Figure 5.12B, 5.13E). Ventral anchors  $36 \pm 3.9$  (28-42), inner root  $12 \pm 1.8$  (9-14), outer root  $6 \pm 1.4$  (3-8), shaft  $25 \pm 3.0$  (20-28), tip  $4 \pm 0.7$  (3-5) (Figure 5.12B, 5.13D). Ventral bar length  $29 \pm 4.8$  (20-38), ventral bar width  $6 \pm 1.2$  (4-8) (Figure 5.12B, 5.13F). Marginal hooklets; I=  $8 \pm 2.4$  (5-12), II=  $17 \pm 2.4$  (14-22), III=  $19 \pm 3.4$  (12-23), IV=  $19 \pm 4.7$  (13-25), V=  $20 \pm 4.0$  (14-25), VI=  $19 \pm 3.0$  (14-22), VII=  $12 \pm 2.3$  (8-15) (Figure 5.13B, 5.13G). Copulatory organ opens ventrally, posterior to prohaptor (Figure 5.13C, 5.14E), cirrus elongated and tubular, cirrus  $25 \pm 6.1$  (18-37), accessory piece  $22 \pm 5.2$  (16-30). Vagina opening sinistral (Figure 5.14F), not sclerotised.

**REMARKS:** *Annulotrma rhabdalesti* sp.n. from the Okavango delta is distinguished from all existing species as it is the first record from *Rhabdalestes maunensis* and has a unique shaped cirrus resembling none of the existing species. The dorsal anchors are robust and prominent. The ventral anchors differ from the dorsal anchors in having a median root, which is vestigial. The dorsal bar is slightly concave and narrow. The ventral bar has an apron resembling that of *A. armorata* and *A. elongata*. The marginal hooklets are uniformly shaped and are relatively small. Although the opisthaptoral sclerites of *Annulotrema rhabdalesti* resemble those of *Annulotrema armorata* and *A. elongata* morphologically, they differ in size. The copulatory organ consists of an elongated straight cirrus which runs parallel to the accessory piece. The accessory piece is more or less as long as the cirrus and is bifid distally. The copulatory organ of *A. rhabdalesti* has the same components as the rest of the *Annulotrema* species but has a unique shape and cannot be likened to any of the known species, hence *A. rhabdalesti* is described as a new species.

## FIGURE 5.12

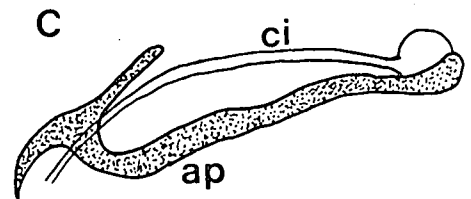
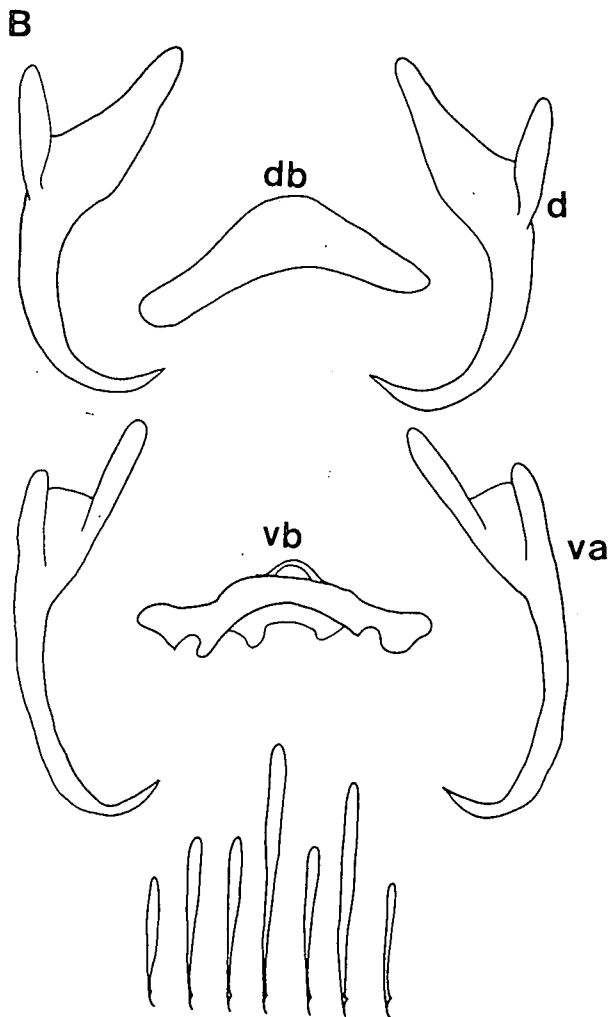
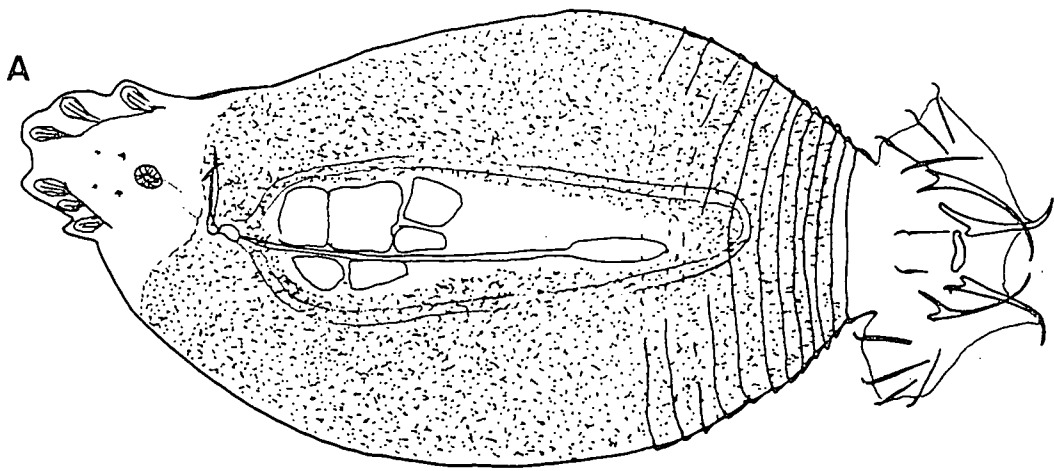
Microscope projection drawings of *Annulotrema rhabdalesti* sp. n., occurring on the gill filaments of *Rhabdalestes maunensis* (Fowler, 1935).

A. Whole mount

B. Opisthaptor sclerites (db-dorsal bar, vb- ventral bar, da- dorsal anchor, va- ventral anchor, mh- marginal hooklets)

C. Copulatory organ (ap- accessory piece, ci- cirrus)

Scale bar: A- 100  $\mu\text{m}$  B&C- 10  $\mu\text{m}$



I II III IV V VI VII

## FIGURE 5.13

Light micrographs of *Annulotrema rhabdalesti* sp. n., occurring on the gill filaments of *Rhabdalestes maunensis* (Fowler, 1935).

A. Whole mount

B. Opisthaptor

C. Dorsal anchor

D. Ventral anchor

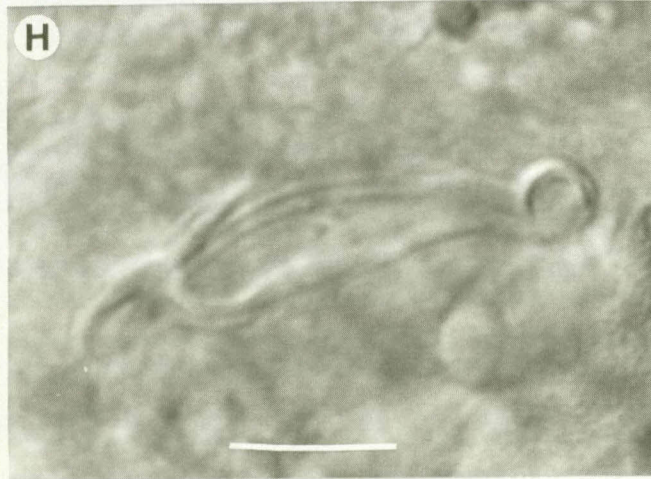
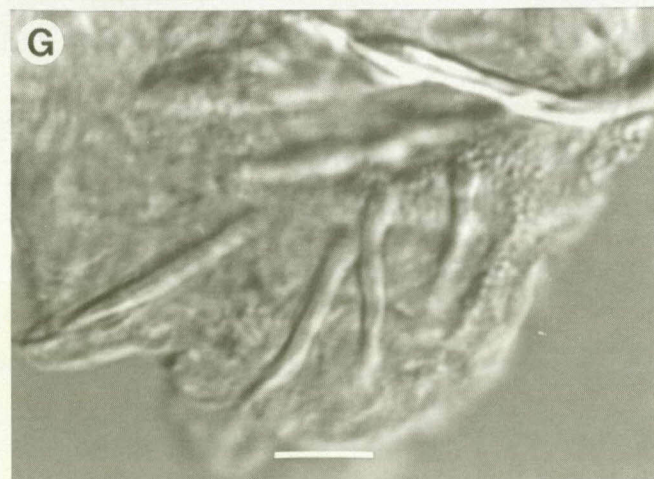
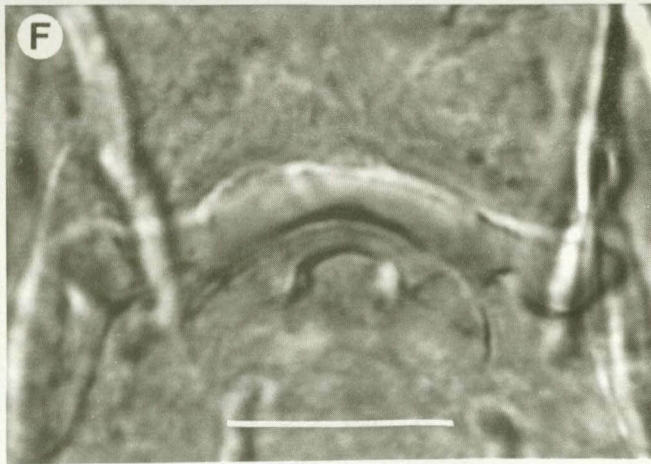
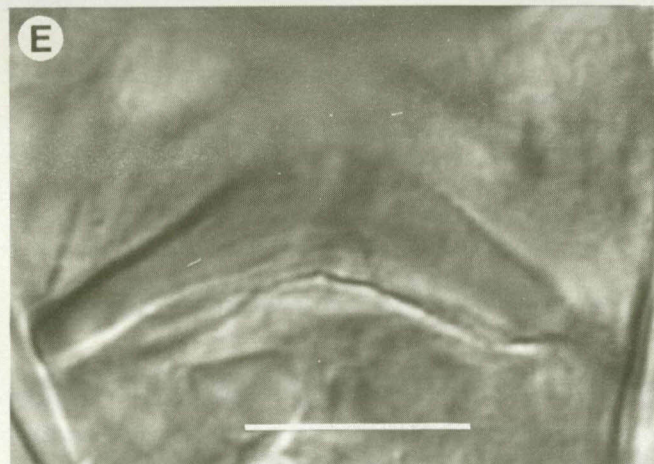
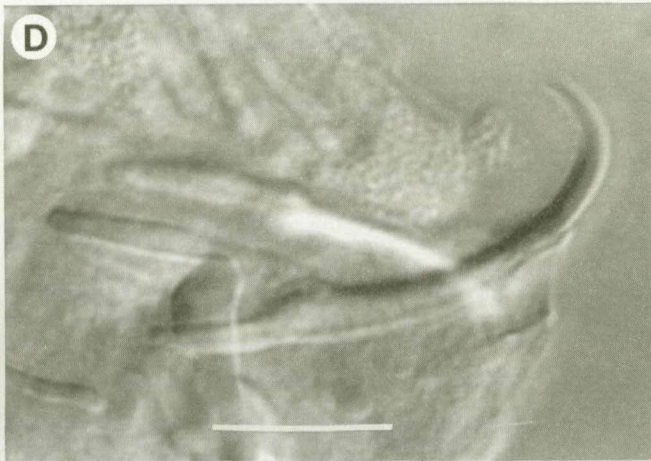
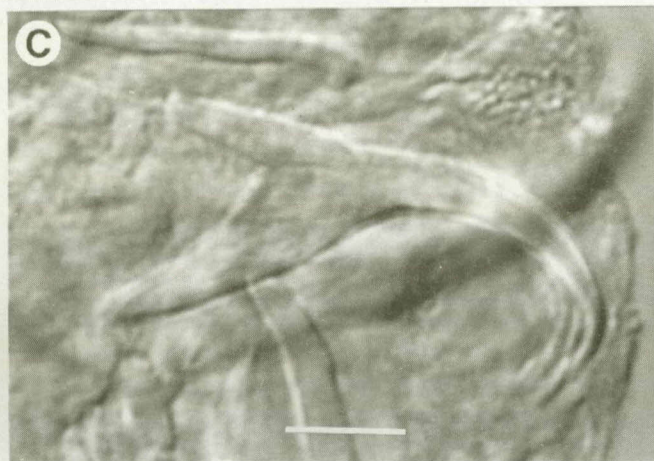
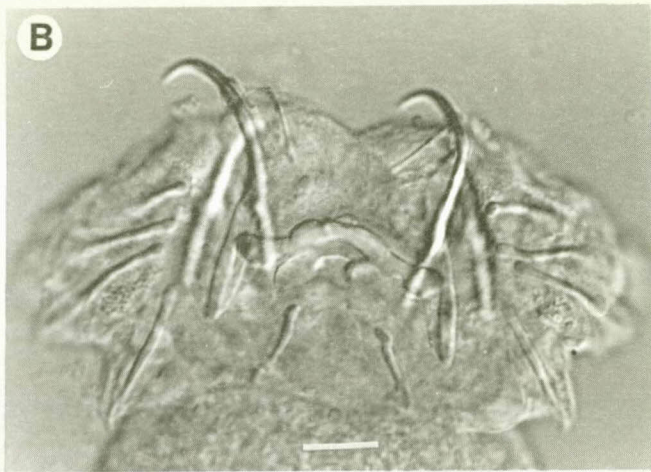
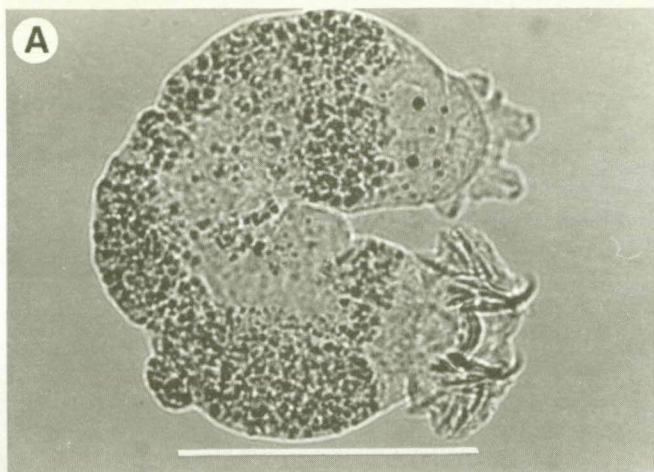
E. Dorsal bar

F. Ventral bar

G. Marginal hooklets

H. Copulatory organ

Scale bar: A- 100  $\mu$ m B-H- 10  $\mu$ m



## FIGURE 5.14

Scanning electron micrographs of *Annulotrema rhabdalesti* sp. n. occurring on the gills of *Rhabdalestes maunensis* (Fowler, 1935).

A. Whole mount

B. Tegumental annulations

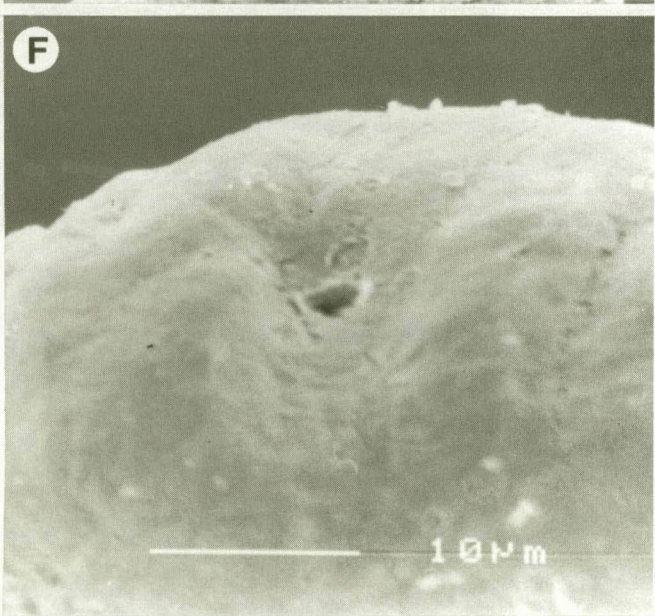
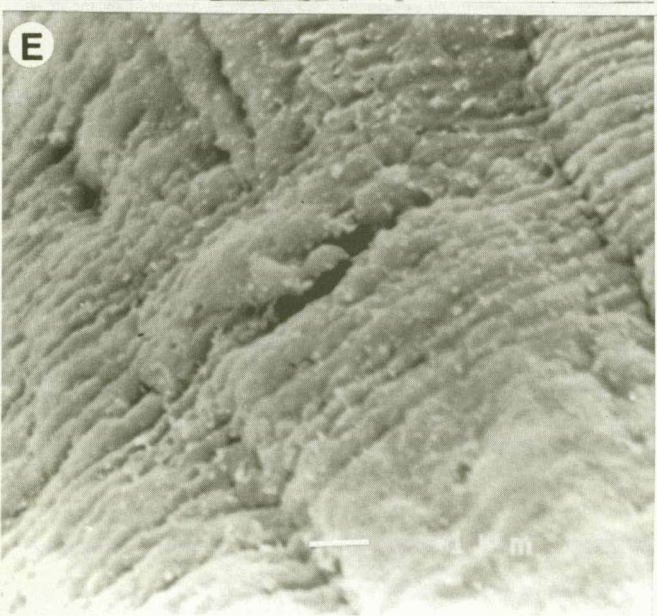
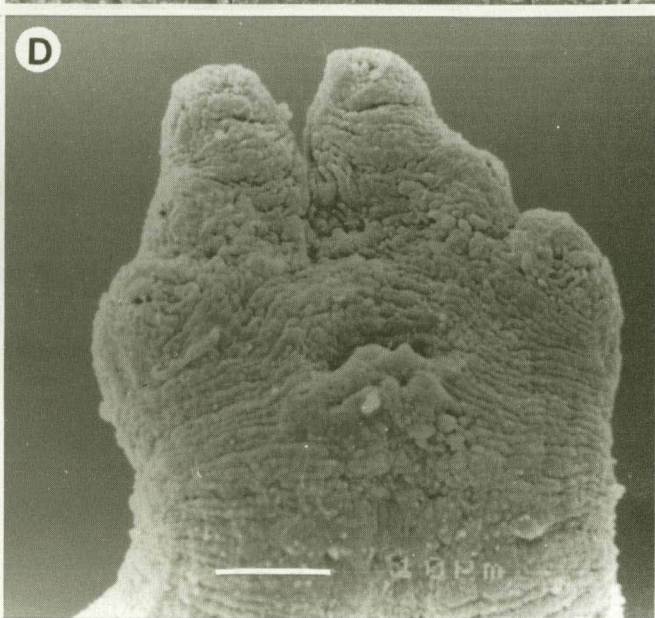
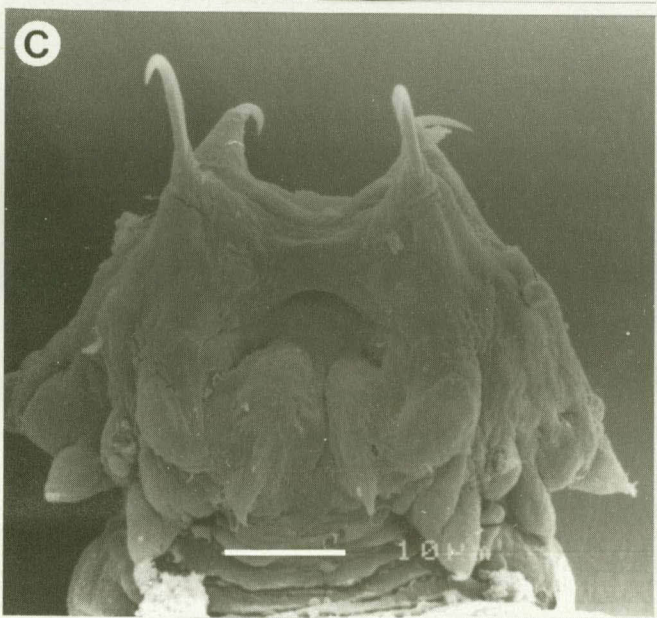
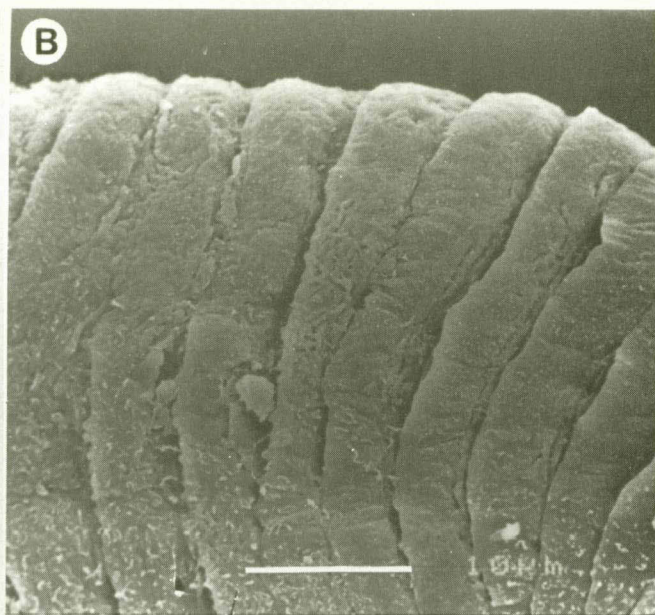
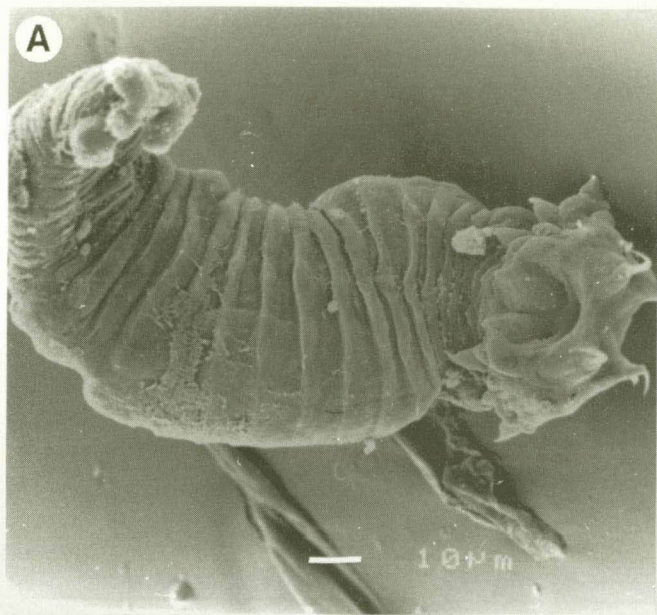
C. Opisthaptor

D. Prohaptor

E. Cirrus opening

F. Vaginal opening

Scale bar: A- 100  $\mu\text{m}$  B-F- 10  $\mu\text{m}$





***Characidotrema nursei* Ergens, 1973****HOST:** *Brycinus lateralis* (Boulenger, 1900)**LOCATION ON HOST:** Gills**LOCALITY:** Mainstream (Xaro) (18°25'23.6"S; 21°56'18.2"E), Lagoon (Xaro) & Guma Lagoon (18°57'44.9"S; 22°22'26.7"E).**REFERENCE MATERIAL:** 98 / 06 / 23 - 11**MATERIAL:** Measurements from 15 specimens mounted in Ammonium picrate.

