A REVIEW OF THE FAMILY ERGASILIDAE (COPEPODA: POECILOSTOMATOIDA) OF AFRICA

by

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Dissertation submitted in fulfilment of the requirements for the degree
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August 2004

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Chapter 1

Introduction

The Aquatic Parasitology Research Group has been involved in the Okavango Fish Parasite Project to identify the fish parasites of the Okavango River and Delta, Botswana. This project has been underway since 1997 with the following main objectives:

1. To compose a complete database of the fish parasites occurring in the Okavango Delta, as well as their distribution.
2. To determine the health status of the fish populations of the Okavango Delta and whether any parasite could pose as a threat towards these fish communities.
3. To determine whether any parasite could pose as a threat towards aquaculture and humans.
4. To better our knowledge of the African freshwater fish parasites as well as describing their lifecycles.
5. To shed light on the largely unknown parasitic crustaceans occurring in Lake Malawi.

All the major groups of parasites are being studied with three M.Sc dissertations on the trematodes (Jansen van Rensburg 2001), monogeneans (Christison 1998) and the myxosporeans (Reed 2000); as well as two Ph.D theses on the monogeneans (Christison 2002) and myxosporeans (Reed 2003). Many papers have been published on a variety of parasites, such as the branchiurans (van As & van As 1999), peritrichs (Basson & van As 2002) and nematodes (Moravec & van As 2001), with many more still to be completed. In addition to these published papers, a large number of papers on the material have been presented at various conferences. During the course of the Okavango Fish Parasite Project many ergasilids have been collected, but nothing has been done with the material to date. It is very unfortunate that there has been such a complete lack of interest in this very interesting group of parasites over the past thirty years, especially in the southern African region, with only two studies having ever been conducted on the ergasilids in southern Africa – Oldewage & Van As (1987) and Douëllou & Ehlwanger (1994). It is imperative to conduct this and further studies on these parasites, in order to improve our knowledge of the group, and hopefully be able to describe their complete lifecycle during future studies. But this would not be possible if the present study was not conducted.

There is a project currently running in Lake Malawi, which concentrates on the monogeneans present on the gills of the cichlids. Many ergasilids have been collected during this study, these were then sent by Prof. Sherman Hendrix, to our research group for study. Studies have been conducted in the past on the ergasilids of the lake, but none have taken place on the lake's southern region. This is because Lake Malawi is the southernmost lake on the great rift valley and the study of the ergasilids collected there will help us begin to reveal the true diversity of these parasites on the African continent.

The Poecilostomatoida is a major order of symbiotic copepods, has a worldwide distribution and comprises forty-seven families. Apart from five, which are mainly found in marine plankton, the majority of the families are symbiotic with marine invertebrates or fish from marine and freshwater habitats (Ho 1991). In this study we are concentrating on the family Ergasilidae von Nordmann, 1832, with three genera present in Africa, *Dermoergasilus* Ho & Do, 1982 – marine and estuarine species; *Ergasilus* von Nordmann, 1832 – marine, estuarine and freshwater species; and *Paraergasilus* Markewitsch, 1937 – freshwater species. Worldwide there are approximately 120 *Ergasilus* spp., 14 *Paraergasilus* spp. and 30 *Dermoergasilus* spp., these figures are approximates because there has not yet been a survey bringing all the species together in one list. More will be discussed further on in the text.

The layout of this dissertation is as follows: **Chapter 2** explains the materials and methods used to collect, preserve and study the specimens collected from the Okavango River and Delta and Lake Malawi. **Chapter 3** discusses the Great African Rift Valley and the geographical, climatological and ecological aspects of the Okavango Delta and Lake Malawi. In **chapter 4** the morphology of the ergasilids is discussed, with a short comparison between the three genera –, *Ergasilus*, *Paraergasilus* and *Dermoergasilus*. In **chapter 5** is the literature overview of all the freshwater species, ten *Ergasilus* species and two *Paraergasilus* species with their descriptions, distribution and hosts provided. **Chapter 6** is the results where the four species that were collected, two from the Okavango Delta and two from Lake Malawi are described. **Chapter 7** discusses the phylogeny of the *Ergasilus* species as well as providing a taxonomic key of the African *Ergasilus* species. **Chapter 8** provides a discussion of the results found in this study as well as the environmental problems facing the two main study areas – the Okavango Delta and Lake Malawi. Finally **chapter 9** gives all the literature referred to in this dissertation, followed by the abstracts and acknowledgements.

Chapter 2

Material and Methods

This study includes material collected in two vastly different areas, the implication was that different methods of collection for the fish and ergasilids were used. Once all the ergasilid specimens were at the Aquatic Parasitology Laboratory in Bloemfontein, all the material was treated in a similar manner.