**DESCRIPTION AND MEASUREMENTS:** Body spindle shaped, total length  $345 \pm 50.4$  (290-470), width  $132 \pm 35.9$  (95-190) (Figure 5.15A, 5.16A, 5.17A). Prohaptor with two poorly developed cephalic lobes (Figure 5.17D). Eyes equidistant, anterior pair smaller than posterior pair. Pharynx spherical,  $15 \pm 2.8$  (10-19) in diameter. Opisthaptor sub-terminal and indistinct, appearing as extension of body trunk (Figure 5.15B, 5.16B, 5.17C). Dorsal anchors  $15 \pm 2.4$  (13-21), inner root  $3 \pm 0.9$  (2-4), outer root  $2 \pm 0.8$  (1-4), shaft  $12 \pm 1.8$  (9-15), tip  $2 \pm 1.0$  (1-4) (Figure 5.15B, 5.16C). Dorsal bar length  $14 \pm 2.6$  (10-19), dorsal bar width  $2 \pm 0.7$  (1-3) (Figure 5.15B, 5.16E). Ventral anchors  $11 \pm 1.3$  (8-12), inner root  $4 \pm 1.1$  (2-6), outer root  $2 \pm 0.7$  (2-4), shaft  $8 \pm 1.1$  (6-10), tip  $2 \pm 0.5$  (1-2) (Figure 5.15B, 5.16D). Ventral bar length  $15 \pm 4.9$  (7-22), ventral bar width  $2 \pm 0.4$  (1-2), sinistral lateral arm  $8 \pm 1.9$  (6-11), dextral lateral arm  $8 \pm 1.1$  (6-9) (Figure 5.15B, 5.16F). Marginal hooklets; I=  $8 \pm 2.9$  (5-13), II=  $9 \pm 2.5$  (6-14), III=  $8 \pm 3.8$  (4-15), IV=  $8 \pm 3.6$  (5-14), V=  $8 \pm 2.5$  (5-11), VI=  $7 \pm 1.7$  (5-9), VII=  $7 \pm 1.7$  (5-9) (Figure 5.15B). Cirrus, long curved shaft,  $16 \pm 2.3$  (13-20). Accessory piece, elongated, associated with cirrus distally  $9 \pm 2.3$  (8-10) (Figure 5.15C, 5.16H, 5.17E). Vagina, opens dextrally, lightly sclerotised with spiralled tubular opening (Figure 5.17F).

**REMARKS:** *Characidotrema nursei* collected from the Okavango resemble the specimens collected by Paperna (1979) and Kritsky, *et al.* (1987), both in general morphology and in size. The tubular vagina is characteristic, although no previous mention has been made of the spiralled cuticularisation observed in the Okavango population. This is the first record of this species from *Brycinus lateralis* and from the Okavango System which hence represents the southern most distribution of *C. nursei*.

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The specimens of *Characidotrema nursei* collected from the Okavango were frequently found associated with an *Ichthyobodo* species which, attached to the opisthaptor, embedding their flagellae into the tissue of the monogeneans (Figure 5.16G, 5.17C).

## FIGURE 5.15

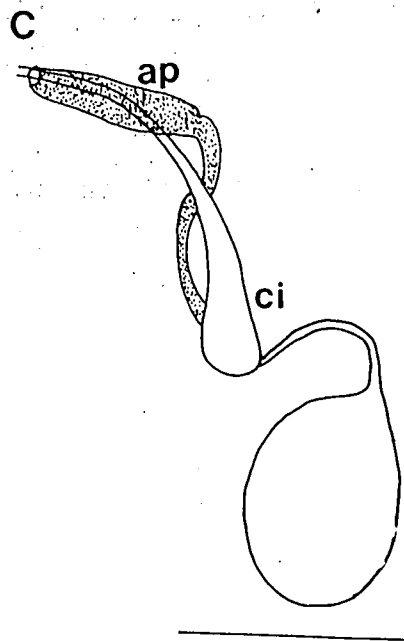
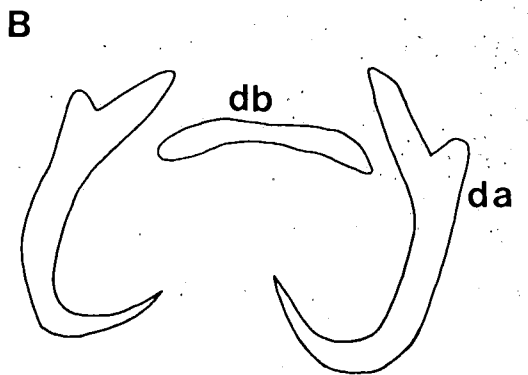
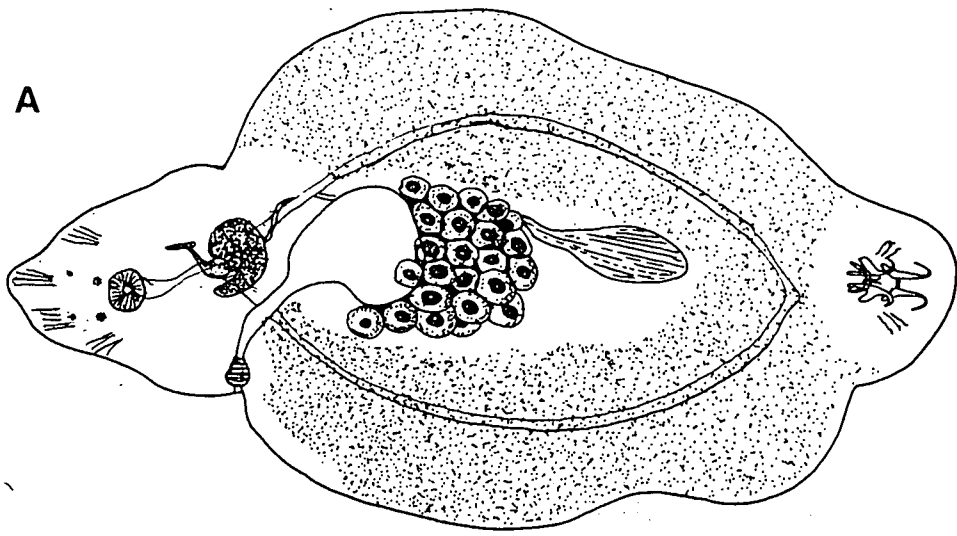
Microscope projection drawings of *Characidotrema nursei* Ergens, 1973, occurring on the gill filaments of *Brycinus lateralis* (Boulenger, 1900).

A. Whole mount

B. Opisthaptor sclerites (db-dorsal bar, vb- ventral bar, da- dorsal anchor, va- ventral anchor, mh- marginal hooklets)

C. Copulatory organ (ap- accessory piece, ci- cirrus)

Scale bar: A- 100  $\mu\text{m}$  B&C- 10  $\mu\text{m}$



I II III IV V VI VII

## FIGURE 5.16

Light micrographs of *Characidotrema nursei* Ergens, 1973, occurring on the gill filaments of *Brycinus lateralis* (Boulenger, 1900).

A. Whole mount

B. Opisthaptor

C. Dorsal anchor

D. Ventral anchor

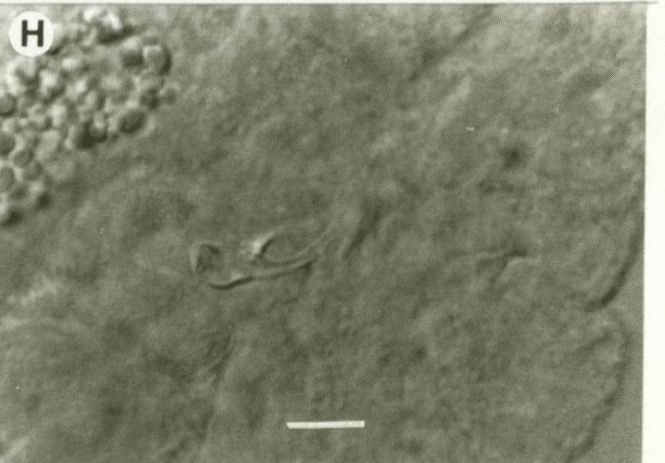
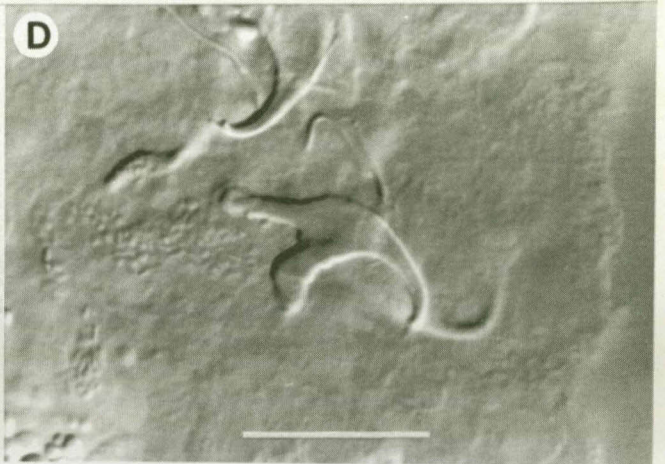
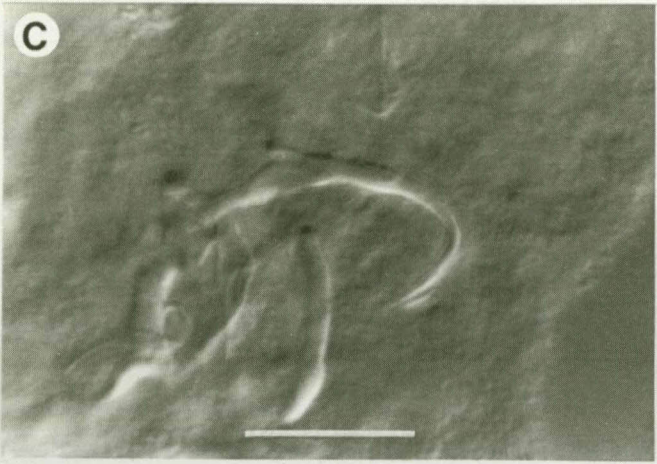
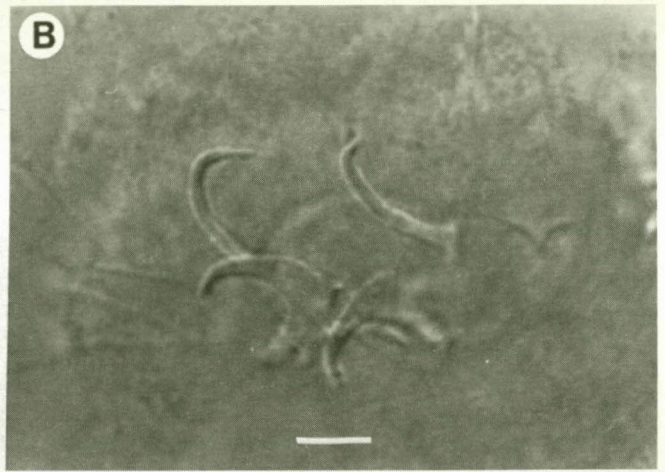
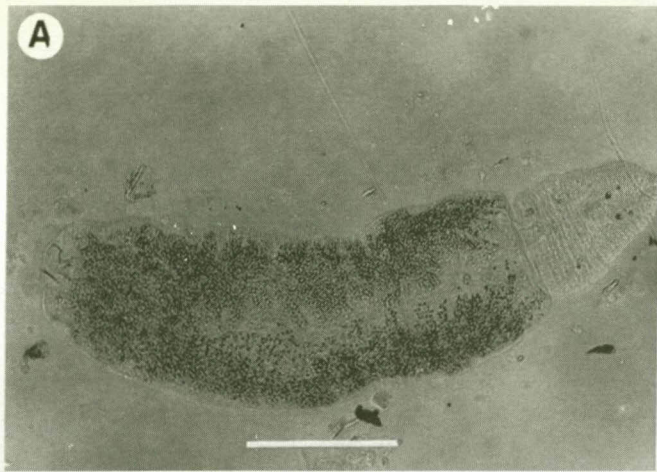
E. Dorsal bar

F. Ventral bar

G. Marginal hooklets

H. Copulatory organ

Scale bar: A- 100  $\mu\text{m}$  B-H- 10  $\mu\text{m}$



## FIGURE 5.17

Scanning electron micrographs of *Characidotrema nursei* Ergens, 1973, occurring on the gills of *Brycinus lateralis* (Boulenger, 1900).

A. Whole mount

B. Tegumental annulations

C. Opisthaptor

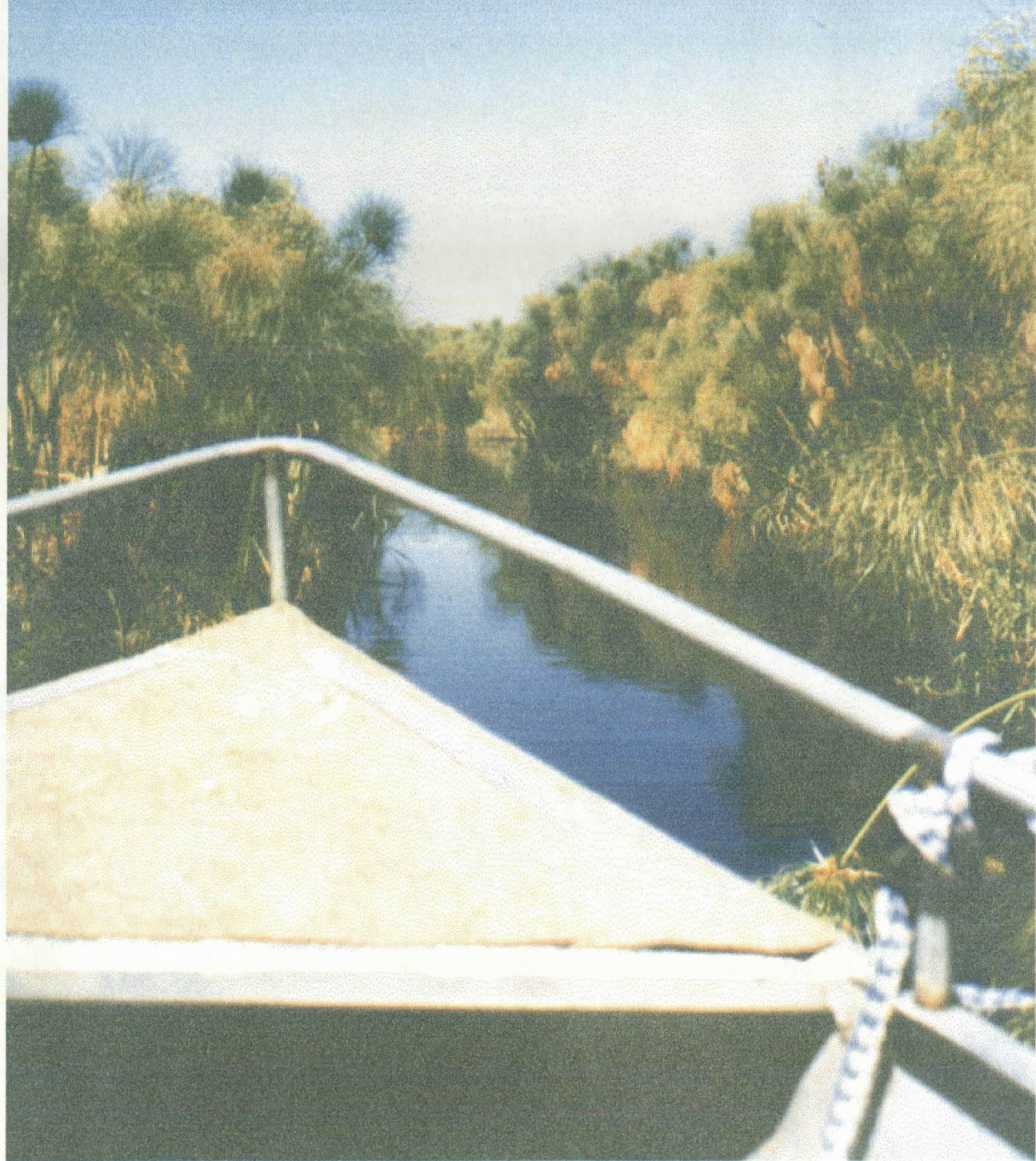
D. Prohaptor

E. Cirrus opening

F. Vaginal opening

Scale bar: A- 100  $\mu\text{m}$  B-F- 10  $\mu\text{m}$

# CHAPTER 6





# ASPECTS OF PARASITE HOST ASSOCIATIONS

Gills of fish are evaginated respiratory organs with large surface areas to facilitate the necessary gaseous exchange to sustain life. Along with this large surface area, it provides a suitable habitat for the colonisation of a variety of symbiotic organisms including monogeneans.

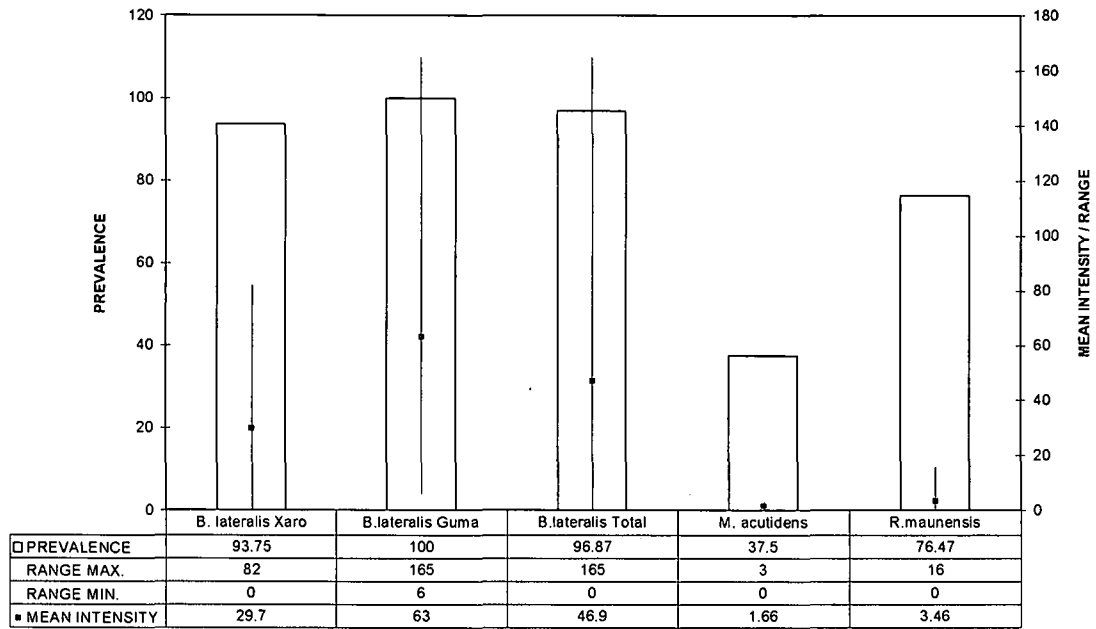
According to Noble & Noble (1982) the monogeneans as a group, are very host specific. This specificity may be physiological or ecological in nature, but the specificity is pronounced and is of phylogenetic significance. This extreme host specificity is clearly noticeable in representatives of the two genera *Annulotrema* and *Characidotrema*. Species from these genera have been recorded from characiform fishes in Africa exclusively. The various species of these two genera are also relatively species specific with only seven of the 44 *Annulotrema* species and four of the 10 *Characidotrema* species being recorded from more than one fish host (Table. 4.3 & Table. 4.6). Site specificity among monogeneans is also clearly exhibited by some species, particularly those with morphological adaptations to attachment on a specific site. Extreme site specificity, according to Noble and Noble (1982), in turn also influences the degree of host specificity as transfer from one host to another becomes more difficult.

Of the six species of monogeneans collected from characiform fish from the Okavango System, five belonged to the genus *Annulotrema* and one to the genus *Characidotrema*. As described below, these monogeneans were collected from different localities within the Okavango System and were found to occur in varying numbers on the gills of the fishes. These infestations were also found to vary between the different species of host and parasite, and from one collection locality to another.

## INFESTATION LEVELS

The prevalence of monogenean infestations on the gills of characiform fish from the Okavango seems to be relatively uniform with almost all of the fishes that were examined being infested by either *Annulotrema* species or *Characidotrema* species or by both (Figure 6.1, 6.2; Appendix 2-8). Both *Annulotrema curvipenis* and *Characidotrema nursei* infested 93.75% of the striped robbers (*Brycinus lateralis*), collected from a lagoon near Xaro Lodge. The population of *B. lateralis* from Guma Lagoon on the other hand showed a 100% prevalence of this mixed infestation. None of the infested striped robbers that were examined from Xaro and Guma Lagoons were exclusively infested by only *Annulotrema curvipenis* or *Characidotrema nursei*, but all showed a mixed infestation which differed in intensity and constitution between the two collection sites (Figure 6.1). The two populations of *B. lateralis* differ quite remarkably in the number of parasites per infested host (mean intensity). The Guma population seems to bear a much larger monogenean burden than the population at Xaro. This is not only illustrated by the mean intensity, but also by the more extensive range in number of parasites of the Guma population (6-165 monogeneans per host) than the Xaro population (0-82 monogeneans per host).

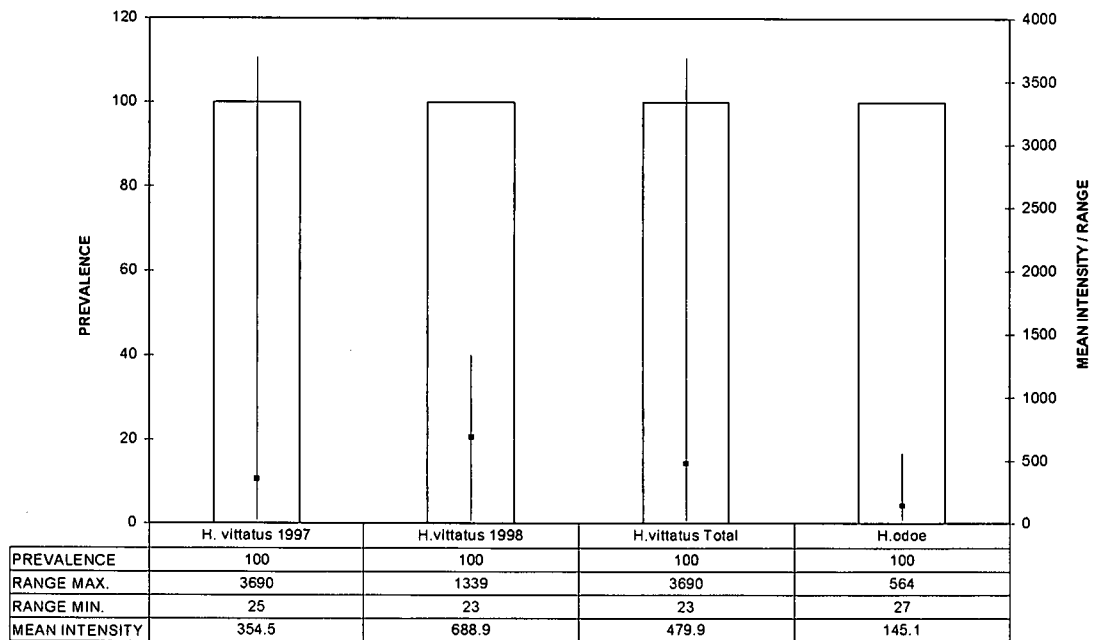
Although it may seem as if *Micralestes acutidens* and *Rhabdalestes maunensis* differ quite remarkably with respect to their monogenean infestations, they are, however, compared as they are very similar not only in size, but in biology and distribution as well. When comparing the infestation levels of these two fish species to those of the other three fish species (Figure 6.1 & 6.2), both *Micralestes acutidens* and *Rhabdalestes maunensis* have very few monogeneans per infested host. The reasons for this may be due to a much smaller sample of these two fish species than that of the other species, but is more accurately ascribed to the extremely small gill area which in turn means a minute microhabitat which can sustain far less monogeneans than the larger species.



**FIGURE 6.1** Graphic representation of monogenean prevalence, mean intensity and range of parasites per host on *Brycinus lateralis* (Boulenger, 1900) from Xaro Lagoon and Guma Lagoon and on *Micralestes acutidens* (Peters, 1852) and *Rhabdalestes maunensis* (Fowler, 1935) from mainstream Xaro.

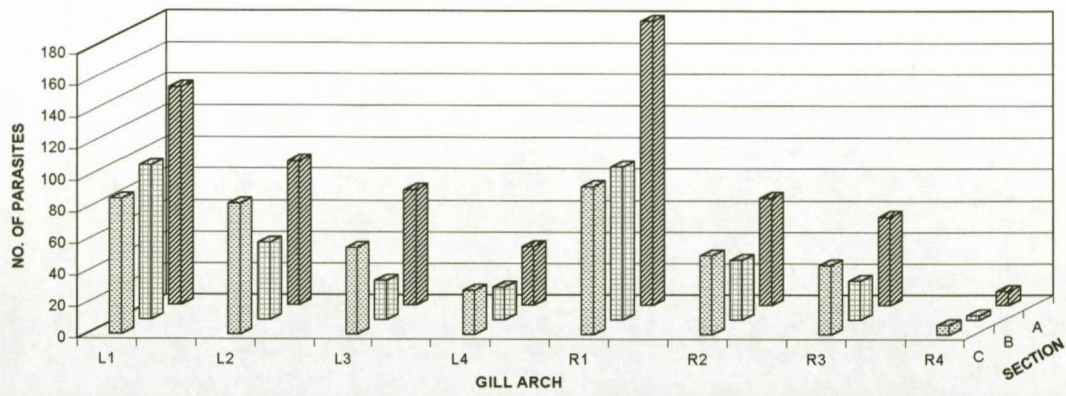
Figure 6.2 indicates that 100% of the tiger fish sampled were infested with a range of 23 to 3690 parasites per host. An interesting difference between the mean intensities of the samples taken in October 1997 and August 1998 is, however, noticeable. In October 1997, only one fish was collected which had more than 1000 monogenean parasites on its gills. This was a specimen of 740mm standard length, which had 3690 monogeneans on its gills. The mean intensity of the infestation on the rest of the specimens without this one specimen is only 173 parasites per host. The August 1998 sample, on the other hand, had three specimens with more than 1000 parasites per host. The rest of the sample had a mean intensity of 565 parasites per host. From these results there seems to be a clear difference in the intensity of *Annulotrema pikei* on the gills of *Hydrocynus vittatus* from late winter (June-August) to early summer (October).

All of the pike were infested with a relatively large number of *Annulotrema hepseti*. A mean intensity of 145.1 parasites per host was recorded with a range of 27 to 564 parasites per host (Figure 6.2). This infestation is comparable to that of *Brycinus lateralis* from Guma lagoon (Figure 6.1) in size and nature. The density of parasites would be expected to be much higher in *Brycinus lateralis* than in *Hepsetus odoe* due to the vast difference in body size and hence in gill surface area.

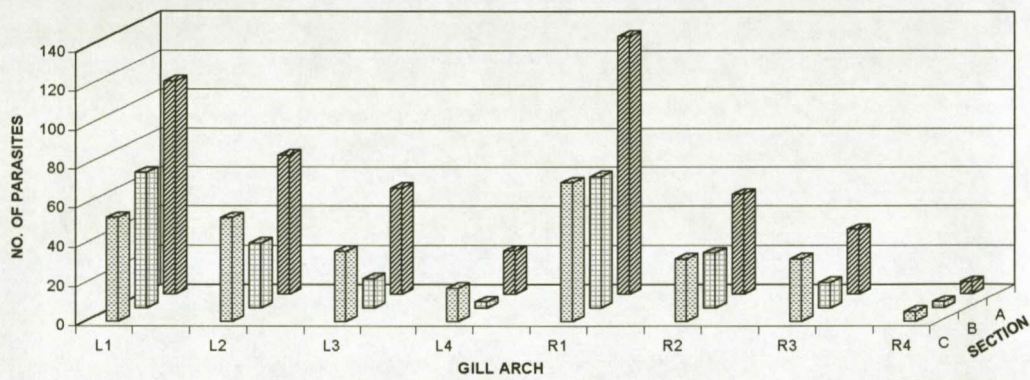


**FIGURE 6.2** Graphic representation of monogenean infestation prevalence, mean intensity and range of parasites per host on *Hydrocynus vittatus* Castelnau, 1861 collected in October 1997 and August 1998 and on *Hepsetus odoe* (Bloch, 1794).

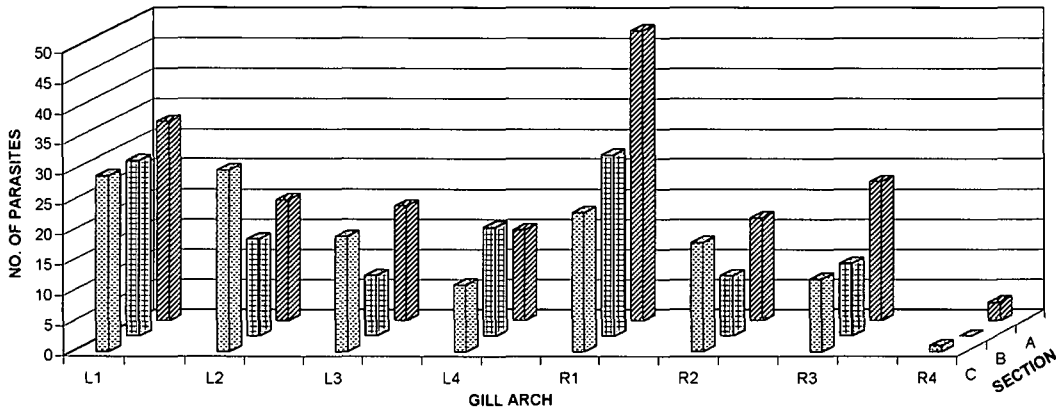
In figures 6.3-6.5, the distribution of the branchial monogeneans on the specific gill arches and gill sections of *Brycinus lateralis* are illustrated. The general trend in both sampling localities is more or less uniform with the first gill arch on either side harbouring the most monogeneans and decreasing to the fourth. Monogeneans also exhibit preference to the first section of each gill arch with sections B and C being about equal. There do not appear to be any significant differences in the distribution of monogeneans on the gills of *Brycinus lateralis* between the two sampling localities, apart from the difference in mean intensity between the two populations.



**FIGURE 6.3** Graphic representation showing the distribution of branchial monogeneans on the gills of *Brycinus lateralis* (Boulenger, 1900) from the Okavango System.



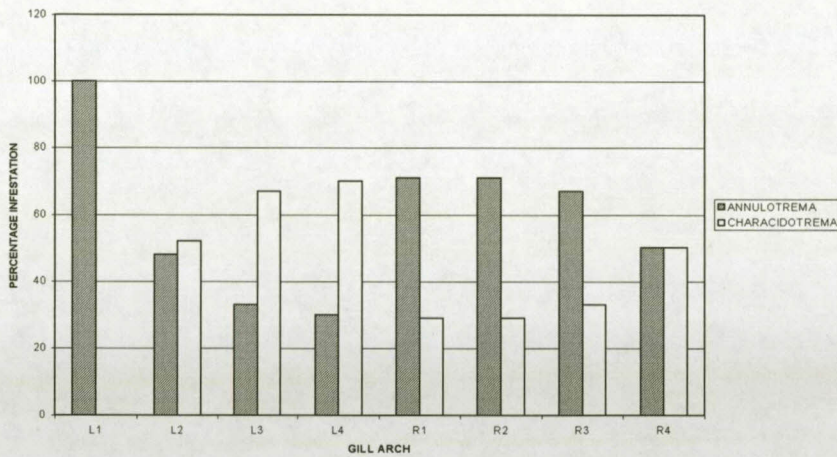
**FIGURE 6.4** Graphic representation showing distribution of branchial monogeneans on the gills of *Brycinus lateralis* (Boulenger, 1900) from Guma Lagoon.



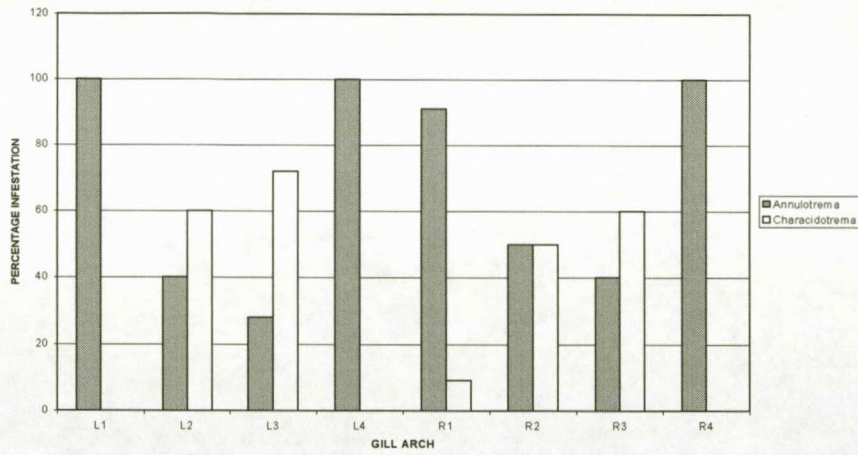
**FIGURE 6.5** Graphic representation showing distribution of branchial monogeneans on the gills of *Brycinus lateralis* (Boulenger, 1900) from Xaro Lagoon.

Site preference was observed between *Annulotrema curvipenis* and *Characidotrema nursei* from *Brycinus lateralis*. These monogeneans show clear preference to certain gill arches. In general *A. curvipenis* showed preference to the first two gill arches whereas *C. nursei* showed preference for the third and fourth gill arches (Figure 6.6-6.8). When considering the two populations individually, the Guma population (Figure 6.7) showed clear adherence to this trend as no *C. nursei* specimens were present in the first left gill arch and no *A. curvipenis* specimens were recorded from the fourth left gill arch. The gill arches on the right hand side were infested by both species on all four gills, but were still in accordance with the general trend represented by Figure 6.6. The Xaro population (Figure 6.8) showed a slightly different pattern with the first and the fourth gill arches being preferred by *A. curvipenis* and the second and third by *C. nursei*. This difference in pattern is adequately explained when one considers which species was dominant and to what degree was it dominant. In the Guma population, 64% of the gill monogeneans were *A. curvipenis* whereas in the Xaro population, 73% of the gill monogeneans were *A. curvipenis*. The lower concentration of *C. nursei* on the gills of

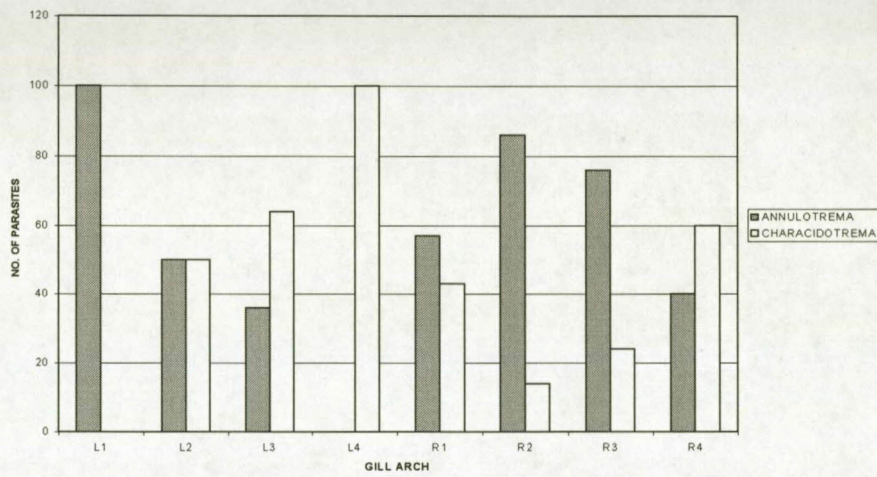
the Xaro population of *Brycinus lateralis* compared to the Guma population contributes to the pattern exhibited on the gills of the Xaro population. When all the data is combined (Figure 6.8), *A. curvipenis* makes up 66% of the total monogeneans found on the gills of *Brycinus lateralis*.



**FIGURE 6.6** Graphic representation showing the distribution of *Annulotrema curvipenis* Paperna, 1969 and *Characidotrema nursei* Ergens, 1973 expressed as a percentage of the total number of parasites on the different gill arches of *Brycinus lateralis* (Boulenger, 1900). L1-4 Gill arches on the left side of the fish, R1-4 gill arches on the right side.



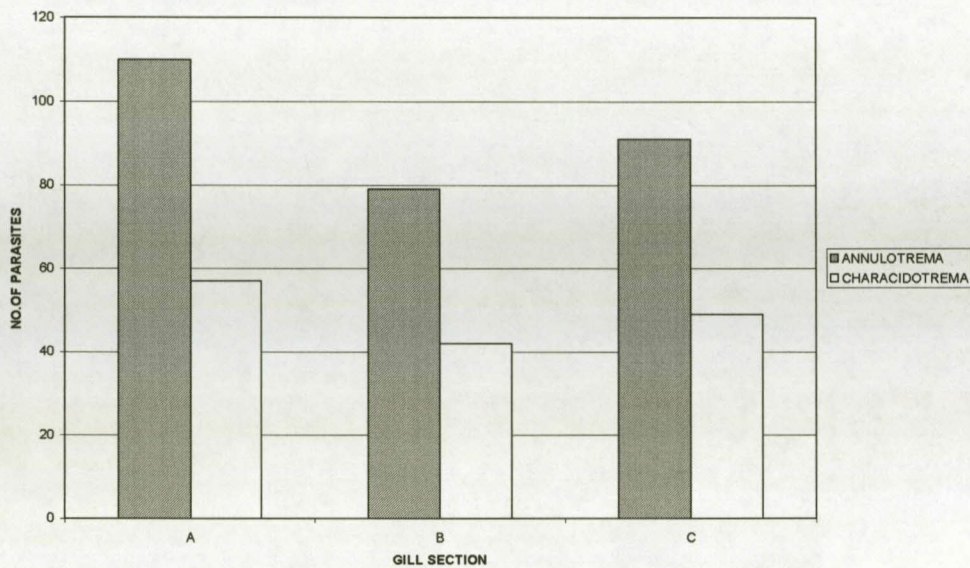
**FIGURE 6.7** Graphic representation showing the distribution of *Annulotrema curvipennis* Paperna, 1969 and *Characidotrema nursei* Ergens, 1973 expressed as a percentage of the total number of parasites on the different gill arches of *Brycinus lateralis* (Boulenger, 1900) from Guma Lagoon.



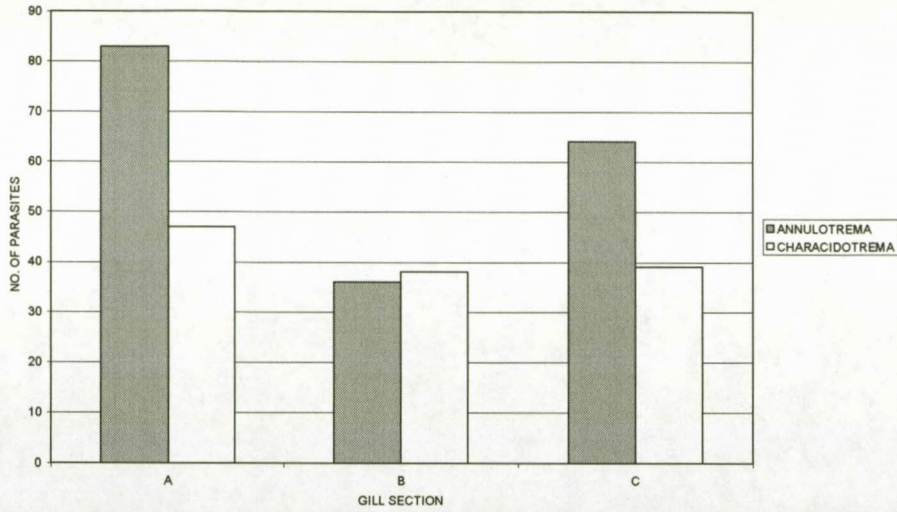
**FIGURE 6.8** Graphic representation showing the distribution of *Annulotrema curvipennis* Paperna, 1969 and *Characidotrema nursei* Ergens, 1973 expressed as a percentage of the total number of parasites on the different gill arches of *Brycinus lateralis* (Boulenger, 1900) from Xaro.



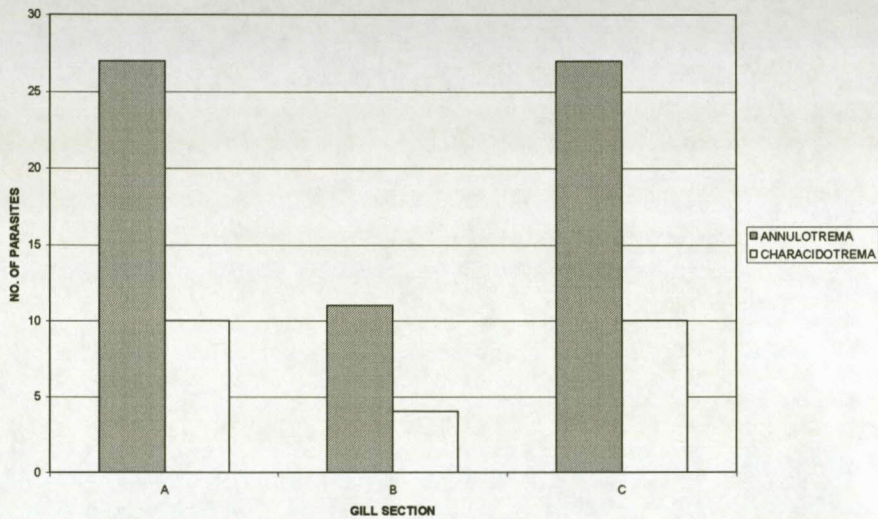
*Characidotrema nursei* and *Annulotrema curvipenis* also showed specific site preference to the region or section of the specific gill arch from where they were collected. In general both species showed a preference for the gill section A followed by section B and then C (Figure 6.9). In most cases the number of *A. curvipenis* outnumbered that of *C. nursei* except for section B in the Guma population (Figure 6.10). In the Guma population where *C. nursei* was more abundant, *A. curvipenis* showed clear preference to section A as opposed to Xaro (Figure 6.11) where *A. curvipenis* showed no preference between the A and B sections of the gill arch.



**FIGURE 6.9** Graphic representation showing the site preferences of monogeneans on the gills arches of *Brycinus lateralis* (Boulenger, 1900).



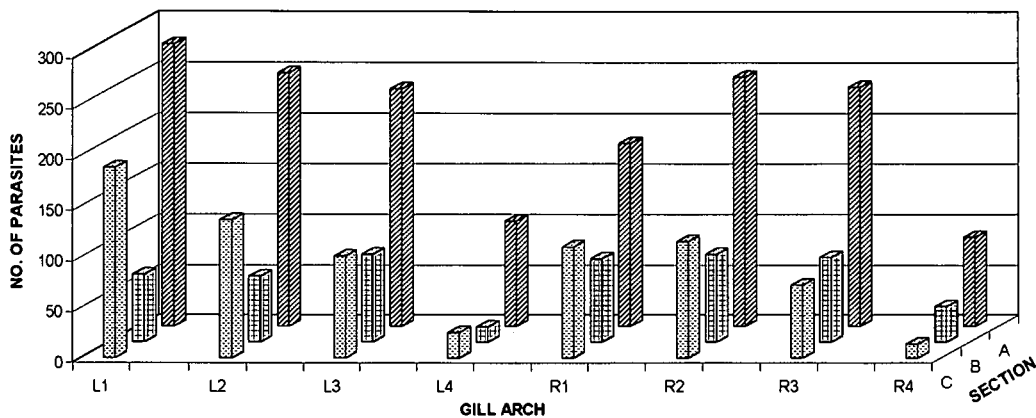
**FIGURE 6.10** Graphic representation showing the site preferences of monogeneans on the gills arches of *Brycinus lateralis* (Boulenger, 1900) from Guma Lagoon.



**FIGURE 6.11** Graphic representation showing the site preferences of monogeneans on the gills arches of *Brycinus lateralis* (Boulenger, 1900) from Xaro.

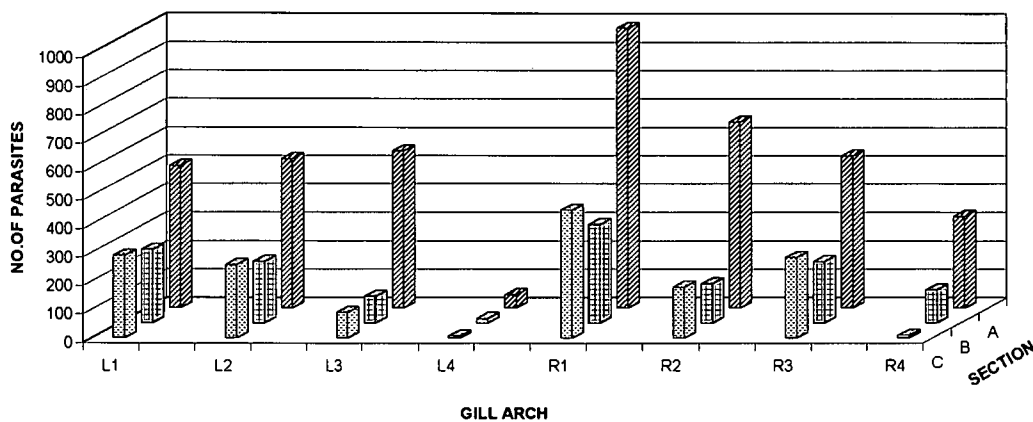
*Annulotrema hepseti* collected from the gills of *Hepsetus odoe* showed a clear preference to section A of the gill arches, followed by section C (Figure 6.12). Section A of the first left gill arch did on average have the most monogeneans, but when combining left and right, the second and third gill arches were the most preferred sites of attachment.

The reason for the relatively low mean intensity of monogeneans on the gills of the pike may be due to the fact that a diversity of parasites were observed on the gills of these fish and seem to be making use of the same niche as *Annulotrema hepseti*. The presence of these other parasites would also directly impact on the distribution of the monogeneans on the gills.

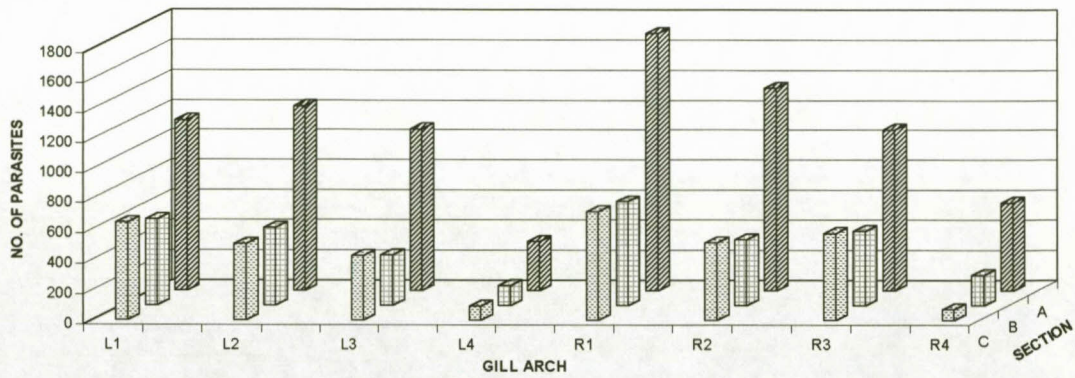


**FIGURE 6.12** Graphic representation showing the distribution of branchial monogeneans on the gills of *Hepsetus odoe* (Bloch, 1794) from the Okavango System.

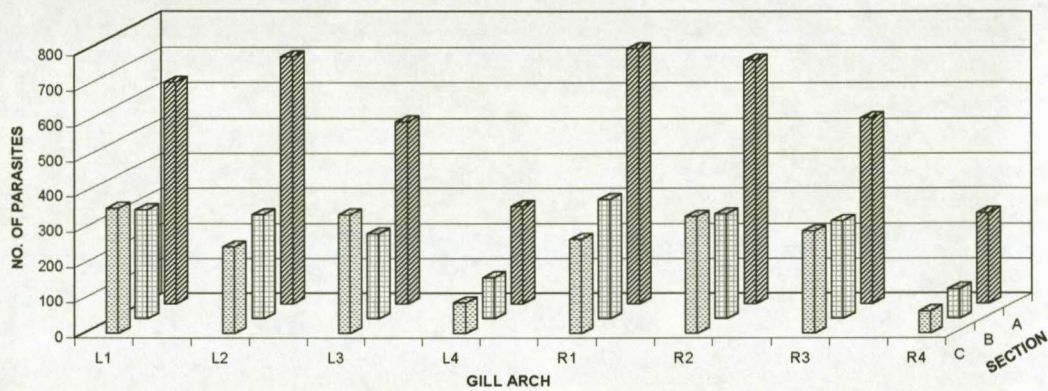
*Annulotrema pikei* in general showed a preference to the first two gill arches, particularly to section A. Section A of the first right gill arch has an exceptionally high monogenean count, this is due to a large tigerfish that was collected in October 1997 which had a total number of 3690 monogeneans on its gills. Of these, 2400 were recorded from section A from all the gill arches, with 600 being counted on section A of the first right gill arch (Figure 6.13). When comparing Figures 6.14 & 6.15, it is notable that the differences between the gill arches and the sections of the gill arches of the 1988 sample are far less pronounced than that of the 1997 sample, which has a lower mean intensity than the 1998 sample (Figure 6.2). The higher degree of site preference, or more pronounced differences between the number of parasites on the various sections of the various gill arches, expressed by the 1997 population is probably as a result of less intra-specific competition for space due to less parasites on average per host.