2.1 Collection and Preparation of the Fish Hosts

In the Okavango River and Delta the fish were collected by using a variety of methods, depending on the species of fish being targeted. The smaller fish species such as *Rhabdalestes maunensis* (Fowler, 1935), *Brycinus lateralis* (Boulenger, 1900) and *Marcusenius macrolepidotus* (Peters, 1852) were collected in the evening at the water's edge, using scoop nets, hand nets and light traps. During the day, they were collected by using scoop nets in the hippo grass at the edge of the papyrus stands in the secluded channels and lagoons (Fig. 2.1B). Another method used for the smaller species was to detach a large clump of papyrus, and lift it into the boat to examine the roots for the fish that use the papyrus as shelter from predators (Fig. 2.1A). The larger predatory fish such as *Hydrocynus vittatus* Castelnau, 1861 were caught in the lagoons and channels using fishing rods and gill nets in the mornings between 7:00 and 11:00 and in the afternoons between 16:00 and 19:00 (Fig. 2.1C).

The cichlids (Fig. 2.1D) were caught in the early mornings by using cast nets, which were cast from the boat and sand banks in the lagoons and channels. The final method used to collect the larger species of fish such as *Serranochromis* spp. Regan, 1920, *Sargochromis* spp. Regan, 1920, *Synodontis* spp. Cuvier, 1816 and *Clarias* spp. Scopoli, 1777 was by setting out gill nets shortly before sunset and clearing the nets approximately an hour after sunset. This method ensured the fish that are primarily day feeders and ones that are primarily night feeders could be collected. Many fish were obtained from the fishermen from the neighbouring fishing lodge and village, most of these fish were caught from the mainstream and floodplains using traditional fishing rods made out of reeds.

The fish were kept in aerated aquaria in the temporary laboratory (Fig. 2.1E) until they could be examined, the anaesthetic MS222 was used to kill them, the fish were then identified using Skelton (2001), sexed and measured. Different groups of parasites are studied by the researchers in the Aquatic Parasitology Research Group. This meant that when a fish was dissected (Fig. 2.1F), each researcher examined the fish for the presence of the parasite of their specific interest. In this case the ergasilids, occurring on the gills, were removed with the gills and examined under the dissection microscope (Fig. 2.1G). Live observations of the ergasilid specimens were conducted on the specimens (Fig. 2.1H) in the field laboratory using a Wild dissection microscope. Once the live observations were completed the ergasilids were fixed in 70% etOH.

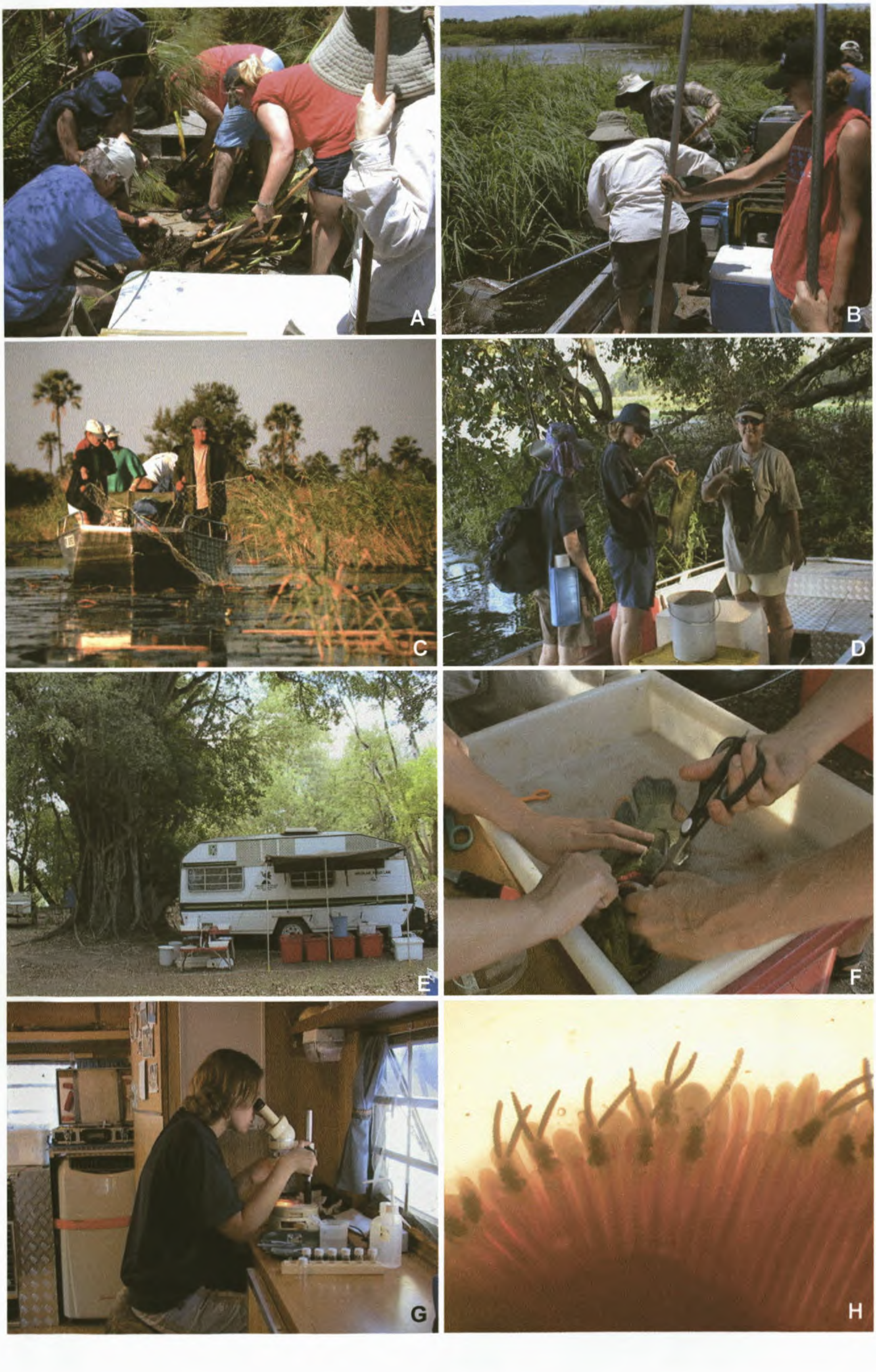
The study presently under way in Lake Malawi deals with the diversity of cichlids and monogeneans of the Lake. The study was concentrated on the eastern arm at the southernmost end of the lake. Because the study was only concerned with the cichlids of the lake, it means that the scientists in charge of collecting the specimens were very specific with the fish they caught. The main method of collection was by herding the fish into nets using SCUBA equipment. The unwanted or non-cichlid fish were released, while the others were brought to shore. Each fish collected was measured and sexed, once all the measurements were completed, the gills were removed and examined for monogenean and copepod parasites by Prof. Sherman Hendrix[1]. The copepod specimens were then sent to the Department of Zoology and Entomology at University of the Free State by Prof. Hendrix where they were sorted and transferred to 70% and examined in the same manner as those collected in the Okavango River and Delta.

[1] Prof. Sherman Hendrix is a expert in the study of the monogeneans and is currently a professor at Gettysburg College in the United States of America.

Figure 2.1

Photographs of the collection and dissection of the fish hosts.

- **A.** Examining papyrus roots for the smaller fish species
- **B.** Using scoop nets in the hippo grass to catch the smaller fish species
- **C.** Using gill nets to collect the fish hosts
- **D.** Some of the cichlid species collected
- **E.** The field laboratory with the aerated containers used to keep the fish alive until they were examined
- **F.** Dissecting the fish
- **G.** Examining the gills using the dissection microscope
- **H.** Photograph of live ergasilids on the gill filaments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2.2 Study and Preparation of the Material

Light and Dissection Microscopy

At the Aquatic Parasitology Laboratory in Bloemfontein the ergasilid specimens were sorted into groups according to the host species on which they were found. The specimens were placed in lactic acid for approximately an hour, this is a very short period, but due to the small body size the lactic acid cleared the specimen very quickly. The lactic acid ensured that the setae were clearly visible and strengthened them to prevent them from breaking. The specimens were examined using the following light microscopes Leitz Laborlux D and Zeiss Axiophot, and a Wild dissection microscope. 20-25 specimens were drawn and measured from each host species, depending on whether there were enough specimens from the host species. The drawings of the *Ergasilus* specimens were made using a drawing tube connected to the Leitz and Wild microscopes. The *Paraergasilus* specimens were too small to draw using these microscopes. Because of this, pictures were drawn from photo prints, which were taken using the Zeiss microscope, which had attachments enabling us to reach a higher magnification. Measurements were taken from the drawings, as illustrated in Figure 2.2. The spine-seta formula is determined by counting the number of spines and setae on each segment of the rami, as well as the presence or absence of setae on the coxa and basis. The spines are represented by roman numerals, while the setae were represented by conventional numbering as in Table 2.1.

Table 2.1: An example of the method used to illustrate the spine-seta formula for ergasilids collected during this study.