**FIGURE 6.13** Graphic representation showing the distribution of branchial monogeneans on the gills of *Hydrocynus vittatus* Castelnau, 1861 from the Okavango System.

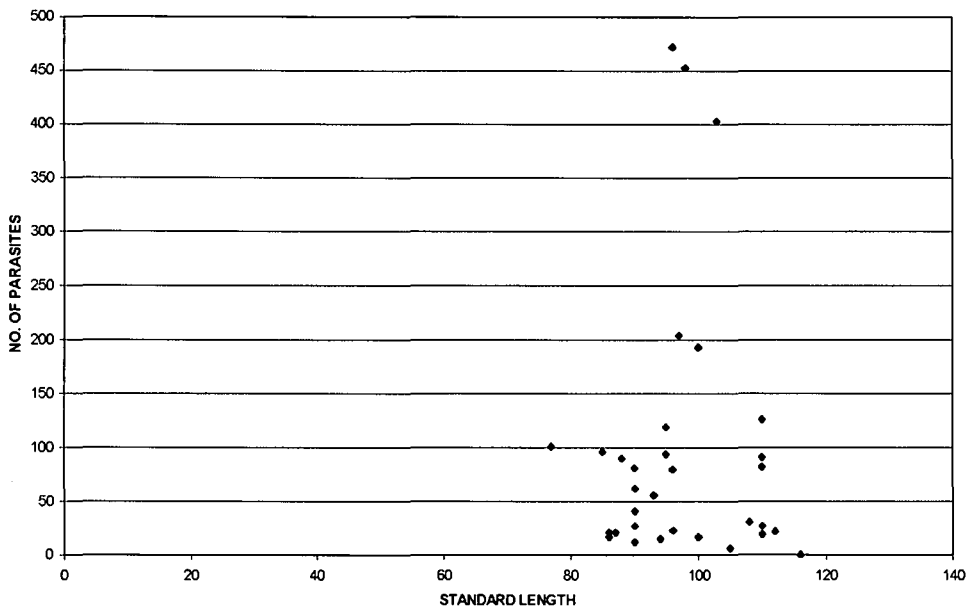


**FIGURE 6.14** Graphic representation showing the distribution of branchial monogeneans on the gills of *Hydrocynus vittatus* Castelnau, 1861 from the Okavango system collected early summer 1997.



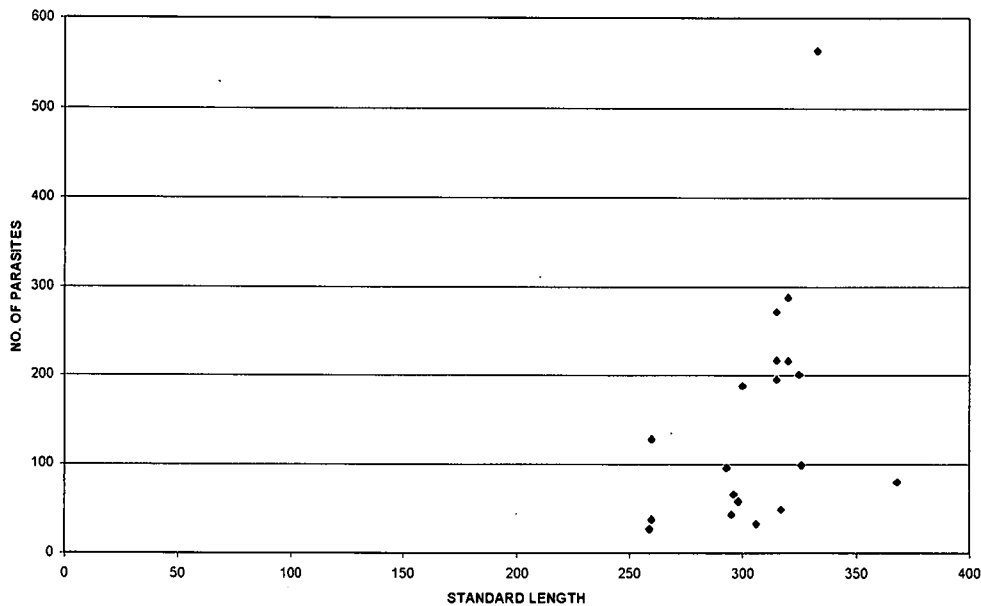
**FIGURE 6.15** Graphic representation showing the distribution of branchial monogeneans on the gills of *Hydrocynus vittatus* Castelnau, 1861 from the Okavango System collected in late winter 1998

Figures 6.16-6.20 and Appendices 2-8 represent the distributions of the branchial monogenean parasites within the various populations of the characins collected from the Okavango System. The combined infestation of *Annulotrema curvipennis* and *Characidotrema nursei* on the gills of *Brycinus lateralis* from both Guma lagoon and Xaro seems to be overdispersed (Figure 6.16). With the exception of three individual fish, which were severely infested, most of the fish had mild infestation of less than 50 monogeneans per host. The number of parasites on the fish *Brycinus lateralis* did not necessarily increase with increased size of the fish host.



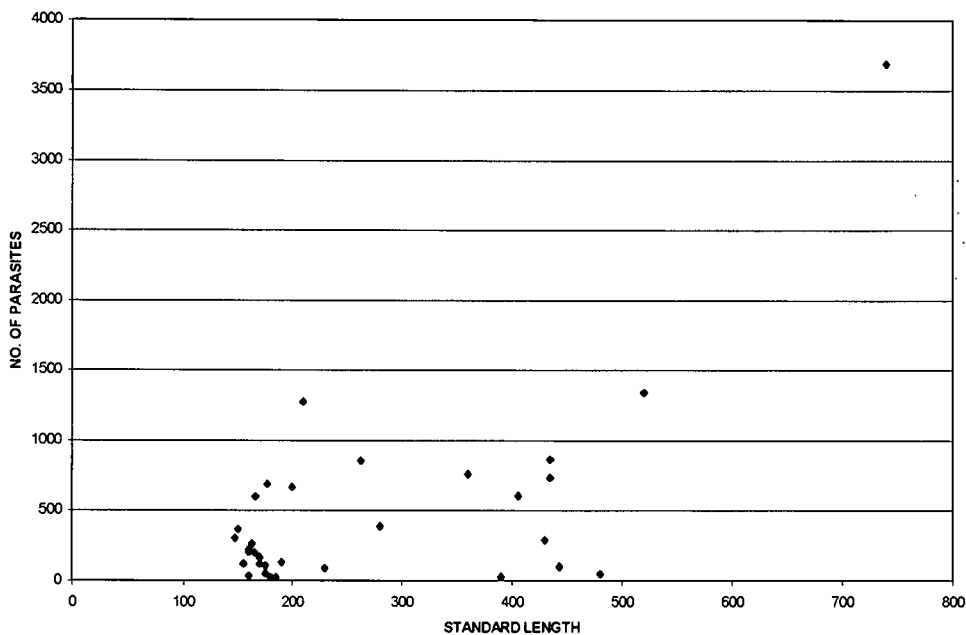
**FIGURE 6.16** Scatter plot diagram illustrating the distribution of *Annulotrema curvipennis* Paperna, 1969 and *Characidotrema nursei* Ergens, 1973 on specimens of *Brycinus lateralis* (Boulenger, 1900).

The infestation of the gills of *Hepsetus odoe* by *Annulotrema hepseti* (Figure 6.17) is very similar to that of the monogenean infestation of *Brycinus lateralis*. The infestation also appears to be overdispersed with the most of the hosts being infested by less than 100 monogeneans. The infestation once again does not necessarily increase with increased host size.



**FIGURE 6.17** Scatter plot diagram illustrating the distribution of *Annulotrema hepseti* Paperna & Thurston, 1969 on specimens of *Hepsetus odoe* (Bloch, 1794).

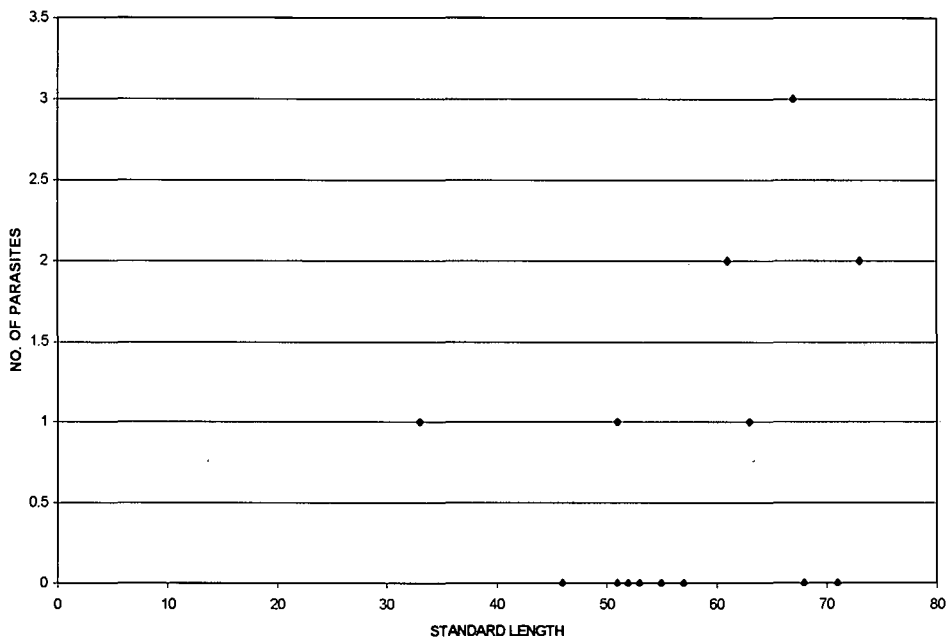
The combined data of infestation by *Annulotrema pikei* recorded from *Hydrocynus vittatus* in 1997 and 1998 from the Okavango system is represented in Figure 6.18. A large spectrum of hosts was examined. One tigerfish specimen had an extremely high infestation of *Annulotrema pikei* ( $n=3690$ ). This host was also the largest specimen collected. Apart from this isolated case, the infestation of the majority of the population is significant yet overdispersed with only 11 individuals bearing infestations of more than 500 monogeneans. Besides the one large individual that was severely infested, it does not appear as if the size of the host has any significant effect on the extent of the infestation.



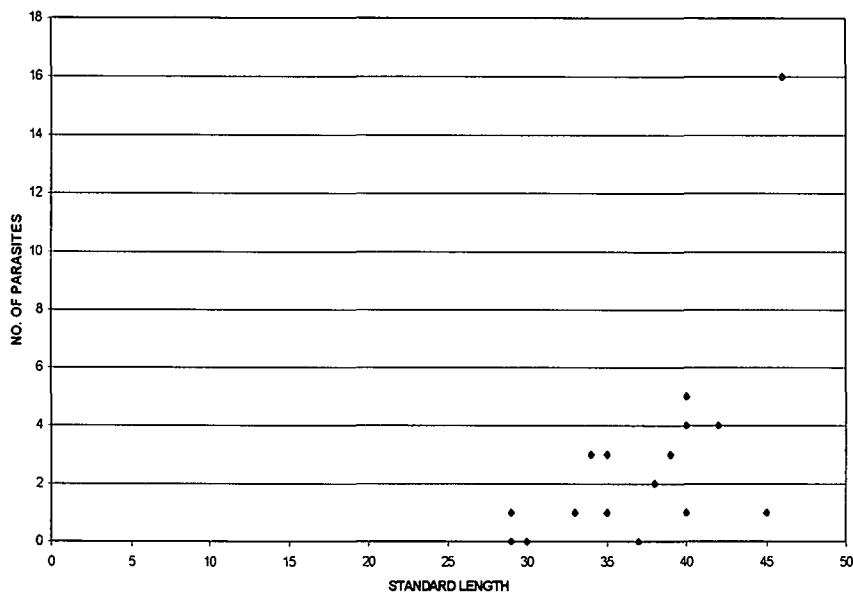
**FIGURE 6.18** Scatter plot diagram illustrating the combined distribution of *Annulotrema pikei* (Price Peebles & Bamford, 1969) on specimens of *Hydrocynus vittatus* Castelnau, 1861.



The infestations of *Micralestes acutidens* (Figure 6.19) and *Rhabdalestes maunensis* (Figure 6.20) by *Annulotrema micralesti* and *A. rhabdalesti*, follow the same pattern as that of the other species. The most significant difference, however is the magnitude of the infestation (Figure 6.1). The infestation of both *M. acutidens* and *R. maunensis* is typically an over-dispersion with only a small proportion of the population being infested by many monogeneans.



**FIGURE 6.19** Scatter plot diagram illustrating the distribution of *Annulotrema micralesti* sp. n. within the population of *Micralestes acutidens* (Peters, 1852).



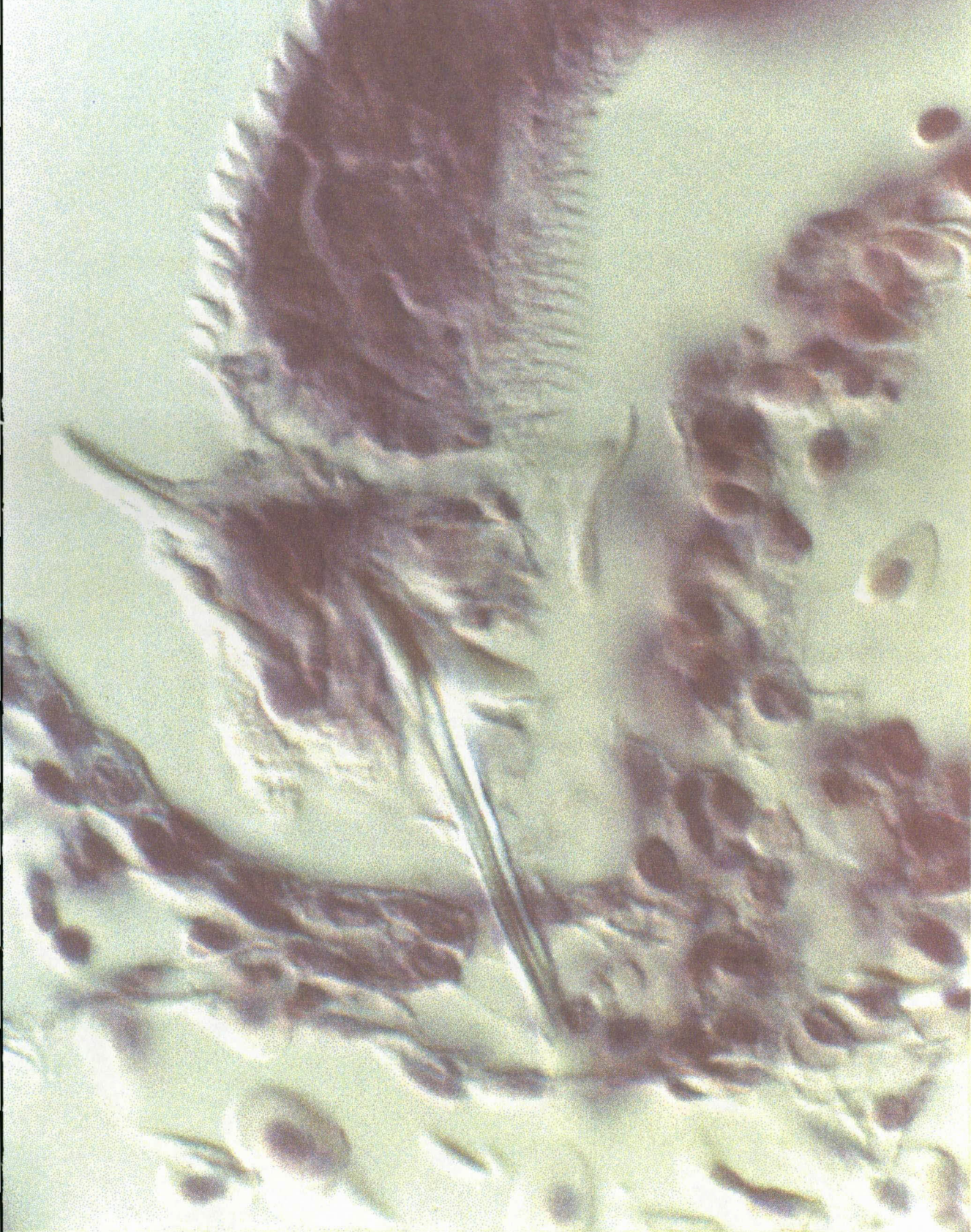
**FIGURE 6-20** Scatter plot diagram illustrating the distribution of *Annulotrema rhabdalesti* sp. n. within the population of *Rhabdalestes maunensis* (Fowler, 1935).

### CONCLUDING REMARKS

From the overall examination of the infestations of the Okavango characins by species of the genera *Annulotrema* and *Characidotrema*, certain general trends are evident. The nature of the infestation seems to be over dispersed and although, in some cases, the infestations are generally high only very few hosts are severely infested. The position of attachment is also specific and representatives of the genus *Annulotrema* specifically show strict site preferences. These preferences are, however, influenced by intra- and inter-specific competition as is illustrated by the infestations of *Brycinus lateralis* and *Hydrocynus vittatus* respectively.

As these infestations do not increase with an increase in the standard length of the host, the infestations are not cumulative. However, the presence of a spectrum of reproductively immature to mature specimens on the same host suggests that the hosts are continually re-infested.

# CHAPTER 7



# GILL PATHOLOGY AS A RESULT OF MONOGENEAN INFESTATION

The anatomical structure of gills is intricate. Each gill arch has a double row of paired filaments or primary lamellae. Each filament has a series of lamellae or secondary lamellae located anteriorly and posteriorly, perpendicular to the filament (Yasutake & Wales, 1983). The entire branchial complex is covered with epithelial tissue, which, according to Eller (1975), forms a barrier between the fish's blood and the surrounding water. According to Yasutake & Wales (1983) the principle function of the gills of fishes is to bring the blood haemoglobin in close proximity with the water, so that oxygen can be absorbed and carbon dioxide released. This ventilatory function necessitates exposing the gills, which consist of a system of capillaries with sufficient surface area to effect the required gas exchange. This exposure in turn makes the gill tissue highly vulnerable to the external environment. The gaseous exchange needed to sustain life takes place across the epithelial barrier and any thickening thereof induced by irritation from toxicants, abrasive particles, parasitic or saprophytic organisms can reduce respiratory efficiency as well as hinder the secretory and excretory functions of the gills.

## GENERAL CHARACTERISTICS OF EPITHELIAL TISSUE

Epithelial tissues are composed of closely aggregated polyhedral cells, with very little intercellular substance, which line or cover the surfaces of the body or organs (Figure 7.1A, 7.1B). Their close contact forms an effective barrier between the external environment and the underlying tissue. One margin of the epithelium is in contact with the environment and is known as the apical border. The basal border on the other end is separated from the underlying tissue by a continuous sheet-like structure called the basal lamina. Epithelial cells are extremely adhesive, and relatively strong mechanical forces are necessary to separate them. This quality of intercellular binding is especially prominent in those epithelial tissues which are exposed to physical pressure and friction

(e.g. fish gills). According to Junqueira, *et al.* (1977) there are a few factors responsible for this adhesion between epithelial cells, but of the most important factors in cell adhesion are special structures, the most frequent of which are desmosomes. According to Leeson & Leeson (1970) desmosomes (Figure 7.1B) are small dense bodies at the sites of intercellular bridges. However, desmosomes are scattered along epithelial and other cell interfaces, and are not confined to the sites of intercellular bridges.

According to Yasutake & Wales (1983) gill epithelium usually consists of unspecialised epithelial cells, dark cells, chloride cells and mucous cells. The so-called unspecialised cells function in protection and support. The dark cells resemble the unspecialised cells and are scattered uniformly throughout the epithelium of the filaments and lamellae. These two types of cells are not easily distinguishable using light microscopy. Large chloride cells are located along the entire lamellar epithelium, but are more numerous at the proximal end of the lamellae. These cells are more spherical than the other epithelial cells and tend to project from the gill surface. According to Yasutake & Wales (1983), the name chloride cells is a physiological misnomer as these cells may be responsible for the transport of various ions across the membrane. The mucous cells are abundant on the surface of the lamellae, appearing as granule filled domes or vacuolated cells in light microscopy. These cells are similar to the chloride cells but differ in having a dark cytoplasm, large round vesicles and large membrane bound bodies near the nucleus (Yasutake & Wales, 1983).

Epithelia are classified according to the number of layers they consist of and the predominant cell shape. The epithelia of the gills consist only of one layer and are thus termed simple epithelium. The type of simple epithelium that covers the gills can either be squamous or cuboidal depending on the predominant shape of the cells. According to Leeson & Leeson (1970) naming of epithelial tissue is difficult at times, as there is a continuum of cellular conformation from squamous to columnar epithelium. The morphology of the epithelial gill cells, however, is ideally suited to the transport of material across their surfaces and hence facilitates the exchange of oxygen and carbon dioxide.

Epithelia of the gills are subject to harsh conditions that result in cells being damaged or lost. Besides this fact, the longevity of individual epithelial cells is not indefinite and therefore, epithelial tissues require the renewal and replacement of lost components. The simple epithelia covering the gills are not highly differentiated for various functions and retain a high mitotic potential hence these cells serve as their own stem cells.

## **PATHOLOGY OF FISH GILLS AS A RESULT OF MONOGENEAN INFESTATION**

According to Cone (1995) monogeneans parasitising fish are either sanguiferous oligonchoineans or grazing polyonchoineans. The oligonchoineans do not produce significant tissue damage due to the delicate manner of attachment to the secondary gill lamellae and the subtle manner in which blood is drawn from the underlying blood vessels. Members of this group are rarely associated with host mortality. Polyonchoineans on the other hand promote significant tissue damage through a more disruptive manner of attachment and grazing on exposed and vulnerable integument. Although the damage is usually minimised because the parasite regularly relocates on the host, members of the group nevertheless have been known to cause significant pathology.

Paperna (1964) recorded severe dactylogyrosis from cultured carp stock. The gills of these fish were examined and showed typical tissue reaction to mechanical irritation namely, strong hyperplasia or proliferation of gill respiratory and lining epithelia and of the mucous goblet cells, resulting in serious deformations of the filaments especially at their apices. These symptoms were followed by the degeneration of the network of blood vessels and the cartilage rods, eventually causing the death of the fish due to damaged respiratory function. Paperna (1964) described the macroscopic appearance of infested gills to have lost their natural red colour, especially at the tips, which became a grey-white colour. The gills were also covered in mucous and were irregularly shaped.

Eller (1975) reported that two species of the genus *Dactylogyrus* caused the mass mortality of carp fry in Russia. In both instances, they caused marked epithelial proliferation. In addition to the epithelial hyperplasia, these monogeneans were also

responsible for causing many of the epithelial cells to degenerate into secretory cells. According to Eller (1975), the excessive amount of mucous secreted by these cells was enough to impair the respiratory functions of the gills. Hwang & Yu (1987) recorded that dactylogyrids cause physical damage to the gills of the fish host by their method of attachment, whereby the monogenean inserts its anchors into the gill tissue of the host and the physical movement of the monogeneans on the gills cause the gills to excrete excess mucus which inhibits respiration. Another potential cause of damage discussed by Hwang & Yu (1987) is the feeding habits of the dactylogyrids, which cause the gills to bleed resulting in minor haemorrhaging, and oedema, which in turn causes respiratory blockage. Monogenean infestations especially those of polyonchoinean monogeneans have also been suspected of undermining non-specific defence mechanisms and thus allowing invasions by microbial pathogens (Eller, 1975). According to Cone (1995), monogeneans may also be the mechanical vectors of various viral and bacterial pathogens of fish.