	Coxa	Basis		Segment 1	Segment 2	Segment 3
Leg 1	0	1	Exopodite	I – 0	I – 1	II – 5
			Endopodite	0 – 1	0 – 1	II – 4
Leg 2	0	1	Exopodite	I – 0	0 – 1	0 – 6
			Endopodite	0 – 1	0 – 1	I – 4
Leg 3	0	1	Exopodite	I – 0	0 – 1	0 – 6
			Endopodite	0 – 1	0 – 1	I – 4
Leg 4	0	1	Exopodite	I – 0	0 – 5	-*
			Endopodite	0 - 1	0 – 1	I – 3

* all *Ergasilus* and *Paraergasilus* species lack this segment

Figure 2.2

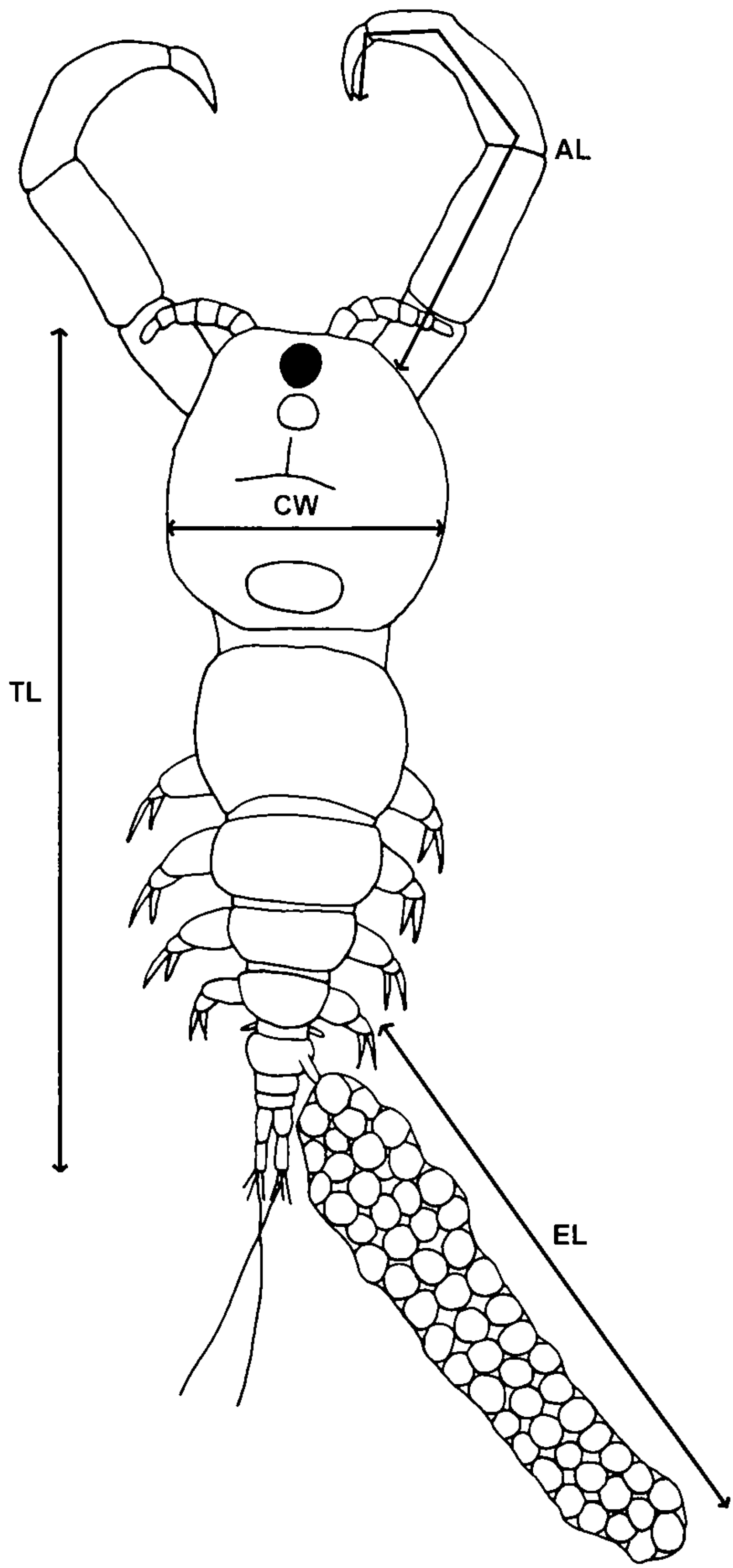
A generalised line drawing illustrating the measurements taken from each specimen.

AL. Antenna length

CW. Carapace width

EL. Egg sac length

TL. Total length


AL
CW
TL
EL

Scanning Electron Microscopy

Specimens were cleaned using a very fine brush, after which they were dehydrated through a series of alcohol concentrations and critical point dried using the standard techniques. Once critical point dried the specimens were glued onto Scanning Electron Microscopy stubs using two different methods, larger specimens were mounted using a mixture of quick drying glue (Pratley putty). The smaller specimens could not be prepared in this way due to the fact that they would be engulfed in the glue; therefore thin double sided tape had to be used.

The setae on the legs tend to cover the ventral sides of the thorax and abdomen; therefore the legs of certain specimens were removed in order to study the ventral surfaces of these structures. Specimens were sputter coated with gold and studied using the JEOL WINSEM JSM 6400 Scanning Electron Microscope (SEM) at the Centre for Confocal and Electron Microscopy, University of the Free State. Black and white photographs of the specimens were taken on the SEM, these were developed by the author in the darkroom at the Department of Zoology and Entomology.

Computer Programmes

All the drawings included in this study were done by the author and were scanned in and edited using Coral Draw 10 and Coral Photo Paint 10. In the case of the literature study in Chapter 5, it was necessary to redraw the original drawings from the species descriptions. A problem was encountered with these drawings because many of the original authors neglected to include scale bars. In some cases it was possible to add scale bars based on known measurements, while in others it was not, therefore a few drawings lack scale bars. A variety of different programmes were used during this study, including Microsoft Excel and Microsoft Word. PAUP 4.4, Nexus was used in Chapter 7 where the taxonomy of the ergasilids is discussed, to determine the relationships between the *Ergasilus* species.

Chapter 3

African Freshwater Habitats

The natural history of the African continent began in the earliest period of geological time, the Pre-Cambrian, which stretched from the beginning of Earth's history to approximately 600 million years ago. On the continent there are certain groups of rocks that are approximately 3500 million years old, these older rocks form three older cratons. The first of these cratons is found in the western lobe of the continent, the second in the Zaire-Angola region, and the third in the Zimbabwe-Transvaal-Free State region (Grove 1998). These cratons contain many of the precious ores important to man and have a distinct influence on the land features such as rivers and lakes.

Following the Pre-Cambrian was the Cambrian period, this is when the first signs of life began to emerge. For the first two-thirds of the Cambrian, Africa was part of the super-continent of Gondwanaland. There was a high rate of erosion at the time, causing a lot of sediment to be deposited, which at present can be seen in the sandstones, shales, limestones and dolomites in the Maghreb (north-west Africa), the western Sahara and the Cape region (Grove 1998). Many of these rock formations are very resistant to erosion and influence the surface features such as the river systems. Approximately 500 to 450 million years ago the seas encroached over north west Africa, and a few million years later, when the northern parts of Africa were situated at the South Pole, a vast glaciation occurred in this area which is now the vast Sahara Desert. And 150 million years later southern Africa had moved to the South Pole and experienced its own glaciation (Grove 1998). All these processes have had a major influence on the landforms, features and diversity of life on the continent. It has been estimated that between 270 and 200 million years ago there was a considerable increase in the seismic activity of the super-continent causing it to break up into the continents we know today (Stuart & Stuart 1995). A process of continental drift then began, which caused the continents to drift away from each other towards the positions that they are found at present. Of these continents Africa is the world's second largest, with the equator crossing it just south of its centre. This extreme size, placement and geological history accounts for its extremely diverse range of habitats ranging from the Sahara Desert in the north to the Equatorial rainforests in the central region.

Changes in precipitation from season to season dominate the river regimes of Africa, this means that many of the African rivers are dry for half the year and in flood for the rest. These changes are more pronounced the further one travels from the equatorial regions. In the equatorial areas precipitation falls throughout the year, this means that the lack of rainfall is not a major factor influencing the rivers, here the amount of evaporation occurring throughout the year is the largest factor influencing the water levels. The water levels of many of the larger African rivers, such as the Niger River (Fig. 3.1), rise and fall several metres throughout the year (Grove 1998). The Congo River is a good example of one with a relatively steady discharge throughout the year. The Congo Basin (Fig. 3.1) covers a very large area and lies across the equator, this means that for half of the year it gets its rainfall from the Southern Hemisphere and for the other half from the Northern Hemisphere.

These factors have a very large influence on the fish fauna of the rivers. The present distribution of freshwater fish is due to the historical drainage patterns. The fish species present in the equatorial rivers are different to those in the rivers of the northern Sudan area. Travelling south of the Zambezi River the number of fish species decreases rapidly, this is mainly due to the fact that the rivers are very seasonal and the water temperatures are much lower than in the northern regions. South of the Zambezi the fish distribution makes it obvious that many of the river systems were linked in the past, for example the Orange River Mudfish *Labeo capensis* (A. Smith, 1841), which is found in the Orange River and the south-eastern Cape rivers the Gouritz, Gamtoos, Sundays and Great Fish Rivers (Gabie 1965). The Cape Fold Mountains are situated in the southernmost region of Africa, because this area is in the overlap of the winter and summer rainfall region where the rivers receive year round rainfall. These areas have a high number of endemic species, possibly due to the unique rainfall pattern.