It is important to note that severe pathogenicity and mortality of a host as a result of monogenean infestation does not promote transmission of the parasite. In most instances the parasite and host have a long evolutionary relationship and parasites have been naturally selected to cause very little or no damage to the host. Host mortalities and severe host pathogenicity are usually a result of the breakdown of usual host-parasite relationships as a result of artificial circumstances.

### **PATHOLOGY OF THE GILLS OF OKAVANGO CHARACINS AS A RESULT OF INFESTATION BY THE GENERA *ANNULOTREMA* AND *CHARACIDOTREMA***

As the prevalence and mean intensity of *Annulotrema* species infesting the Okavango characiform fish as well as that of the species of *Characidotrema* recorded from *Brycinus lateralis* was high, some pathology of the gills of these fish could be expected. Gills from infested specimens of *Hydrocynus vittatus*, *Hepsetus odoe*, and *Brycinus lateralis* were examined to determine the extent and nature of the expected pathology.

The monogeneans were found located on the gill tissue in between the secondary gill lamellae (Figure 7.2A-B). They attached by anchoring themselves to the primary lamella by means of their dorsal and ventral anchors (Figures 7.2B-C). The marginal hooklets are used as counter hooks and are hooked into the secondary lamellae on either side of the fluke (Figure 7.2D).

An initial inflammatory reaction from the host on the parasite was expected, either directly as a result of the parasite or as a result of secondary infection by various microorganisms on the lesions left by the parasite. According to Wolke (1975), there are three major categories of lesions, those associated with inflammation, those associated with cellular degeneration and necrosis and abnormalities of cell growth, including neoplasia. Wolke (1975) further subdivides these three basic categories to allow for the subtle differences brought about by the various agents. Inflammatory responses, involved with infectious agents, are categorised on the basis of cell type and vascular change.

Acute inflammation is characterised by sudden localised vascular dilation resulting in congestion, oedema and hemorrhage and by the influx of polymorphonuclear cells (neutrophils, heterophils) (Wolke, 1975). According to Yasutake & Wales (1983), polymorphonuclear leucocytes are usually slightly larger than the lymphocytes averaging about 9-13  $\mu\text{m}$ . The nuclei are multi-lobulated and are frequently connected by thin strands of nuclear material.

Chronic inflammation, or inflammation of a longer duration is characterised by vascular proliferation and the influx of mononuclear cells such as lymphocytes and plasma cells (Wolke, 1975). According to Yasutake & Wales (1983) lymphocytes are small spherical cells which are about 7-10  $\mu\text{m}$  in diameter. The nucleus is slightly off-center and is also spherical in shape, which sometimes has a slight indentation. Cytoplasmic granules are frequently but not always present.

According to Wolke (1975) inflammation characterised by a mass of inflamed granular tissue or granulomatous inflammation is a proliferative inflammatory response characterised by phagocytic cells, especially histocytes (macrophages) and monocytes.



In addition epithelioid and giant cells are also present. According to Yasutake & Wales (1987), the monocytes are ovoid in shape and are generally large, 9-25  $\mu\text{m}$  in diameter. The monocytes are believed to be precursors to macrophages. Differentiation of phagocytes usually takes place when they become extravascular. The cytoplasm of monocytes often have a granular cytoplasm with a large nucleus. Macrophages in fish are often found in various tissues and are seldom seen in circulating blood.

None of these cells or steps of the expected inflammatory reaction could be observed from both the transmission micrographs (Figures 7.1A-F) as well as the histological sections (Figures 7.2A-F). Circulating leucocytes were, however, observed in some of the blood vessels but as they were not localised they could not be ascribed to the presence of the monogeneans on the gills. It thus appears as if all three fish hosts do not show an allergic or inflammatory reaction to the presence of the parasites.

As there appeared to be no inflammatory reaction to the parasites, it was expected that the parasites at least caused physical lesions or gross proliferation of the gill epithelium as was found by Paperna (1964); Eller (1975) and Hwang & Yu (1897). On first observation of the histological sections, there were regions of excessive masses of unconnected cells that were not membrane bound, much like the region ventral to the monogenean in Figure 7.2E. As these cells were all nucleated, spherical and relatively uniformly sized, they were thought to have been erythrocytes. It appeared as if these were possible regions of bleeding or hemorrhaging, which would have been an indication of acute inflammation. This led to closer investigation using the transmission electron microscope. These cells were subsequently identified as epithelial cells showing typical epithelial characteristics including the presence of desmosomes, which would not be found in erythrocytes (Figures 7.1A-B). The occurrence of these masses of epithelial cells was ascribed to imperfections during the fixation and preparation procedures.

In the immediate region of the opisthaptor (Figure 7.1C, 7.2A-F), not much damage was visible. As some of the anchors penetrated directly into blood vessels (Figures 7.1C, 7.2B), some bleeding or aggregation of tissue fluid was expected, but was not observed. The only sign of damage that was observed was that of the epithelial cells directly in the

path of hook or anchor penetration. As each hook only affects three or four individual cells at a time it appears as if the damage is negligible as it would be expected that the epithelial cells of the gills of fish get replaced regularly due to the amount of friction and exposure they undergo.

The epithelium in the immediate vicinity of the parasites (Figure 7.1D) did show some signs of thickening which could be as a result of irritation by the parasite and may be indicative of mild hyperplasia or proliferation of the epithelium. There were, however, other regions that also showed areas where the epithelium was two or more cell layers thick (Figure 7.1E & Figure 7.1 F). These could be previous attachment sites of monogenean attachment or could be as a result of some other irritant. Figure 7.1E shows a region, between the two blood vessels, that appears as if there may be some mild hyperplasia or proliferation of epithelial cells. This region could be a remaining scar of a previous site of attachment of a monogenean. In Figure 7.1F there are once again indications of hyperplasia, where the epithelium on the left side of the blood vessel appears to be at least twice as thick as the epithelium on the right hand side. This could be as a result of matrix proliferation, where the cytoplasm proliferates as opposed to cellular proliferation (Figure 7.1E). The adjacent lamella on the right hand side also appears to have some thickening of the epithelium and these thickened regions could once again be the remains of a previous attachment site (Figure 7.1F).

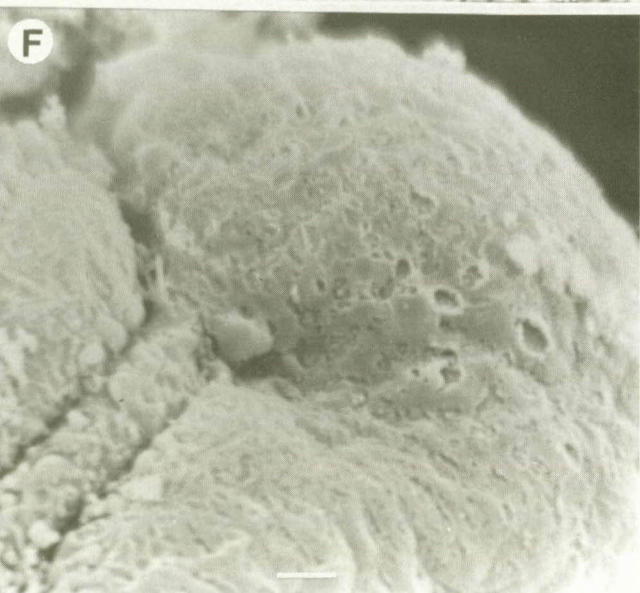
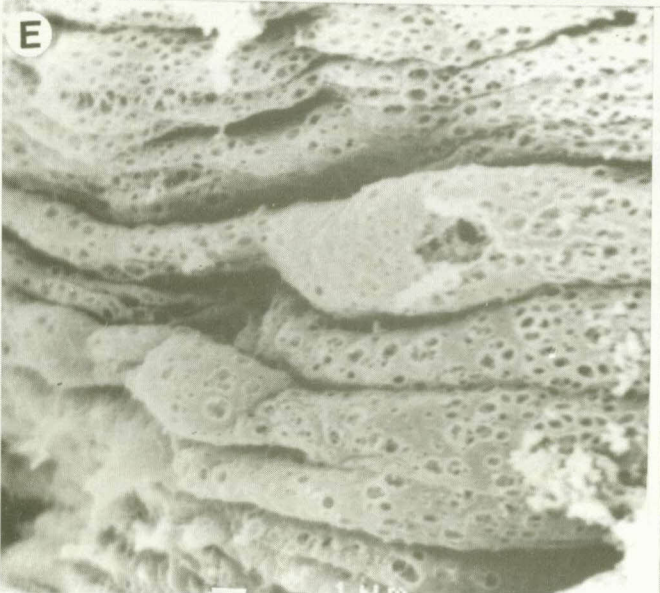
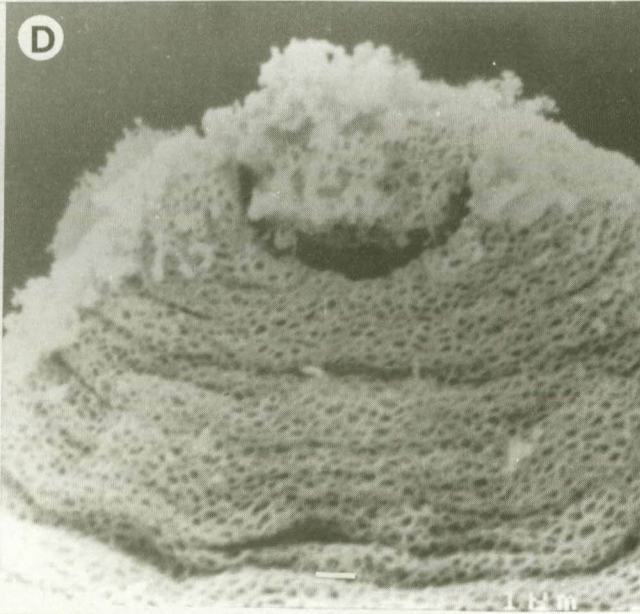
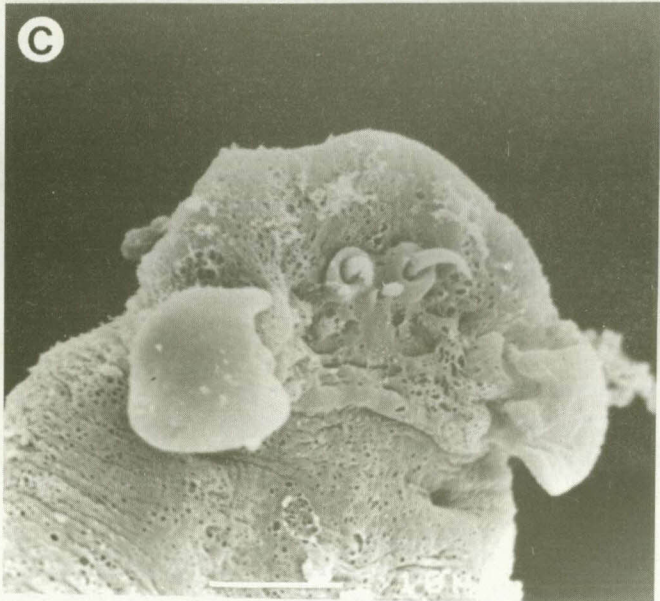
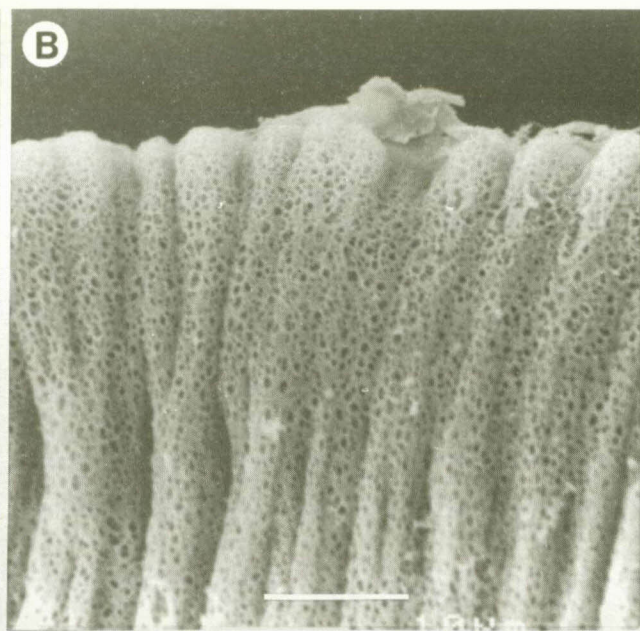
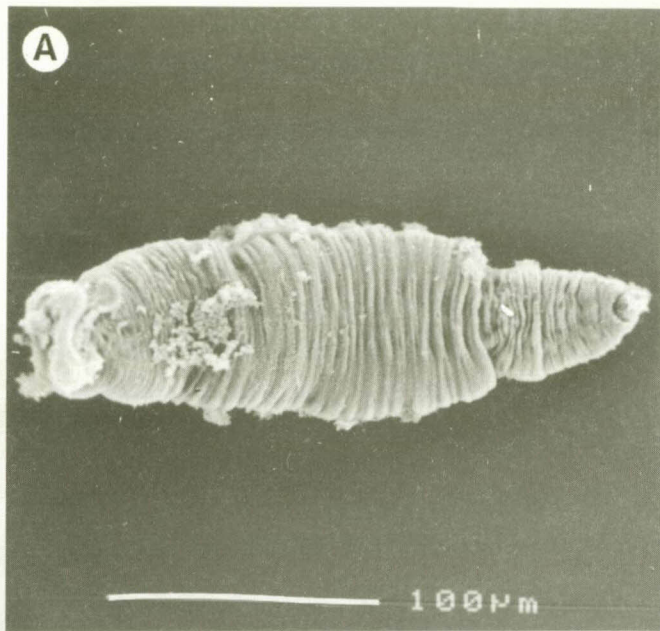
In most cases it seemed as if the monogeneans may have caused only mild mechanical damaged to the gills, which was represented by mild hyperplasia of the lamellar epithelium. This could be in accordance with the findings of Cone (1995) in which some dactylogyrid monogeneans facilitate their parasitism through the disruption of host epithelia causing epithelial hyperplasia to ensure firm attachment to the host and a localised replenishment of food. This may also be seen as microhabitat or niche reservation when taking into consideration the numbers in which these parasites occur on the gills of their fish hosts.

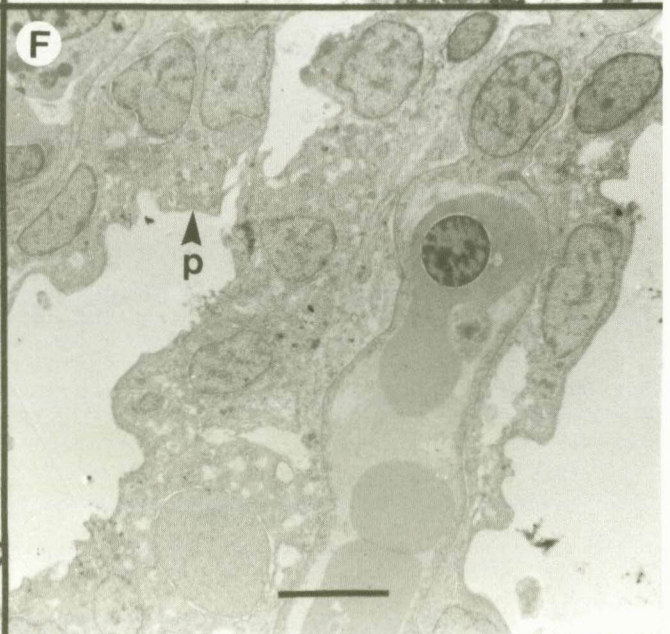
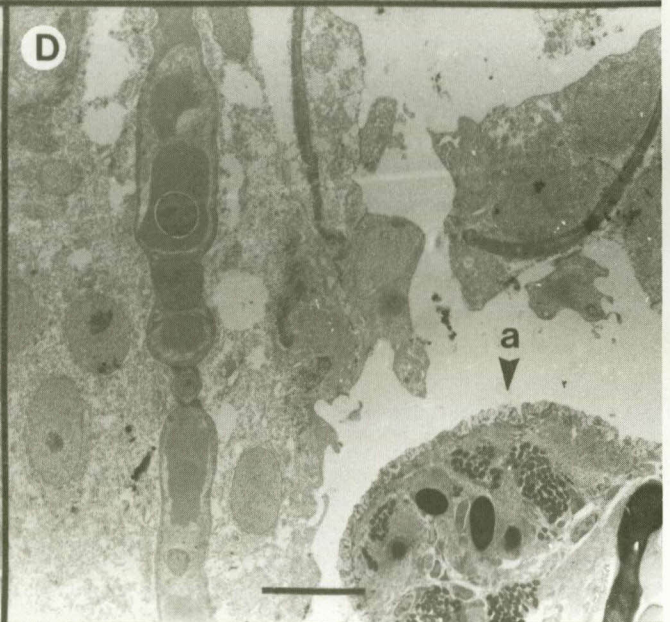
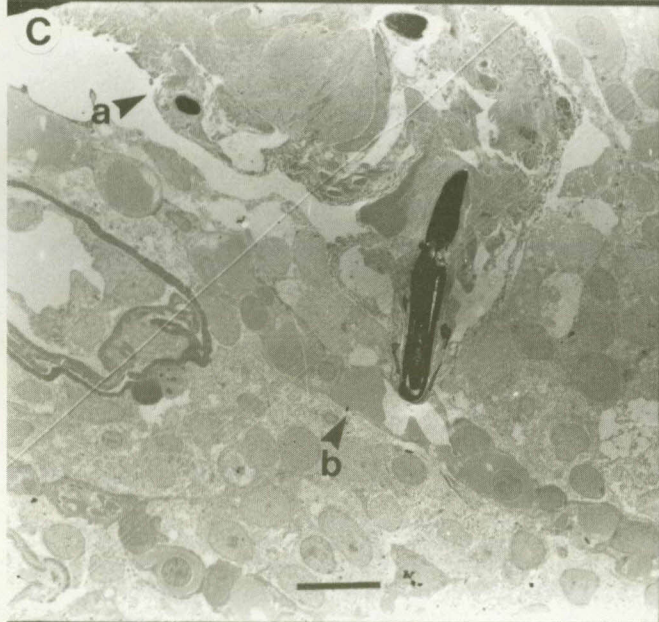
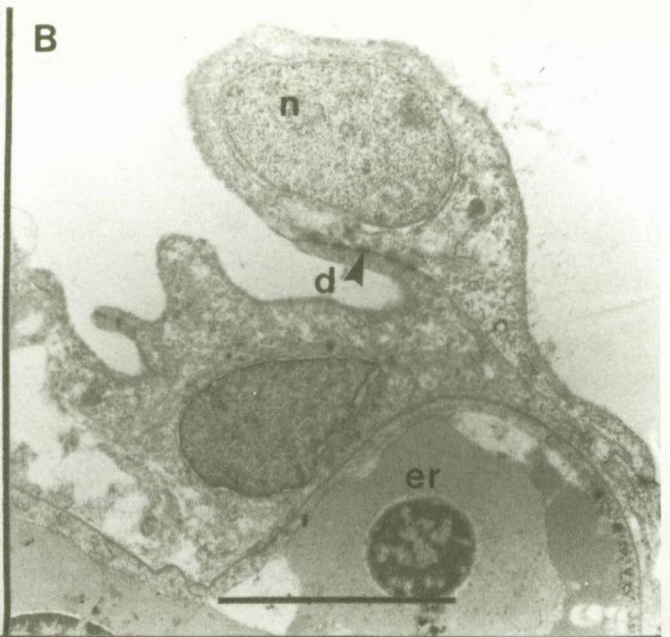
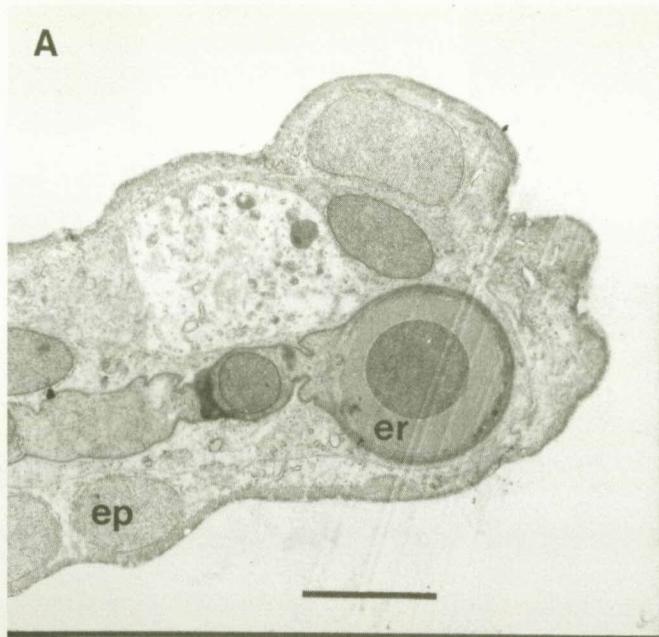
## FIGURE 7.1

Transmission electron micrographs of sections of gill tissue from *Hydrocynus vittatus* Castelnau, 1861 infested by *Annulotrema pikei* (Price, Peebles & Bamford, 1969)

- A. Gill filament (er-erythrocyte, ep- epithelial cell)
- B. Epithelial tissue (n- nucleus, d- desmosome, er- erythrocyte)
- C. *A. pikei* attached to the gill filament of *H. vittatus*
- D. Gill filament of *H. vittatus* infested by *A. pikei*
- E. Possible cellular hyperplasia between two gill filaments of *H. vittatus*
- F. Possible matrix proliferation of gill filament of *H. vittatus*

Scale Bar: A-B 5  $\mu\text{m}$ , C-E 10  $\mu\text{m}$ , F 5  $\mu\text{m}$ ,



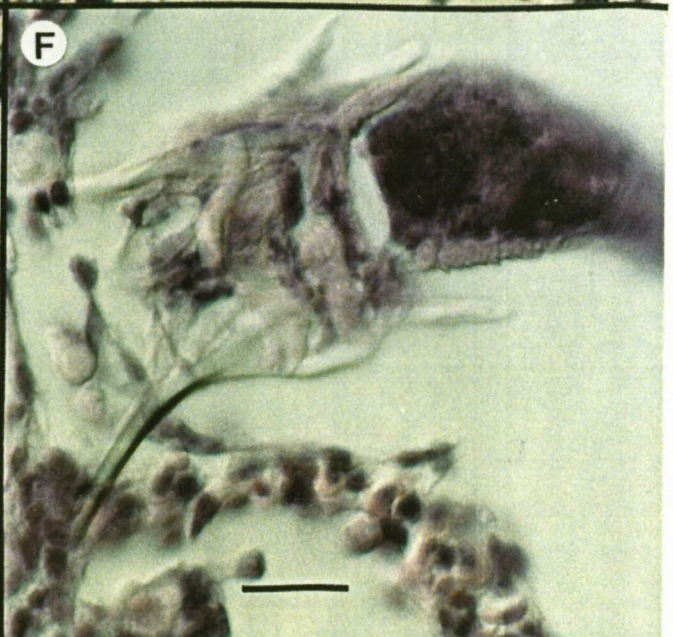
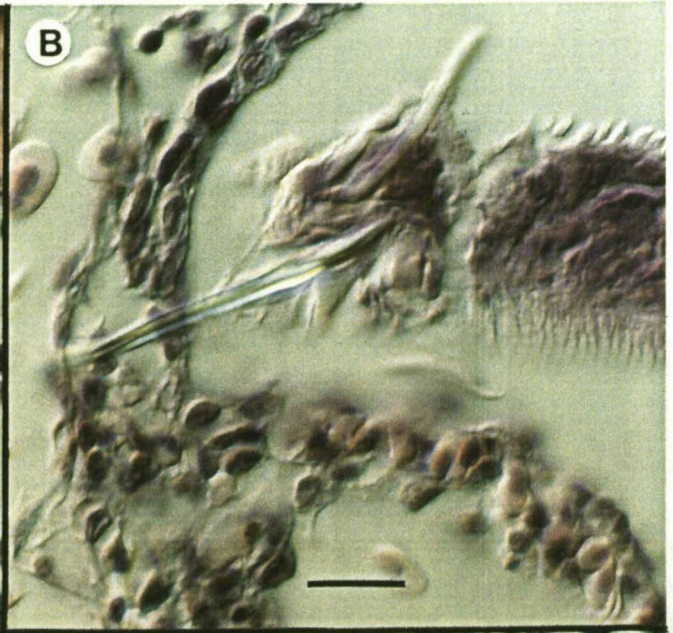
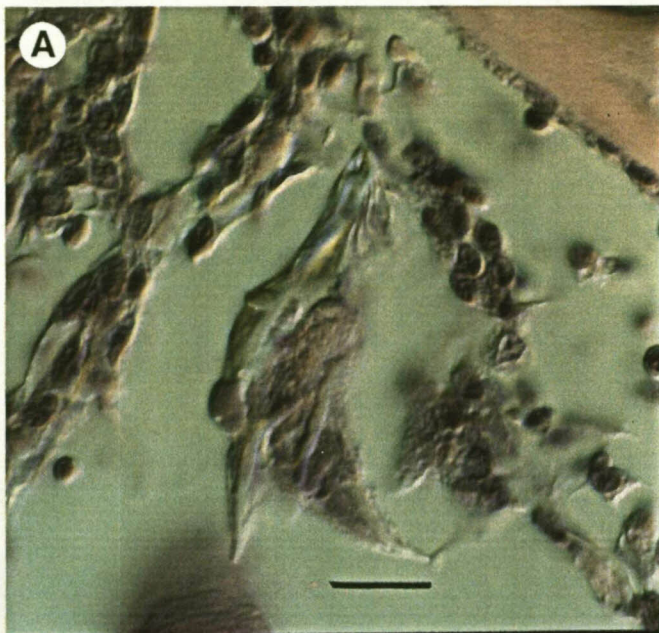


## FIGURE 7.2

Light micrographs of histological sections of the gills of *Hydrocynus vittatus* Castelnau, 1861 infested with *Annulotrema pikei* (Price, Peebles & Bamford, 1969).