3.1 The Great Rift Valley

The Great Rift Valley stretches from Lebanon to Moçambique and has been developing over the last 20 million years ever since a series of enormous tectonic activities tore through the Middle East and North Eastern Africa. The main fault line runs from northern Ethiopia to Lake Malawi (Fig. 3.1). A few smaller faults branch off the main fault, they are the Gulf of Suez, which stretches to the north west from the northern part of the Red Sea, and a smaller fault branching off from Lakes Albert and Tanganyika (Fig. 3.1) through to the Okavango Delta. The main fault is still slowly drifting apart, which has led scientists to the conclusion that the entire eastern section will in millions of years, detach from the continent.

The Great Rift Valley is considered one of the worlds most impressive volcanic regions, most of the volcanoes in the area are extinct, but there are at least thirty that are dormant or active (Willock 1974). The volcanic origin of the area has a very big effect on the lakes of the Rift Valley; many of the smaller lakes are very high in salts which make it very difficult for any organisms to survive. Lakes Magadi and Natron are the two most caustic lakes but are still able to support a wide variety of animal life. In Lake Magadi many fish species are able to survive in the hot springs found in the southern region of the lake and Lake Natron is one of the main breeding grounds for flamingos in East Africa (Willock 1974). Even though many of the smaller lakes in the rift valley are salt lakes, others are wonders of the natural world, for example Lake Tanganyika and Lake Malawi which have an amazing diversity of fish species.

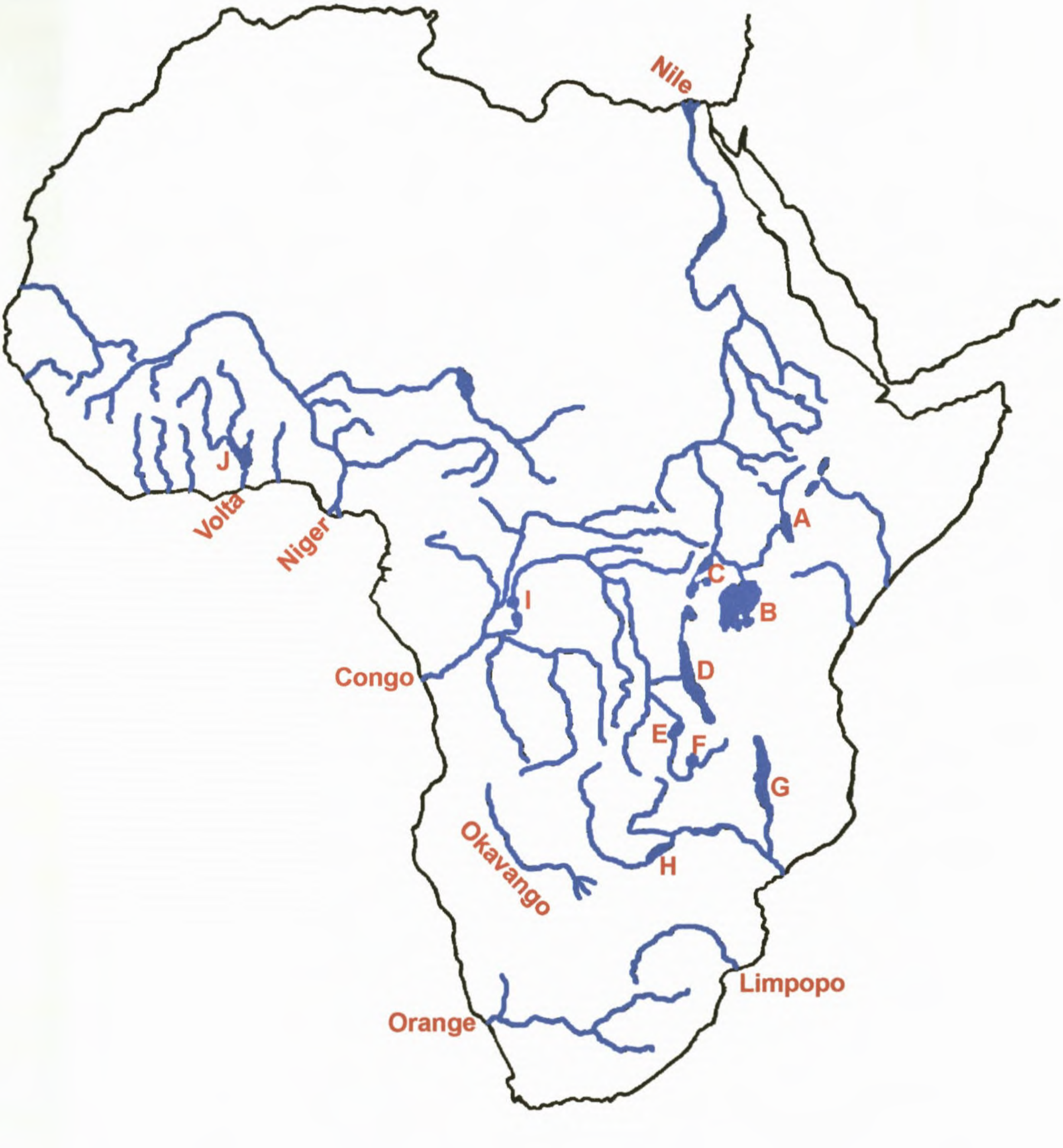


Figure 3.1: Map of the African continent with the major river systems and lakes. **A.** Lake Turkana **B.** Lake Victoria **C.** Lake Albert **D.** Lake Tanganyika **E.** Lake Mweru **F.** Lake Bangweulu **G.** Lake Malawi **H.** Lake Kariba **I.** Lake Tumba **J.** Lake Volta [Map adapted from Grove (1998)].

3.2 The Okavango River and Delta, Botswana

The Okavango River is very unique, this is due to the astonishing fact that it is located in one of the driest regions of southern Africa, the Kalahari Desert. The Kalahari Desert extends from the Democratic Republic of Congo to the Orange River, covering a total area of 2500km^2, this has earned it the distinction of being the largest continuous expanse of sand in the world (Ross 1987). The Okavango Delta is the largest delta in Africa, but is actually not a delta at all, it is an alluvial fan. A delta forms when a river flows into a larger body of water, like a lake or sea. But due to its size and delta-like appearance the Okavango Delta will always be known as a delta and not an alluvial fan. The Delta proper covers an approximate area of 22,000km^2 (Fig. 3.4), the total area changes annually depending on the season.

Geographical Aspects

The Okavango Delta is situated in northern Botswana, where the approximate average annual rainfall is a mere 450mm (Pallett 1997). This means that the Delta receives the majority of its water from elsewhere. It originates as many small streams on the southern slopes of the Angolan highlands (Fig. 3.3) at an elevation of 1800m (Sefe & Leburu-Sianga 2001). These small headwater streams flow towards the southeast joining along the way to form the large mainstream called the Cubango River (Fig. 3.3). The river's flow changes towards an easterly direction where it is met by a major tributary, the Cuito River (Fig. 3.3). Once it crosses the Botswana border it becomes the meandering Okavango River, which can be as much as 4m deep and 200m wide. This section of the river, before it reaches the Delta region, is known as the Panhandle, and is prevented from spreading out excessively due to the fact that its course runs through a Graben structure. This means that due to a small local fault the land that the river flows over is slightly lower than the surrounding regions. A very distinctive feature of the Okavango is the papyrus plants *Cyperus papyrus*, that line vast reaches of the river's course. At the end of the Panhandle it encounters three different faults (Fig. 3.4) that mark the end of the East African Rift system, i.e. the Gumare, Kunyere and Thamalakane Faults (McCarthy & Ellery 1997). Once it has crossed the

Gumare Fault it fans out forming the Delta area. When the water has passed the Panhandle region, it loses a lot of momentum, this means that the water will begin to deposit its sediment load. This sedimentary deposition is one of the main factors influencing channel formation in the Delta.