- A. *A. pikei* attached to gill filaments of *H. vittatus*
- B. Anchor of *A. pikei* penetrating the gill filament of *H. vittatus*
- C. Gill filament of *H. vittatus* infested with *A. pikei*
- D. Marginal hooklets of *A. pikei* used as counter hooks between the lamellae of the gills of *H. vittatus*
- E. Unbound cell mass ventral to *A. pikei*
- F. *A. pikei* attached to gill filaments of *H. vittatus*

Scale Bar: 10  $\mu$ m



## NOTES ON HYPERPARASITISM

Species from both genera of monogeneans parasitising Okavango characins were infested by ecto-hyperparasites. Both *Annulotrema* and *Characidotrema* specimens were infested by a yeast like fungus, which attached all over the body of the monogenean (Figure 7.3C), but seemed to show preference to the cephalic region (Figure 7.3A). The morphology of these cells resembles that of brewers yeast, *Saccharomyces cerevisiae*. This fungus as well as most of the fungi causing fungal diseases in animals are part of the group Ascomycetes (Van Denmark & Batzing, 1987). These fungi seemed to have an asexual reproductive stage where reproduction takes place by the budding off of spores (Figure 7.3B). The spores in Figures 7.3C-D have a coarser surface than those in Figure 7.3B. This could be due to one of two reasons, these spores may represent different reproductive stages of the same fungus, or they may be spores of two different species. The fungus in Figure 7.3B was found mainly on *Annulotrema* species especially *Annulotrema pikei*, where they would be firmly attached to the prohaptor. The fungi in Figures 7.3C-D on the other hand were found mainly on the parasites of *Brycinus lateralis* where they attached randomly on the body of the monogeneans showing no clear signs of site preference. This fungus often also infested the gills of *B. lateralis* and in some cases the hyphae were clearly visible.

Fungal infection is one of the most common diseases of freshwater fishes and is characterised by the growth of thin threads on the skin and gills of the fish. According to Van Duijn (1967) fungi attack only fishes that have been wounded or whose resistance has been lowered by the presence of parasites or other pathogens. No pathology was observed on the gills of the Okavango fish as a result of fungal infestation. It could be hypothesised that the monogeneans may be the vectors of fungal infections on the fish host. This is unlikely as monogeneans have a direct life cycle, having no intermediate hosts, and do not translocate from one host to another.

Another hyperparasite of the Okavango monogeneans was an *Ichthyobodo* species which was found infesting *Characidotrema nursei*. *Characidotrema nursei* specimens collected from both Xaro and Guma Lagoon were infested by *Ichthyobodo* species. These parasites were attached to the posterior end of the monogenean on either side of



the opisthaptor. Although this is not the first record of *Ichthyobodo* species infesting representatives of the genus *Characidotrema* (Paperna, 1969; Paperna, 1979) it is still quite a curious phenomenon as *Ichthyobodo necator* (Henneguy, 1883) is essentially a parasite of fish.

Lom & Dykova (1992) describe *Ichthyobodo* as being a dangerous ectoparasite of practically all freshwater fishes. This parasite attacks the whole surface of the host, even its roe and is of cosmopolitan distribution. It has two forms, a free swimming infective form and a feeding attached form. The free non-feeding form has a flat, slightly asymmetrical, oval body, is strongly convex dorsally and slightly concave ventrally. A longitudinal groove traverses the posterior 2/3 of the ventral surface near its right margin and plunges into a funnel-shaped flagellar pocket. Two unequal flagella extend from the pocket, the longer flagellum being closer to the right cell margin (Lom & Dykova, 1992).

The feeding attached form (Figure 7.3E-F), fixed to the epithelial cells, is highly modified. The cell curls in a pyriform shape, the flagella pointed away from the host surface. The pellicle around the cytostome becomes an attachment plate, through which the cytostome and the associated cytopharyngeal canal protrude as a finger-like process into the host cell. The transformation from the swimming to the attached form takes place within a few seconds (Lom & Dykova, 1992).

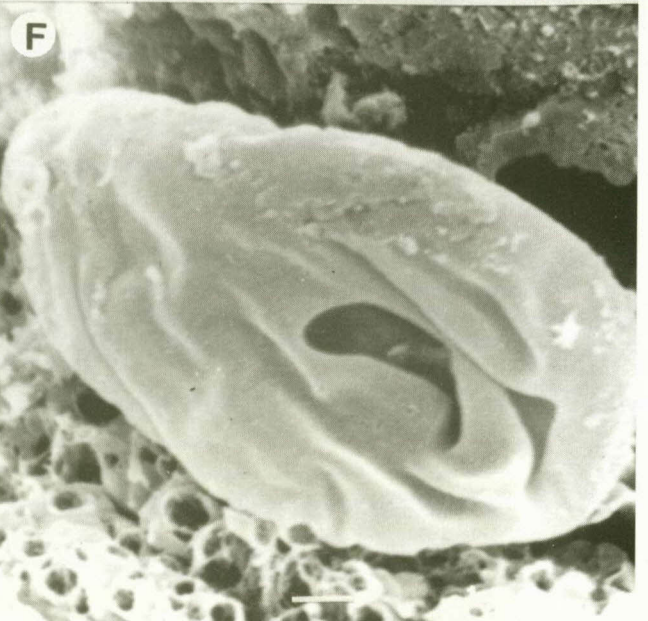
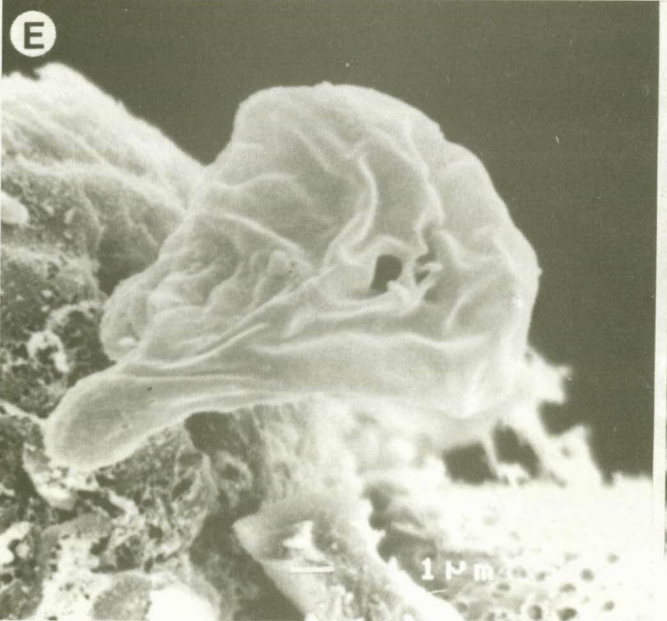
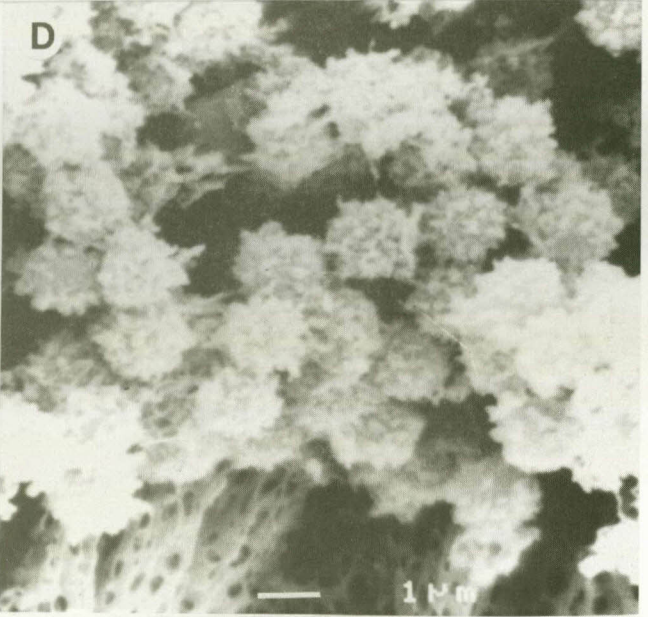
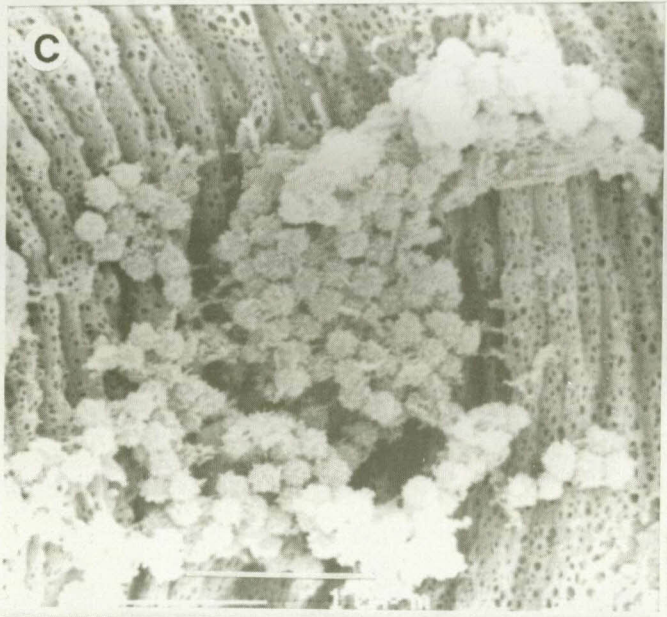
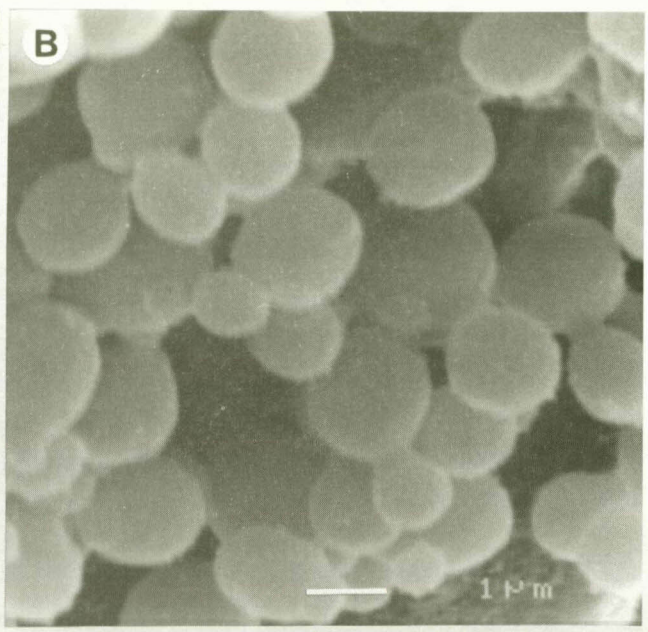
As the *Ichthyobodo* specimens attach randomly to the surface of the host, it is possible that it would then also attach to the monogenean parasites, which in turn are attached to the host. This being the case, one would then expect to find the fish being infested by the same *Ichthyobodo* species. Due to its mode of attachment, this flagellate has been known to cause damage to epithelial or epidermal cells and bring about widespread pathological changes. No *Ichthyobodo* specimens were observed from the gills or skin of *Brycinus lateralis*, neither were there any signs of their potential pathology. This, however is only an observation and more attention will be given to this in forthcoming surveys.

## FIGURE 7.3

Scanning electron micrographs of hyperparasites infesting *Annulotrema pikei* (Price, Peebles & Bamford, 1969) and *Characidotrema nursei* Ergens, 1973.

- A. Yeast like fungus on the prohaptor of *A. pikei*
- B. Yeast like fungus, on the body trunk of *A. pikei*, in the process of budding
- C. Fungal spores on the body trunk of *C. nursei* Ergens, 1973
- D. Enlargement of fungal spores on the body trunk of *C. nursei* Ergens, 1973
- E. *Ichthyobodo* species infesting *C. nursei* Ergens, 1973
- F. *Ichthyobodo* species infesting *C. nursei* Ergens, 1973

Scale Bar: 1  $\mu\text{m}$



# CHAPTER 8



## DISCUSSION

### THE NATURE OF MONOGENEAN INFESTATION ON OKAVANGO CHARACINS

High species diversity is a well documented phenomenon in the neotropics and is also true of the Ethiopian zoogeographical region. Although the mechanisms of speciation in river systems have been less frequently discussed than those for terrestrial systems, the monogeneans have probably been exposed to the same geologic and paleoecologic events effecting the speciation of their fish hosts. Kritsky, *et al.* (1997) suggest that the variation in sea level during the glacial and interglacial periods of the Quaternary may have provided many vicariant opportunities for speciation of some fishes. Such re-occurring speciation opportunities coupled with coevolutionary scenarios associated with speciation rates could explain the high diversity and occurrences of representatives in the family Dactylogyridae on their hosts.

Although Kritsky, *et al.* (1997) referred specifically to the dactylogyrids effecting Neotropical serrasalmids, this hypothesis can be extended to other systems in other zoogeographical regions. This hypothesis is supported when considering the similarities between the Ethiopian genera *Annulotrema* and *Characidotrema* and the Neotropical genera *Annulotrematoides* and *Jainus* respectively. The species of *Annulotrema* and *Annulotrematoides* share common features and host preferences, suggesting that they may share a common ancestor. Both genera are characterised by species possessing cuticular annulations, and while restricted to their respective biogeographical regions, are exclusively parasites of characiform fish. Kritsky, *et al.* (1987) state that their resurrection of the genus *Characidotrema* for the Ethiopian fauna suggests that vicariant speciation occurred since the break-up of Gondwanaland with speciation events in this group of monogeneans progressing at a similar or slightly slower rate than that of their hosts. Kritsky, *et al.* (1987) further suggest that *Characidotrema* and *Jainus* will likely

be shown to be sister groups that developed from a common ancestral group present in Gondwanaland prior to the separation of the African and South American continents.

According to Jubb (1958) and Gaigher & Pott (1973), the water bodies represented by the distribution of *H. vittatus* in southern Africa, must at least at some stage in their history have been linked. This hypothesis is supported by the distribution of certain fish species within these systems including *H. vittatus*. Since the separation of these systems, due to various geological and environmental factors over a vast period of time, unique systems have developed with unique conditions having only the similarity of fish fauna as a reminder of their previous connection. It is evident in the breeding behaviour of *H. vittatus* that this fish species had to adapt to survive the changes in each of these unique systems regarding spawning and the timing and stimulus thereof.

In Lake Kariba tigerfish gather in the estuaries prior to the rains, and then migrate upstream to suitable spawning sites when the river floods, usually from January to March. As the gravid females migrate upstream, they are accompanied by ripe-running males which outnumber the females 7:1 (Kenmuir, 1989).

According to Gaigher (1967), the breeding behaviour of the tigerfish in the Inkomati system contradicts that of the tigerfish in the Zambezi system. Tigerfish in the Inkomati system apparently migrate into Lake Chualo to spawn whereas in the Zambezi system, tigerfish are known to migrate out of the lakes and into the rivers and tributaries to spawn. Gaigher (1967), states that spawning in the Inkomati River system starts as soon as the rivers rise after the first heavy rains, usually from October to November.

The tigerfish in the Pongola flood plain system are totally flood dependant in their spawning. The reproductive organs mature apparently in response to increasing water temperatures during spring and early summer, but the spawning will only take place once the summer floodwaters inundate the marginal land. These flooded margins are rich in organic matter and support a wealth of invertebrate fauna of a suitable size range to promote rapid growth of the young fish. In addition this breeding ground is shallow thus protecting the fingerlings from predators (Heeg, Breen & Rogers, 1980).

In the Okavango, however, the pattern exhibited by the tigerfish is somewhat different to all of the above. The tide travelling down the main stream is a signal to the tigerfish, which travel upstream to spawn. The exact location of their spawning is as yet still a mystery, though it may be the secluded reedy flats of the upper Okavango River. After spawning the fish return to overwinter in the deeper lagoons (Ross, 1987). Merron (1987) proposed the hypothesis that although the effect of catfish runs on the spawning of tigerfish was unknown, the tigerfish breed before the onset of the annual floods so that their young reach an optimum size and can take advantage of the increased food supply brought about by a large scale spawning of other species during the flood. Adults, which have lost condition due to spawning, then take advantage of the catfish runs to feed and build up condition before the floods arrive. Merron (1987), also suggests that in the time of flood, the food supply of the tigerfish may be limited due to the dilution of fish brought about by the increased water level, making prey items more difficult to locate.

The occurrence of *Annulotrema pikei* from *Hydrocynus vittatus* from both the Okavango and Pongola Systems elucidates the hypothesis proposed by Jubb (1958) and Gaigher & Pott (1973). The presence of fish parasites and their relationships between the parasites and fishes of neighbouring water bodies, or water bodies on either side of a watershed can confirm the origins or relationships between these water bodies.

The gills of fishes provide a suitable microhabitat for various parasites. The large numbers of monogeneans collected from the gills of the Okavango characins, were found occurring syntopically with numerous other parasites (Table 8.1). Although these parasites all occur on the gills of the fish, they each occupy a different niche thereon. In some cases, the number of parasites certainly impact on each other due to a competition for space. Many of these parasites are specialised for inhabitation of the gills of a fish and many are also species specific. The number of parasites occurring on the gills of a fish serve as a major driving force for niche preservation, which is measurable in the degree of host or site specificity or preference of the particular parasite.

**TABLE 8.1** Table indicating other parasites occurring syntopically with the branchial monogeneans of the Okavango characins.

PARASITE	<i>Brycinus lateralis</i>	<i>Hepsetus odoe</i>	<i>Hydrocynus vittatus</i>	<i>Micralestes acutidens</i>	<i>Rhabdalestes maunensis</i>
<i>Trichodina</i> sp.	✓	✓			
<i>Tripartiella</i> sp.		✓	✓		✓
<i>Chilodinella</i> sp.				✓	
<i>Apiosoma</i> sp.		✓			
<i>Ichthyobodo</i> sp.		✓			
<i>Annulotrema</i> sp.	✓	✓	✓	✓	✓
<i>Characidotrema</i> sp.	✓				
Nematoda sp.		✓			
<i>Lamproglena</i> sp.	✓	✓			

### HOST SPECIFICITY

Included in the strategies adopted by animals to fulfil their energy requirements, is predation, where the larger animal eats the smaller animal, and parasitism, where a smaller animal makes use of a microhabitat supplied by the larger animal. Predation is by definition a radical strategy, especially for the prey, whereas the parasite host relationship is more subtle. As the host supplies both food and shelter, the parasites establish a relationship with the host in which the parasite causes as little disruption as possible. If not, by destroying their hosts they destroy their habitat and their own biotope (Lambert & Gharbi, 1995).

The monogeneans have frequently been cited as having comparatively high host specificity. Bychowsky (1957) stated that 711 (74.2 %) of the 958 known monogenean species occur on a single host species and 806 (84.1 %) on species of a single host genus. Rhode (1978) relates the high host specificity to tendencies for K-strategies of ecological selection. Among other traits, monogeneans produce fewer eggs per individual than members in most other parasite groups, have a direct life-cycle with larval



stages actively seeking an appropriate host, and possess complex attachment structures that are frequently specialised into specific sites on hosts (Kritsky, *et al.* 1997).

The concept of host specificity according to Lambert & Gharbi (1995) is a way of characterising the relationships between the host and parasite in a given environment. The equilibrium that results is determined by physiological factors, like host immune reaction, nutritional requirements of the parasite and ethological and ecological factors. Poulin (1992) states that, host-parasite associations evolve through coevolution, host switching or through a combination of these two processes. Tight coevolution results in strict host specificity whereas frequent host switching results in low host specificity. Euzet & Combes (1980) defined three types of host specificity, depending on the influence of the determining factors.

1. Oioxenic specificity: a parasite species found only on a single host species.
2. Stenoxenic specificity: a parasite species infests a few closely related hosts (e.g. species of the same genus).
3. Euryxenic specificity: a parasite species found on several distantly related hosts, which have ecological similarities.

Oioxenic specificity is frequent in dactylogyrid monogeneans of teleost fishes. In such cases, parasite presence can be used as a diagnostic criterion for the host species (Lambert & Gharbi, 1995). The value of monogeneans as a criterion for identifying host species can be demonstrated by using a parasitological comparison of two sympatric characin fish species occurring in the Niger Basin, namely *Hydrocynus forskallii* and *H. vittatus*. Guegan, *et al.* (1988) showed these two species to be distinct due to the discovery of *Annulotrema pikoides*, which is strictly specific to *Hydrocynus vittatus*, alongside other stenoxenic *Annulotrema* species, like *A. pikei*, *A. nili* and *A. longipenis*, which occur on both *Hydrocynus forskallii* and *H. vittatus*.

Based on the information discussed in chapter four about the fish hosts of the species of the genera *Annulotrema* and *Characidotrema* it appears as though these monogeneans exhibit strict host specificity. Of the 44 species of *Annulotrema*, 79.5 % exhibit oioxenic

specificity with the rest exhibiting varying degrees of stenoxenic and euryxenic specificity (Table 4.3). The species of the genus *Characidotrema* show a similar trend with 60 % of the species exhibiting oioxenic specificity (Table 4.6). According to Poulin (1992) this would suggest that species of both *Annulotrema* and *Characidotrema* have long evolutionary relationships with their fish hosts. This is also supported by the limited pathology caused by these parasites on their hosts as well as the numbers in which these monogeneans occur on the gills of the fishes.

Apart from host specificity, species of the genera *Annulotrema* and *Characidotrema* exhibit site preferences which are influenced by the number of parasites of the same species as well as the total number and diversity of parasites on the gills. Species of the genus *Annulotrema* from the Okavango seemed to show site preferences to the specific gill arch and region within a single gill arch. This preference is governed by the availability of space on the gill arches. These site preferences are clearly illustrated in fish with low infestations as opposed to those with high infestations where the numbers of parasites per gill arch and gill region become more or less uniform. The site preferences are also influenced by the presence of other parasites, which will also exert pressure on the availability of space on the preferred site of attachment.

### **TRANSMISSION OF *Annulotrema* AND *Characidotrema* SPECIES**

Cone (1995) describes the life cycle of polyonchoineans as being direct and involving no intermediate hosts. Most polyonchoineans are oviparous and produce eggs. These eggs are either released into the surrounding water or attached to an appropriate attachment site by the means of filaments, which form part of the egg casing. On hatching, a crawling or free-swimming oncomiracidium actively seeks and invades a suitable host. As post oncomiracidia, they migrate over the gills or body to the final site of attachment. The egg hatching rate and longevity of the oncomiracidia are dependant on environmental factors like photo-period, temperature, salinity and pH (Ogawa, 1998).

As the eggs of *Annulotrema* and *Characidotrema* species do not possess filaments it is suspected that these eggs would be released directly into the water. This, however, would not promote the transmission of these parasites as some of the hosts, like the

tigerfish for example, occur mainly in fast flowing waters of the main stream. On releasing eggs in flowing water, the eggs and ciliated oncomiracidia would be flushed down stream where chances of finding a suitable host become negligible. Another proposed method of transmission would be if the release of eggs were seasonal and occurring simultaneously with the spawning of the fish hosts. At this time, the fishes leave the fast flowing waters and migrate to the shallower stationary waters of the marginal floodplains.

The latter proposal is supported by the observation made during field work, of a single egg, in which the oncomiracidium undergoes intrauterine development, in some of the *Characidotrema mursei* specimens collected. Normally eggs may be deposited rapidly from the uterus during oviposition, as reproduction comes to an end some eggs may remain in utero long enough to complete development. According to Tinsley (1978) this ovoviviparity has been recorded in certain polystomatid monogeneans. A strategy of intra-uterine embryo development clearly gives freedom from many of the hazards and constraints of the external environment and eliminates the time delay between oviposition and infestation. This is achieved necessarily at the cost of producing fewer offspring (Tinsley, 1983).

During the recent field trip to the Okavango (August 1998), an interesting observation was from the gills of tigerfish which had been kept in a well aerated aquarium for a few days before examination. The *Annulotrema pikei* specimens produced eggs, which were thought to have been caught up in the mucus of the gills, and were visible on gill smears. These eggs promptly hatched and gave rise to ciliated oncomiracidia, which were also visible on these smears. This once again suggests that a certain degree of in utero development of the oncomiracidium takes place making it viable soon after oviposition.

The advantage of this ovoviviparity in the representatives of the genera *Annulotrema* and *Characidotrema* is that direct infestation of the same host is possible. Cross infestation can also occur as the order Characiformes consists mainly of shoaling species. This is especially probable in times of spawning, when the fish hosts congregate in shallow stationary water.

To summarise, the hypothetical mode of transmission of species of the genera *Annulotrema* and in particular *Characidotrema* takes place when the hosts are stimulated to spawn. The parasites simultaneously also produce many eggs which they liberate into the water concurrent to the spawning of the fish. The advantage of this is that most of the characin species will be concentrated in shallow stationary water in which the oncomiracidia can easily swim, seek and infest a new host. These monogeneans, however retain an egg within the uterus. This egg undergoes inutero development and the oncomiracidium develops inside. When oviposition takes place, the egg immediately hatches liberating the oncomiracidium which will in turn directly infest the original host. This is especially effective when the fish hosts are not gregarious or when they occur in rapid flowing water like that encountered in the Okavango mainstream.

## ANNUAL FISH KILLS IN THE OKAVANGO

Within this labyrinth of channels and waterways a variety of creatures, in constant interaction with each other and their environment, enact the daily drama of their lives while the seasonal rhythm of the Okavango's waters provides the tempo that guides their activities from one year to the next. One of the effects man has on this ecosystem is becoming more prevalent year after year and can be measured by the declining fish stocks of the Delta. This decrease in fish numbers may be caused directly or indirectly by a number of factors, being anthropogenic or natural.

According to Lafferty (1997), there are a variety of ways in which environmental changes affect parasites, suggesting that information on parasites can indicate human impacts. Parasites may increase if the human impacts inhibit or reduce host resistance. Parasitism may decrease if the human impacts decrease the number of definitive hosts or if the parasites suffer mortalities either directly or indirectly as a result of such impacts. The monogeneans can serve as good models for parasitic indicators of environmental change as they have a direct one-host life cycle and exhibit species specificity and site preference as was discussed in chapters four and six.

Definite contributors to the declining fish stocks are the massive fish mortalities documented by Bills (1996). These fish kills are an annual event in the Okavango,

although their magnitude and extent of occurrence vary (Bills, 1996). The fish kills are associated with the new floodwaters entering the floodplains and swamps of the Delta and generally do not effect the panhandle. It is the opinion of the residents in the Delta that the annual fish kills are associated with the seasonal burning of papyrus. The burning of papyrus takes place either due to natural catastrophe or due to the burning by farmers who graze their live stock on the new shoots or due to campfires of local fisherman and tourists camping on the numerous islands. The probable explanation for the fish kills is as proposed by Bills (1996). In papyrus swamps, dead vegetation rots and falls to the bottom of the swamp as peat. In closed papyrus swamps there is little or no water flow and little sunlight reaching the water. Because of this, the water below the papyrus is typically anoxic. Swamps or lagoons, which have been closed for long periods, may build up large oxygen debts.

As the new waters enter the Delta with the annual flood, the stagnant water is flushed out of lagoons. The extent to which this anoxic water is flushed out is dependent on various hydrological factors, but the dominant one is probably the blocking and unblocking of lagoons. Lagoons may become unblocked by high water levels lifting papyrus mats, water currents or winds, which break papyrus mats apart, and burning or cutting for human access.

The flushing of lagoon water results in a changed water chemistry, which is characterised by enormous changes in conductivity. These changes appear to coincide with a change in fish composition. The economic implications of these fish kills can only be speculated but clearly significant stock losses result (Bills, 1996). The main fish affected, according to Bills (1996), are *Hydrocynus vittatus*, *Oreochromis andersonii* (Castelnau, 1861) and *Synodontis* species.

Fish like *H. vittatus* have a reduced gill surface area, hence their preference for open fast flowing water. When these fish are infested with gill parasites like *Annulotrema pikei* for example, which occur in vast numbers, the gill surface area suitable for effective respiration is further reduced. Any subsequent reduction in the oxygen in water as a

result of natural or human induced circumstances makes effective respiration impossible and hence results in the mortality of the fish.

Although parasites and in particular monogeneans may not be directly responsible for the declining fish stocks in the Okavango System, they cannot be ignored as at least a contributing factor.

# CHAPTER 9



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# REFERENCES

- BAILEY, A. 1998. *Okavango Africa's Wetland Wilderness*. Struik Publishers (Pty) Ltd. Cape Town, South Africa. 176pp.
- BALFOUR, D. & BALFOUR, S. 1997. The Okavango delta: Destination Botswana. *Africa Environment and Wildlife* 5: 70-78.
- BASSON, L. & VAN AS, J. G. 1989. Differential diagnosis of the genera in the family Trichodinidae (Ciliophora: Peritrichia) with the description of a new genus ectoparasitic on freshwater fish from southern Africa. *Systematic Parasitology* 13: 153-160.
- BELL-CROSS, G. & MINSHULL, J.L. 1988. *The fishes of Zimbabwe*. Trustees of the National Museums and Monuments of Zimbabwe, Harare, Zimbabwe. 294 pp.
- BILLS, R. 1996. Fish stock assesment of the Okavango river (May 1996). *J.L.B. Smith Institute Of Ichthyology Investigational Report No. 56*. 110 pp.
- BIRGI, E. 1988. Les Monogenes de Characoidea de la zone forestiere Camerounaise. *Annales de la Faculte des Sciences de la Biologie et Biochemie* 3: 59-111.
- BLACKMAN, J. 1990. Americans in the Okavango. *Hengel / Angling March*, 42-43.
- BOEGER, W. A. & KRITSKY, D. C. 1993. Phylogeny and a revised classification of the Monogenoidea Bychowsky, 1937 (Platyhelminthes). *Systematic Parasitology* 26: 1-32.



- BOEGER, W.A. & KRITSKY, D.C. 1997. Coevolution of the Monogenoidea (Platyhelminthes) based on a revised hypothesis of parasite phylogeny. *International Journal For Parasitology* 27: 1495-1511.
- BRUTON, M. N. & MERRON, G. S. 1985. The Okavango Delta- Give credit where credit is due. *African Wildlife* 39: 59-63.
- BYCHOWSKY, B. E. 1937. Ontogenesis and phylogenetic relationships of parasitic flatworms. *Investiz Akademia Nauk SSSR., Ser. Biol.* 4: 1353-1383.
- BYCHOWSKY, B. E. 1957. Monogenetic trematodes their systematics and phylogeny. American Institute Of Biological Sciences, Washington, 627pp.
- \*CARUS, J. V. 1863. Räderthiere, Würmer, Echinodermen, Coelenteraten und Protozoen. In PETERS, W. C. H., CARUS, J. V. & GERSTAECKER, C.E.A. (eds). *Handbuch der Zoologie* 2: 422-600.
- CHRISTISON, K. W. VAN AS, J. G. & BASSON, L. 1998. *Annulotrema* gill parasites of Okavango characins. *Proceedings Of The Microscopy Society Of Southern Africa* 28: 83.
- CONE, D. K. 1995. Monogenea (Phylum Platyhelminthes). in WOO, P. T. K. (eds.) *Fish Diseases And Metazoan Infections*. CAB International. Wallingford, United Kingdom. 808pp.
- DOUELLOU, L. 1993. Monogeneans of the genus *Cichlidogyrus* Paperna, 1960 (Dactylogyridae: Ancyrocephalinae) from cichlid fishes of Lake Kariba (Zimbabwe) with descriptions of five new species. *Systematic Parasitology* 25: 59-186.
- \*DOUELLOU, L. & CHISHAWA, A. M. M. 1995. Monogeneans of three siluriform fish species in Lake Kariba, Zimbabwe. *Journal of African Zoology* 109: 99-115.

- ELLER, L. L. 1975. Gill lesions in freshwater teleosts. In RIBELIN, W. E. & MIGAKI, G. (eds.). *The Pathology Of Fishes*. The University of Wisconsin press. Wisconsin, U.S.A. 1004 pp.
- \*ERGENS, R. 1973. *Charaidotrema nursei* sp. nov. from the gills of *Alestes nurse* from River Nile. (Vermes, Trematoda; Monogenoidea). *Revue de Zoologie et de Botanique Africaines* 87: 195-197.
- ERGENS, R. 1988. Four species of the genus *Annulotrema* Paperna et Thurston, 1969 (Monogenea: Ancyrocephalinae) from Egyptian freshwater fish. *Folia Parasitologica* 35: 209-215.
- \*EUZET, L. & COMBES, C. 1980. Les problèmes de l'espèce chez les animaux parasites. In Les problèmes de l'espèce dans le règne animal, ed. Bocquet, C. Genermont, J. & Lamotte, M. *Mémoires Société Zoologique de France*. 40: 239-285.
- GAIGHER, I. G. & POTT, R. M. C. 1973. Distribution of fishes in southern Africa. *South African Journal Of Science* 69: 25-29.
- GAIGHER, I. G. 1967. *Aspects of the ecology of the tigerfish Hydrocynus vittatus Castelnau in the Inkomati river system*. Masters Dissertation. Faculty of Science, Pretoria University. 182 pp.
- GUEGAN, J. F., LAMBERT, A. & BIRGI, E. 1988. Observations sur le parasitisme branchial des Characidae du genre *Hydrocynus* en Afrique de l'ouest. Description d'*Annulotrema pikoides* n. sp. (Monogenea, Ancyrocephalidae) chez *Hydrocynus vittatus* (Castelnau, 1861). *Ann. Parasitol. Hum. Comp.* 63: 91-98.

- HEEG, J. BREEN, C.M. & ROGERS, K.H. 1980. The Pongolo floodplain: A unique ecosystem threatened. In Bruton, M.N. & Cooper, K.H. *Studies on the ecology of Maputaland*, Rhodes University, Grahamstown. 560 pp.
- HWANG, S. L. & YU, T. C. 1987. The investigation of eel (*Anguilla japonica*) infected with Dactylogyrid. *Bulletin of Taiwan Fisheries Research Institute* 43: 329-343.
- JUBB, R.A. 1958. The distribution of freshwater fishes: A note on some Zambezi river species. *South African Journal Of Science* 54 (8):218.
- JUNQUEIRA, C., CARNEIRO, E. & CONTOPOULOS, L. 1977. *Basic Histology*. Lange Medical Publications. Canada. 468pp.
- JUSTINE, J. L. 1991. Cladistic study in the Monogenea (Platyhelminthes), based upon a parsimony analysis of spermiogenetic and spermatozoal ultrastructural characters. *International Journal for Parasitology* 21: 821-838.
- JUSTINE, J. L., LAMBERT, A. & MATTEI, X. 1985. Spermatozoon ultrastructure and phylogenetic relationships in the monogeneans (Platyhelminthes). *International Journal for Parasitology* 15: 601-608.
- KENMUIR, D. 1989. *Fishes of Kariba: Revised edition*. Longman Zimbabwe. Zimbabwe. 135pp
- KHALIL, L. F. & POLLING, L. 1997. *Check List Of The Helminth Parasites Of African Freshwater Fishes*. Department Of Zoology / Biology, University of the North. Pietersburg, South Africa. 185pp.
- KRITSKY, D.C. & BOEGER, W.A. 1995. Neotropical Monogenoidea. 26. *Annulotrematoides amazonicus*, a new genus and species (Dactylogyridae: Ancyrocephalinae), from the gills of *Psectrogaster rutiloides* (Kner) (Teleostei:

- Characiformes: Curimatidae) from the Brazilian Amazon. *Proceedings Of The Biological Society of Washington* 108: 528-532.
- KRITSKY, D. C., BOEGER, W. A. & JEGU, M. 1997. Neotropical Monogenoidea. 29. Ancyrocephalinae (Dactylogyridae) of Piranha and their relatives (Teleostei, Serrasalmidae) from Brazil: Species of *Amphithecium* Boeger and Kritsky, 1988, *Heterothecium* gen. n. and *Pithanothecium* gen. n. *Journal of the Helminthological Society of Washington* 64: 25-54.
- KRITSKY, D. C., KULO, S. D. & BOEGER, W. A. 1987. Resurrection of *Characidotrema* Paperna and Thurston, 1968 (Monogenea: Dactylogyridae) with description of two new species from Togo, Africa. *Proceedings of the Helminthological Society of Washington* 54: 175-184.
- LAMBERT, A. & GHARBI, S. E. 1995. Monogenean host specificity as a biological taxonomic indicator for fish. *Biological Conservation* 72: 227-235.
- LAFFERTY, K. D. 1997. Environmental Parasitology: What can parasites tell us about human impacts on the environment? *Parasitology Today* 13: 251-255.
- \* LEBEDEV, B. I. 1986. *Monogeneans Of Suborder Gastrocotylinea*. Publishing House Nauka. Leningrad. 200pp.
- LEBEDEV, B. I. 1988. Monogenea in the light of new evidence and their position among platyhelminths. *Angewandte Parasitologie* 29: 149-167.
- LEBEDEV, B. I. 1995. *Biodiversity and Evolution of Oligonchoinean Monogenoidea*. The Russian Academy Of Sciences, Far East Branch, Institute Of Biology & Pedology. Vladivostok. 31pp.
- LEESON, T. S. & LEESON, C. R. 1970. *Histology*. W. B. Saunders Company. Philadelphia. 525pp.

- LOM, J. & DYKOVA, I. 1992. *Developments In Aquaculture And Fisheries Science Volume 26: Protozoan Parasites Of Fishes*. Elsevier Science Publishers, Amsterdam, Netherlands. 315pp.
- MALMBERG, G. 1957. Om förekomsten av *Gyrodactylus* på svenska fiskar. *Skrifter Utgivna Av Södra Sveriges Fiskeriförening Arsskrift* 19-76.
- MALMBERG, G. 1990. On the ontogeny of the haptor and the evolution of the Monogenea. *Systematic Parasitology* 17: 1-65.
- MASHEGO, S. N. 1983. South African monogenetic parasites of the genus *Dactylogyrus*: new species and records (Dactylogyridae: Monogenea). *Annals of the Transvaal Museum* 33: 337-346.
- MCCARTHY, T. S., BARRY, M., BLOEM, A., ELLERY, W. N., HEISTER, H., MERRY, C. L., RUTHER, H. & STERNBERG, H. 1997. The gradient of the Okavango fan, Botswana, and its sedimentological and tectonic implications. *Journal of African Earth Sciences* 24: 65-78.
- MERRON, G. S. 1987. Predator-Prey interactions in the Okavango delta: The annual catfish run, October - December, 1986. Investigational Report 25. JLB Smith Institute of Ichthyology, Grahamstown.
- MERRON, G.S. 1991. The ecology and management of the fishes of the Okavango Delta, Botswana, with particular reference to the seasonal floods. Ph.D. Thesis.
- MERRON, G. S. 1993. The diversity, distribution and abundance of the fishes in the Moremi Wildlife Reserve, Okavango Delta, Botswana. *South African Journal Of Wildlife Research* 23: 115-122.
- MERRON, G. S. & BRUTON, M. N. 1986. Where are all the Okavango fishes. *Kalahari Conservation Society Newsletter* 13: 4-5.

- MERRON, G. S., HOLDEN, K. K. & BRUTON, M. N. 1990. The reproductive biology and early development of the African pike, *Hepsetus odoe*, in the Okavango Delta, Botswana. *Environmental Biology Of Fishes* 28: 215-235.
- N'DOUBA, V., PARISELLE, A. & EUZET, L. 1997. Espèces nouvelles du genre *Annulotrema* Paperna et Thurston, 1969 (Monogenea, Ancyrocephalidae) parasites de *Hepsetus odoe* (Bloch, 1794) (Teleostei, Hepsetidae) en Côte D'Ivoire. *Parasite* 4: 55-61.
- NOBLE, E. R. & NOBLE, G. A. 1982. *Parasitology: The Biology Of Animal Parasites*. Lea & Febiger Publishers, 566pp.
- NORMAN, C. 1990. Diary of a plastic worm angler in the Okavango. *Tight Lines* February, 6-10.
- ODHNER, T. 1912. Die homologeien der weiblichen genitalwege bei den Trematoden und Cestoden. Nebst bemerkungen zum naturlichen system der monogenen Trematoden. *Zoologischer Anzeiger* 39: 327-351.
- OGAWA, K. 1998. Egg hatching of the monogenean *Heterobothrium okamotoi*, a gill parasite of cultured tiger puffer (*Takifugu rubripes*), with a description of its oncomiracidium. *Fish Pathology* 33: 25-30.
- OLDEWAGE, W. H. & VAN AS, J. G. 1988. A key for the identification of African piscine parasitic Ergasilidae (Copepoda: Poecilostomatoida). *South African Journal Of Zoology* 23:42-46.
- PAPERNA, I. 1964. Host reaction to infestation of carp with *Dactylogyrus vastator* Nybelin, 1924 (Monogenea). *Bamidgeh* 16: 129-141

- PAPERNA, I. 1969. Monogenetic trematodes of the fish of the Volta Basin and South Ghana. *Bulletin de l'Institut Francais d'Afrique Noire*. 31: 840-880.
- PAPERNA, I. 1973. New species of Monogenea (Vermes) from African Freshwater Fish. A preliminary report. *Revue de Zoologie et de Botanique Africaines* 87: 505-518.
- PAPERNA, I. 1979. *Monogenea of inland water fish in Africa*. Musee Royal De L'Afrique Centrale. Elat, Israel. 131pp.
- PAPERNA, I. & THURSTON, J. P. 1968. Monogenetic trematodes (Davctylogyridae) from fish in Uganda. *Revue de Zoologie et de Botanique Africaines* 78: 284-294.
- PAPERNA, I. & THURSTON, J. P. 1969. *Annulotrema* n. gen., a new genus of monogenetic trematodes (Dactylogyridae, Bychowski, 1957) from African characin fish. *Zoologischer Anzeiger* 182: 444-449.
- PIENAAR, U. D. 1968. *The freshwater fishes of the Kruger National Park*. National Parks Board, South Africa. 82pp.
- POULIN, R. 1992. Determinants of host-specificity in parasites of freshwater fishes. *International Journal For Parasitology* 22: 753-758.
- PRICE, E.W. 1937. North American monogenetic trematodes. I. The superfamily Gyrodactyloidea. *Journal of the Washington Academy of Sciences*, 27:114-130, 146-164.
- PRICE, C. E., KORACH, K. S. & McPOTT, R. 1969. The monogenian parasites of African fishes. V. Two new *Dactylogyrus* species from Natal cyprinids. *Review de Zoologie et de Botanique Africaine* 79: 273-279.

- PRICE, C. E. & McCLELLAN, E. S. 1969. The monogenean parasites of African fishes. IX. A new genus, *Gussevstrema*, recovered from the gills of *Terapon jarbua* (Forskål) from South Africa. *Proceedings Of The Biological Society Of Washington* 82: 171-176.
- PRICE, C. E., McLELLAN, E. S., DRUCKENMULLER, A. & JACOBS, L. G. 1969. The monogenean parasites of African fishes. X. Two additional *Dactylogyrus* species from South African *Barbus* hosts. *Proceedings of the Biological Society of Washington* 82: 461-468.
- PRICE, C. E., PEEBLES, H. E. & BAMFORD, T. 1969. The monogenean parasites of African fish. -IV. Two new species from South African hosts. *Revue de Zoologie et de Botanique Africaines* 79: 117-124.
- PRUDHOE, S. & HUSSEY, C. G. 1977. Some parasitic worms in freshwater fishes and fish predators from the Transvaal, South Africa. *Zoologica Africana*. 12: 113-147.
- REED, C. C. VAN AS, J. G. & BASSON, L. 1998. Myxosporea (Protozoa: Myxozoa) of some Southern African fish. *Proceedings Of The Microscopy Society Of Southern Africa* 28: 82.
- ROHDE, K. 1978. Latitudinal differences in host-specificity of marine Monogenea and Digenea. *Marine Biology* 47: 125-134.
- ROSS, K. 1987. *Jewel of the Kalahari: Okavango*. BBC Books, London. 256pp.
- SCHMIDT, G. D. & ROBERTS, L. S. 1977. *Foundations Of Parasitology*. The C. V. Mosby Company. Missouri, United States. 604pp.



- SKELTON, P. 1988. The distribution of African freshwater fishes. In LEVEQUE, C., BRUTON, M. N. & SSENTONGO, G.W. (eds.) *Biology and Ecology of African Freshwater Fishes*. Institut Francais de recherche scientifique pour le développement en coopération collection TRAVAUX et DOCUMENTS 216, Paris. 508 pp.
- SKELTON, P. 1993. *A complete guide to the freshwater fishes of southern Africa*. Southern Book Publishers, South Africa. 388pp.
- SKELTON, P., BRUTON, M. N. & MERRON, G. S. 1985. The fishes of the Okavango drainage system in Angola, South West Africa and Botswana: Taxonomy and distribution. *Ichthyological Bulletin Of The J.L.B. Smith Institute Of Ichthyology* 50: 1-21.
- THURSTON, J.P. 1970. The incidence of Monogenea and parasitic Crustacea on the gills of fish in Uganda. *Revue de Zoologie et de Botanique Africaines* 82: 111-130.
- TINSLEY, R. C. 1978. The role of ovoviviparity in the transmission of polystomatid monogeneans. *Parasitology* 77:5-6.
- TINSLEY, R. C. 1983. Ovoviviparity in platyhelminth life-cycles. *Parasitology* 86: 161-196.
- VAN AS, J. G. 1992. A new species of *Chonopeltis* (Crustacea: Branchiura) from the Zambesi River System. *Systematic Parasitology* 22: 221-229.
- VAN AS, J.G. & BASSON, L. 1992. Trichodinid ectoparasites (Ciliophora: Peritrichida) of freshwater fishes of the Zambesi River System, with a reappraisal of host specificity. *Systematic Parasitology* 22: 81-109.

- VAN AS, J. G. & VAN AS, L. L. 1996. A new species of *Chonopeltis* (Crustacea: Branchiura) from the southern Rift Valley with notes on larval development. *Systematic Parasitology* 35: 69-77.
- VAN AS, J. G. & VAN AS, L. L. (in press). *Chonopeltis liversedgei* sp. n. (Crustacea: Branchiura) parasite of the Western Bottlenose *Mormyrus lacerda* (Mormyridae) from the Okavango Delta, Botswana. *Folia Parasitologia* (In Press).
- VAN DENMARK, P. J. & BATZING, B. L. 1987. *The Microbes: An Introduction To Their Nature And Importance*. Benjamin / Cummings Publishing Company, United States. 979pp.
- VAN DUIJN, C. 1967. *Diseases Of Fishes*. Iliffe Books LTD. London, United Kingdom. 309pp.
- \*WEDL, C. 1861. Zur helminthenfauna Aegyptiens (2 Abt.). *Sber. Dt. Akad. Landwiss. Wien*, 44: 463-482.
- WELCOMME, R. L. 1979. *Fisheries Ecology Of Floodplain Rivers*. Longman Group Limited. New York, United States. 315pp.
- WHEELER, T.A. & CHISHOLM, LESLIE. A. 1995. Monogenea versus Monogenoidea: the case for stability in nomenclature. *Systematic Parasitology* 30: 159-164.
- WINEMILLER, K.O. & KELSO-WINEMILLER, L.C. 1994. Comparative ecology of the African pike, *Hepsetus odoe*, and tigerfish, *Hydrocynus forskahlii*, in the Zambezi River floodplain. *Journal Of Fish Biology* 45: 211-225.
- WOLKE, R. E. 1975. Pathology of bacterial and fungal diseases affecting fish. In RIBELIN, W. E. & MIGAKI, G. (eds.). *The Pathology Of Fishes*. The University of Wisconsin press. Wisconsin, U.S.A. 1004 pp.

---

YAMAGUTI, S. 1963. *Systema Helminthum: Volume 4 Monogenea and Aspidocotylea*. Interscience Publishers. New York, 699pp.

YASUTAKE, W. T. & WALES, J. H. 1983. *Microscopic anatomy of salmonids: An atlas*. United States Department Of The Interior Fish And Wildlife Service Resource Publication 150. Washington D.C. 190pp.

\* Articles not seen in original form.

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# ABSTRACT

The fishes of the Okavango System, Botswana, are of considerable economical and ecological importance. Recently, scientists and local fishermen have reported a dramatic decline in the fish stocks of the Okavango River and Delta. There are many reasons for this decline to which fish parasites may at least be a contributing factor. In recent surveys to the Okavango, monogeneans have been found to be of the most prominent parasites infesting the Okavango fishes. The tigerfish, *Hydrocynus vittatus* Castelnau 1861, especially, show high infestations of the branchial monogeneans, *Annulotrema pikei* (Price, Peebles & Bamford 1969).

The genera *Annulotrema* Paperna & Thurston 1969 and *Characidotrema* Paperna & Thurston 1968, are exclusively parasites of characiform fish in Africa. In the Okavango the characiforms are represented by five species, *Brycinus lateralis* (Boulenger 1900), *Hepsetus odoe* (Bloch 1794), *Hydrocynus vittatus*, *Micralestes acutidens* (Peters 1852) en *Rhabdalestes maunensis* (Fowler 1935), all of which, are infested by species of the genus *Annulotrema* and only one, *Brycinus lateralis* (Boulenger 1900), is infested by a species of the genus *Characidotrema*.

During two field trips to the Okavango System, five *Annulotrema* species were collected; three of which are known species and two new species. This is the first record of monogeneans from Botswana and represents the southern most distribution recorded of *A. curvipenis* Paperna 1969 & *A. hepseti* Paperna & Thurston 1969. Comparative descriptions of the three known species are given and the two new species are described as *A. micralesti* sp. n. and *A. rhabdalesti* sp. n. Mixed infestations of *A. curvipenis* and *Characidotrema nursei* Ergens 1973 were also recorded from the gills of *Brycinus lateralis*. This also represents the southernmost, recorded distribution of *C. nursei*.

Investigation of histological sections revealed that although these monogeneans occurred in relatively high numbers on the gills of the fish, the pathology they caused was limited. Examination of the infestation statistics showed that these parasites exhibit site preferences to the gills on which they occurred. This preference is influenced by

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the number of monogeneans of the same or other species as well as the number of other parasites occurring on the gills of the fish hosts.

When considering the results, these monogenean parasites do not seem to cause severe harm to the host fish. Any changes in the environment could alter the face of this parasite-host relationship dramatically and hence the potential pathogenicity of these parasites should, however, not be ignored.

# OPSOMMING

Die visse van die Okavango rivier en Delta is van aansienlike ekologiese sowel as ekonomiese waarde vir Botswana en sy inwoners. Gedurende die laaste aantal jare het wetenskaplikes, sowel as plaaslike vissers aangedui dat daar 'n afname in die visvangste in die Okavango stelsel was. Daar kan 'n hele aantal redes vir die afname wees, maar die invloed van parasiete en siektes kan nie weggelaat word as 'n moontlike bydraende faktor nie. Tydens loodsopnames wat gedurende 1997 uitgevoer is, het dit aan die lig gekom dat verteenwoordigers van die Monogenea die mees prominente parasiete van die Okavango visse is. Hieronder was die tiervis, *Hydrocynus vittatus* Castelnau 1861, een van die visse wat swaar besmet was.

Die genus *Annulotrema* Paperna & Thurston 1969 en *Characidotrema* Paperna & Thurston 1968, is parasiete wat uitsluitlik met die tiervis groep geassosieer is. Hierdie visse word in die Okavango verteenwoordig deur vyf spesies, *Brycinus lateralis* (Boulenger 1900), *Hepsetus odoe* (Bloch 1794), *Hydrocynus vittatus*, *Micralestes acutidens* (Peters 1852) en *Rhabdalestes maunensis* (Fowler 1935). Al hierdie visse was met verteenwoordigers van die genus *Annulotrema* besmet terwyl *Brycinus lateralis* (Boulenger 1900) ook deur 'n verteenwoordiger van die genus *Characidotrema* besmet was.

Gedurende veldwerk, wat vir hierdie studie uitgevoer is, is drie bekende sowel as twee nuwe spesies van die genus *Annulotrema* versamel. Hierdie vonds verteenwoordig die eerste verslag van enige verteenwoordigers van die klas Monogenea in Botswana. Dit verteenwoordig ook die mees suidelike verspreiding van *A. curvipenis* Paperna 1969 en *A. hepseti* Paperna & Thurston 1969. Vergelykende beskrywings van die bekende spesies word verskaf en die nuwe spesies is beskryf as *A. micralesti* sp. n. en *A. rhabdalesti* sp. n.

Besmettings met *A. curvipenis* sowel as *C. nursei* Ergens 1973 is op die kieuë van *Brycinus lateralis* aangetref en 'n vergelykende beskrywing van *C. nursei* word verskaf. Dit verteenwoordig die mees suidelike verspreiding van *C. nursei* in Afrika.



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'n Histopatologiese ondersoek het aangetoon dat, hoewel die visse 'n baie hoë infestasië van *Monogenea* parasiete gehad het, daar geen duidelike tekens van weefsel beskadiging was nie. Verwerkings van infestasië statistieke het aangetoon dat die parasiete voorkeure ten opsigte van sekere areas op die kieuë getoon het. Hierdie voorkeure was beïnvloed deur die bevolkingsdigtheid van parasiete van dieselfde, sowel as dié van ander spesies .

In die bespreking van al die resultate is daar tot die slotsom gekom dat hierdie parasiete nie hulle gasheer direk beskadig nie. Wanneer omgewingsfaktore verander kan dit moontlik 'n nadelige invloed op die parasiet-gasheer verwantskap hê, wat moontlik tot nadeel van die visbevolking kan wees.

# APPENDIX

# APPENDIX 1

TELEGRAMS: PULA 0 6 AUG 1996  
TELEPHONE: 350800  
FAX: 350858



OFFICE OF THE PRESIDENT  
PRIVATE BAG 001  
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

Infestation Levels of *Annulotrema pikei* on *Hydrocynus vittatus*. October 1997

No.	Size/mm	R 1			R 2			R 3			R 4			L1			L2			L3			L4			TOTAL			TOT
		A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	
1	147	24	8	9	13	6	8	24	6	1	11	2	2	28	5	8	37	35	17	23	16	16	2	2	0	162	80	61	303
2	150	50	6	17	44	7	17	34	6	9	9	3	2	39	9	16	29	2	10	22	16	8	7	0	5	234	49	84	367
3	155	14	6	8	13	0	0	4	1	5	2	1	0	12	11	4	9	2	5	9	2	2	6	4	0	69	27	24	120
4	160	24	15	25	17	3	7	18	3	8	0	3	2	16	7	7	8	7	11	10	2	5	2	1	1	95	41	66	202
5	160	7	2	5	1	0	0	5	0	1	0	0	0	3	3	2	3	1	0	0	0	0	0	0	0	19	6	8	33
6	160	8	17	6	16	15	8	26	14	10	4	2	2	6	9	18	20	13	7	4	12	1	3	0	0	87	82	52	221
7	163	45	2	22	18	4	13	6	0	6	0	0	0	15	6	30	20	11	39	4	3	14	4	0	1	112	26	125	263
8	170	11	2	2	28	7	11	26	11	8	1	0	0	16	3	10	0	0	0	10	6	12	0	0	0	92	29	43	164
9	170	9	10	0	0	10	0	0	0	0	0	0	0	33	12	20	19	3	0	3	1	0	0	0	0	64	36	20	120
10	175	0	0	0	0	0	0	0	0	0	0	0	0	8	0	4	20	3	9	2	0	1	4	0	0	34	3	14	51
11	175	14	3	7	16	5	3	4	1	5	1	0	0	10	2	10	9	2	4	11	0	0	0	0	0	65	13	29	107
12	180	3	3	3	1	1	1	1	0	0	3	2	2	0	0	0	2	0	0	1	1	1	0	0	0	11	7	7	25
13	190	24	11	13	8	7	3	3	4	0	2	2	0	23	0	6	11	0	6	0	0	0	6	2	0	77	26	28	131
14	230	6	0	3	15	5	10	6	2	3	0	0	0	4	5	0	13	3	4	6	1	4	0	0	0	50	16	24	90
15	390	4	0	0	14	1	1	1	0	1	0	0	0	3	0	0	1	0	0	1	0	0	0	0	0	24	1	2	27
16	430	21	42	12	20	21	36	3	8	3	5	0	0	24	12	10	6	11	15	22	13	6	1	0	0	102	107	82	291
17	435	100	54	45	60	39	60	66	38	17	32	0	0	44	15	44	15	20	30	18	16	12	5	7	0	340	189	208	737
18	443	16	5	11	16	4	1	7	0	4	2	0	0	12	5	0	1	1	1	5	1	5	2	0	0	61	16	22	99
19	480	4	1	2	5	4	1	2	2	3	0	0	0	4	4	1	1	3	1	1	3	3	4	0	0	21	17	11	49
20	740	600	160	260	350	0	0	300	120	200	250	100	0	200	150	100	300	100	100	400	0	0	0	0	0	2400	630	660	3690
TOTAL	5303	984	347	450	655	139	180	536	216	284	322	115	10	500	258	290	524	217	259	552	93	90	46	16	7	4119	1401	1570	7090
AVE.	265.15	49.2	17.35	22.5	32.75	6.95	9	26.8	10.8	14.2	16.1	5.75	0.5	25	12.9	14.5	26.2	10.85	12.95	27.6	4.65	4.5	2.3	0.8	0.35	205.95	70.05	78.5	354.5
STD	163.25	132	36.4	57	76.1	9.2	15	66	27	44	56	22	0.9	43	33	23	65	22.7	23	88	6.1	5.2	2.4	1.8	1.1	522.4	139	145	802

Infestation Levels of *Annulotrema pikei* on *Hydrocynus vittatus*. June - August 1998

No.	Size/mm	R 1			R 2			R 3			R 4			L1			L2			L3			L4			TOTAL			
		A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	TOT
1	165	22	0	15	16	9	16	12	3	15	5	0	5	18	15	10	8	0	0	8	5	7	10	0	0	99	32	68	199
2	166	65	22	23	53	33	25	27	11	15	24	5	3	47	18	40	41	21	28	39	10	7	26	7	10	322	127	151	600
3	177	55	16	38	46	38	22	38	27	20	19	5	0	56	18	48	50	32	19	56	34	23	29	0	0	349	170	170	689
4	185	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	20	0	0	0	2	1	20	23
5	263	64	39	7	71	21	34	69	66	36	47	5	2	59	50	12	66	40	8	68	5	50	27	5	4	471	231	153	855
6	280	48	9	17	27	0	0	10	22	27	10	7	12	34	13	26	51	3	11	25	1	17	15	0	2	220	55	112	387
7	360	123	37	3	59	25	54	28	11	4	4	2	4	109	40	78	40	11	10	43	19	23	20	7	8	426	152	184	762
8	520	116	100	40	129	60	104	70	40	50	24	19	10	120	56	50	100	59	19	23	52	22	37	27	12	619	413	307	1339
9	200	41	10	15	45	12	18	68	10	22	20	8	7	53	18	18	57	53	16	65	16	61	20	8	7	369	135	164	668
10	210	103	42	35	118	38	32	80	32	38	71	12	8	84	37	36	140	16	45	94	60	60	47	20	25	737	257	279	1273
11	435	30	23	47	86	28	13	88	45	46	24	8	6	30	33	28	90	24	60	57	15	26	27	20	12	432	196	238	866
12	406	57	41	27	41	34	15	40	10	18	10	12	5	20	11	8	57	37	29	40	25	21	19	22	7	284	192	130	606
TOTAL	3367	724	339	267	692	298	333	530	277	291	258	84	62	630	309	354	701	296	245	518	242	337	277	116	87	4330	1961	1976	8267
AVE.	280.6	60.3	28.3	22.3	57.7	24.8	27.8	44.2	23.1	24.3	21.5	7.0	5.2	52.5	25.8	29.5	58.4	24.7	20.4	43.2	20.2	28.1	23.1	9.7	7.3	216.5	98.1	98.8	688.9
STD	121.1	37.5	27.3	15.4	38.4	17.6	28.2	29.9	19.7	15.7	20.1	5.4	3.7	36.5	17.1	22.2	38.2	20.0	17.9	26.8	19.5	18.6	12.2	9.9	7.2	238.3	117.7	103.6	383.5

Infestation Levels of *Annulotrema hepseti* on *Hepsetus odoe*. June -August 1998

No.	Size/mm	R 1			R 2			R 3			R 4			L1			L2			L3			L4			TOTAL			TOT
		A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	
1	259	4	4	2	1	2	0	1	1	0	0	0	0	0	0	5	3	1	1	2	0	0	0	0	12	12	3	27	
2	260	7	7	4	12	6	7	12	3	2	4	1	0	10	4	8	4	4	8	10	5	4	4	2	0	63	32	33	128
3	260	0	0	0	0	0	0	0	0	0	0	0	0	10	4	8	4	4	8	0	0	0	0	0	0	14	8	16	38
4	293	9	1	4	5	1	7	5	10	5	3	2	0	10	0	8	4	1	0	5	1	5	5	0	5	46	16	34	96
5	295	0	0	0	1	4	4	4	2	0	4	2	0	3	1	14	0	1	1	1	1	0	0	0	13	11	19	43	
6	295	0	0	0	1	4	4	4	2	0	4	2	0	3	1	14	0	1	1	1	1	0	0	0	13	11	19	43	
7	296	7	4	8	3	0	0	4	0	0	0	0	0	6	0	8	8	0	5	3	0	3	6	1	0	37	5	24	66
8	298	2	2	2	4	1	2	7	4	0	3	0	0	5	0	3	2	0	4	10	2	0	5	0	0	38	9	11	58
9	300	7	4	12	18	4	9	13	7	8	15	5	2	20	0	13	7	0	13	6	6	7	8	2	2	94	28	66	188
10	306	0	2	0	3	2	0	8	1	0	5	2	0	0	1	0	3	0	0	0	3	0	0	3	0	19	14	0	33
11	315	7	2	4	13	4	10	16	0	2	7	4	3	43	15	29	23	1	5	13	0	5	10	1	0	132	27	58	217
12	315	26	12	14	12	10	24	11	8	12	9	3	0	6	3	10	12	7	16	29	18	12	15	3	0	120	64	88	272
13	315	10	8	8	20	8	9	0	0	0	4	4	0	7	7	3	15	10	10	28	14	12	8	3	7	92	54	49	195
14	317	6	2	1	4	1	0	2	2	0	0	0	0	3	2	3	6	0	0	8	0	0	9	0	0	38	7	4	49
15	320	18	4	4	18	0	0	60	7	8	5	0	3	62	2	10	35	2	25	10	2	13	0	0	0	208	17	63	288
16	320	21	8	7	24	11	10	14	10	11	7	0	0	14	7	3	12	8	5	15	5	8	9	0	7	116	49	51	216
17	325	17	1	12	22	9	6	12	9	8	9	2	2	16	3	8	9	5	5	19	5	16	6	0	0	110	34	57	201
18	326	15	4	3	10	3	11	2	0	4	0	0	0	8	0	7	10	2	5	3	1	8	3	0	0	51	10	38	99
19	333	25	18	25	70	17	12	62	18	12	9	8	4	41	10	29	64	16	20	60	16	8	16	0	4	347	103	114	564
20	368	0	0	0	0	0	0	0	0	0	0	0	0	12	7	10	28	0	5	13	5	0	0	0	0	53	12	15	80
TOTAL	6116	181	83	110	241	87	115	237	84	72	88	35	14	279	67	188	251	65	137	235	87	101	104	15	25	1616	523	762	2901
AVE.	305.8	9.1	4.2	5.5	12.1	4.4	5.8	11.9	4.2	3.6	4.4	1.8	0.7	14.0	3.4	9.4	12.6	3.3	6.9	11.8	4.4	5.1	5.2	0.8	1.3	80.8	26.2	38.1	145.1
STD	26.3	8.5	4.6	6.3	15.8	4.6	6.1	17.6	4.9	4.5	4.0	2.2	1.3	16.2	4.0	7.9	15.2	4.2	6.9	14.2	5.4	5.2	5.0	1.2	2.4	81.0	24.7	30.1	129.9

Infestation Levels of Branchial monogeneans on *Brycinus lateralis*, Xaro. June -August 1998

No.	Size/mm	R 1			R 2			R 3			R 4			L1			L2			L3			L4			TOTAL			TOT	
		A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C		
1	86	4	0	0	2	1	1	0	0	0	1	0	0	0	1	0	1	1	1	2	1	0	0	1	0	10	5	2	17	
2	86	3	2	3	3	0	0	1	0	1	0	0	1	2	0	2	0	0	0	0	0	1	2	0	0	11	2	8	21	
3	87	0	5	0	2	3	0	0	2	1	0	0	0	2	1	0	0	0	0	0	1	0	1	1	2	5	13	3	21	
4	90	5	2	3	3	2	1	1	0	0	1	0	0	5	5	4	4	3	6	3	3	5	2	4	0	24	19	19	62	
5	90	4	6	5	1	0	0	4	0	0	0	0	0	0	0	2	0	0	0	0	2	3	0	0	0	9	8	10	27	
6	93	4	2	3	0	3	3	2	1	0	1	0	0	3	4	4	5	2	6	1	0	0	2	6	4	18	18	20	56	
7	94	4	2	0	0	0	1	1	1	0	0	0	0	1	0	3	0	0	0	0	0	0	1	1	0	7	4	4	15	
8	96	0	0	5	3	0	3	2	1	0	0	0	0	3	0	6	0	0	0	0	0	0	0	0	0	8	1	14	23	
9	100	3	1	0	0	0	0	1	0	0	0	0	0	2	2	0	1	2	0	3	1	0	0	0	1	10	6	1	17	
10	105	3	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	4	2	0	6	
11	108	3	5	0	1	1	0	0	0	0	0	0	0	4	2	3	2	0	3	0	0	0	1	3	3	11	11	9	31	
12	110	5	0	0	0	0	3	3	4	0	0	0	0	1	2	0	0	2	2	3	1	0	0	0	1	12	9	6	27	
13	110	8	5	4	2	0	6	4	2	4	0	0	0	3	7	4	0	5	6	5	0	9	6	2	0	28	21	33	82	
14	110	2	0	0	0	0	0	2	0	2	0	0	0	2	3	2	0	1	1	2	1	1	0	0	0	8	5	6	19	
15	112	0	0	0	0	0	0	2	1	4	0	0	0	0	0	3	7	0	5	0	0	0	0	0	0	9	1	12	22	
16	116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL	1593	48	30	23	17	10	18	23	12	12	3	0	1	29	29	33	20	16	30	19	10	19	15	18	11	174	125	147	446	
AVE.	99.6	3.0	1.9	1.4	1.1	0.6	1.1	1.4	0.8	0.8	0.2	0.0	0.1	1.8	1.8	2.1	1.3	1.0	1.9	1.2	0.6	1.2	0.9	1.1	0.7	8.7	6.3	7.4	27.9	
STD	10.5	2.2	2.2	2.0	1.2	1.1	1.7	1.4	1.1	1.4	0.4	0.0	0.3	1.5	2.1	1.9	2.2	1.5	2.5	1.6	0.9	2.5	1.6	1.8	1.3	7.7	6.9	8.8	21.3	



Infestation Levels of Branchial monogeneans on <i>Brycinus lateralis</i> Guma. June -August 1998																													
No.	Size/mm	R 1			R 2			R 3			R 4			L1			L2			L3			L4			TOTAL			TOT
		A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	
1	77	5	5	3	4	0	0	1	0	3	0	0	0	4	5	1	2	0	0	3	0	2	0	1	0	19	11	9	39
2	85	3	0	1	4	2	0	1	1	1	0	0	3	1	2	3	4	0	0	4	2	2	0	0	0	17	7	10	34
3	88	6	3	4	0	0	0	0	0	1	0	0	1	8	3	4	0	0	0	0	0	2	3	0	0	17	6	12	35
4	90	3	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	5	0	1	6
5	95	8	2	0	2	0	1	2	1	3	0	0	0	1	1	2	4	3	6	0	1	0	0	0	1	17	8	13	38
6	95	9	7	3	2	0	0	1	0	0	1	0	0	2	4	2	2	0	0	6	1	4	3	1	1	26	13	10	49
7	96	1	0	0	2	1	5	1	0	4	0	0	0	1	5	0	2	2	0	1	0	2	0	0	1	8	8	12	28
8	96	22	10	8	9	6	3	6	6	6	0	0	0	22	10	8	17	6	12	5	2	10	6	0	4	87	40	51	178
9	97	4	4	5	0	0	0	0	0	0	0	0	0	13	5	9	3	2	4	8	1	6	6	1	4	34	13	28	75
10	98	12	16	15	16	10	10	4	3	5	0	0	0	21	13	8	7	8	2	7	5	2	0	0	1	67	55	43	165
11	100	14	4	5	0	0	0	0	0	0	0	0	0	8	6	4	13	3	12	4	1	1	0	0	0	39	14	22	75
12	103	21	10	12	1	4	8	3	2	3	2	1	1	20	13	11	8	4	14	9	0	4	0	0	2	64	34	55	153
13	90	8	2	0	2	2	1	3	0	4	0	0	0	1	1	1	3	2	0	3	0	0	0	0	0	20	7	6	33
14	110	3	2	3	4	0	2	8	0	2	1	1	0	3	0	0	0	0	2	0	0	1	0	0	3	19	3	13	35
15	110	9	0	10	4	2	2	1	0	0	1	1	0	3	1	0	3	1	0	4	2	0	4	0	0	29	7	12	48
16	90	4	2	1	1	1	0	2	0	0	1	0	0	0	0	0	2	2	1	0	0	0	0	0	0	10	5	2	17
TOTAL	1520	132	67	71	51	28	32	33	13	32	6	3	5	109	69	53	71	33	53	54	15	36	22	3	17	478	231	299	1008
AVE.	95.0	8.3	4.2	4.4	3.2	1.8	2.0	2.1	0.8	2.0	0.4	0.2	0.3	6.8	4.3	3.3	4.4	2.1	3.3	3.4	0.9	2.3	1.4	0.2	1.1	23.9	11.6	15.0	63.0
STD	7.2	7.0	4.9	4.8	4.8	3.2	3.5	1.9	1.8	2.1	0.6	0.3	0.9	8.4	4.3	3.7	5.2	2.6	5.5	3.2	1.4	2.8	2.4	0.5	1.5	26.1	16.5	18.1	59.0

Infestation levels of *Annulotrema micralesti* on *Micralestes acutidens* June - August 1998

No.	Size/mm	No. of monogeneans
1	33	1
2	46	0
3	46	0
4	51	1
5	51	0
6	52	0
7	53	0
8	55	0
9	57	0
10	57	0
11	61	2
12	63	1
13	67	3
14	68	0
15	71	0
16	73	2
TOTAL	904	10
AVE	56.5	0.6
STD	10.5	1.0

Infestation levels of *Annulotrema rhabdalesti* on *Rhabdalestes maunensis* June - August 1998

No.	Size/mm	No. of monogeneans
1	35	1
2	40	5
3	42	4
4	45	1
5	38	2
6	35	3
7	30	0
8	29	0
9	40	4
10	46	10
11	39	3
12	29	0
13	34	3
14	33	1
15	37	0
16	40	1
17	29	1
TOTAL	621	39
AVE	36.5	2.3
STD	5.4	2.5