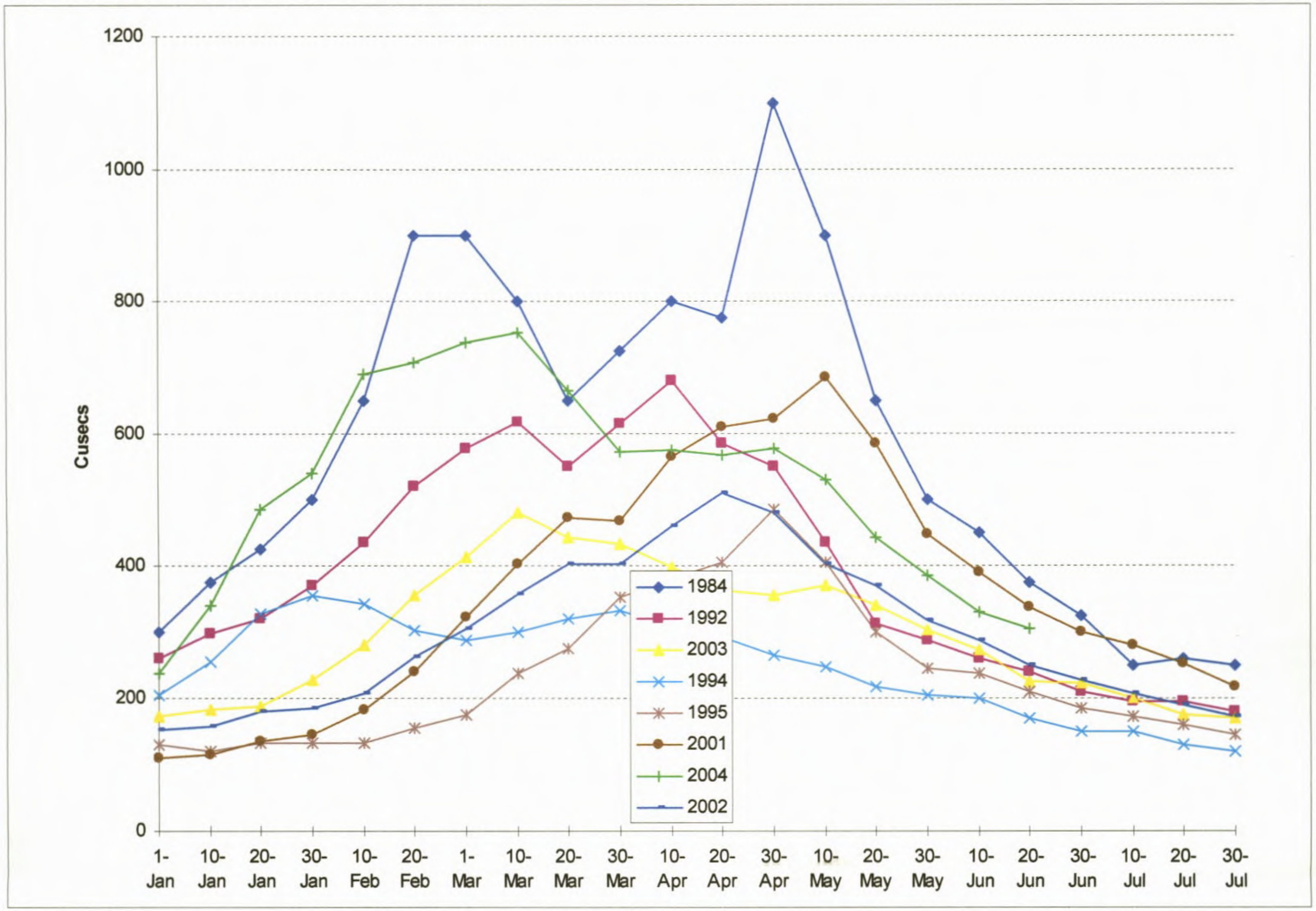
Climatological Aspects

The Okavango Delta is composed of permanent river channels (Fig. 3.5E), semi-permanent drainage channels, lagoons and floodplains, all of these features are totally dependant on the annual flood cycle (Figure 3.2). The floodwaters flowing from the Angolan highlands usually arrive in Shakawe in January, exit the Panhandle at Seronga in March and reach Maun in June. The water level in the upper regions of the Delta is usually at its lowest between July and December. Most of the water loss in the Delta is due to evapotranspiration, an approximate of 450mm/year, much more than the average rainfall of 400mm/year (Pallett 1997), with very little water flowing out of the Delta via the Thamalakane River.

Ecological Aspects

The Okavango Delta possesses many different types of ecosystems, more than other deltas, because it is situated in such a unique area. The following are the main ecosystems present in the system: riverine panhandle, upper swamp, lower swamp, drainage rivers and sump lakes. The two most dominant areas are the riverine panhandle and upper swamp (Fig. 3.5F), which covers at least two-thirds of the total area. In the riverine Panhandle the water has a steady flow and is relatively clear. The main river channel can be up to 100m wide, there are also many tributaries, oxbow lagoons (Fig. 3.5D) and floodplains found in this area. Most of the channels and lagoons in the Panhandle area are lined by papyrus stands (Figs. 3.5B&C), while the vegetation in the floodplains mainly consists of sawgrass (Fig. 3.5A). These floodplains receive an annual flood between February and June. Once the river reaches the upper swamp it divides into two main channels, the Nqoqa and Jao, with many smaller tributary channels present. The lower swamp covers approximately a third of the Delta, the floodplains in this region are vegetated by shallow grass and sedge. The total area included in the lower swamp is dependent on the size of the annual flood and the amount of rainfall falling locally. The Boro and Santandadibe Rivers are the main drainage channels in the Delta, once they reach the Thamalakane Fault they join to form the Thamalakane River, which meets up with the Boteti River (Fig. 3.4), flowing to the Makgadikgadi Salt Pans (McCarthy & Ellery 1997). The presence of so many different habitats has enabled a huge diversity of life forms to live here. This includes 164 species of mammals with the hippopotamus a keystone species (Fig. 3.5H), over 400 species of birds of which many depend on fish for food, i.e. the fish eagle (Fig. 3.5G), 157 different reptile species, 90 fish species (in the total system) (Table 3.1) and over 5000 insect species (Ross 1987). There are many small rural villages scattered along the Okavango River in the Panhandle region, but very few villages are located in the Delta region, mainly because a vast majority of this area is protected.

Figure 3.2: Graph providing the flood data of the Okavango River, measurements are in cubic metres/second and were taken every ten days from Mohembo [Provided by www.aliboats.co.za]



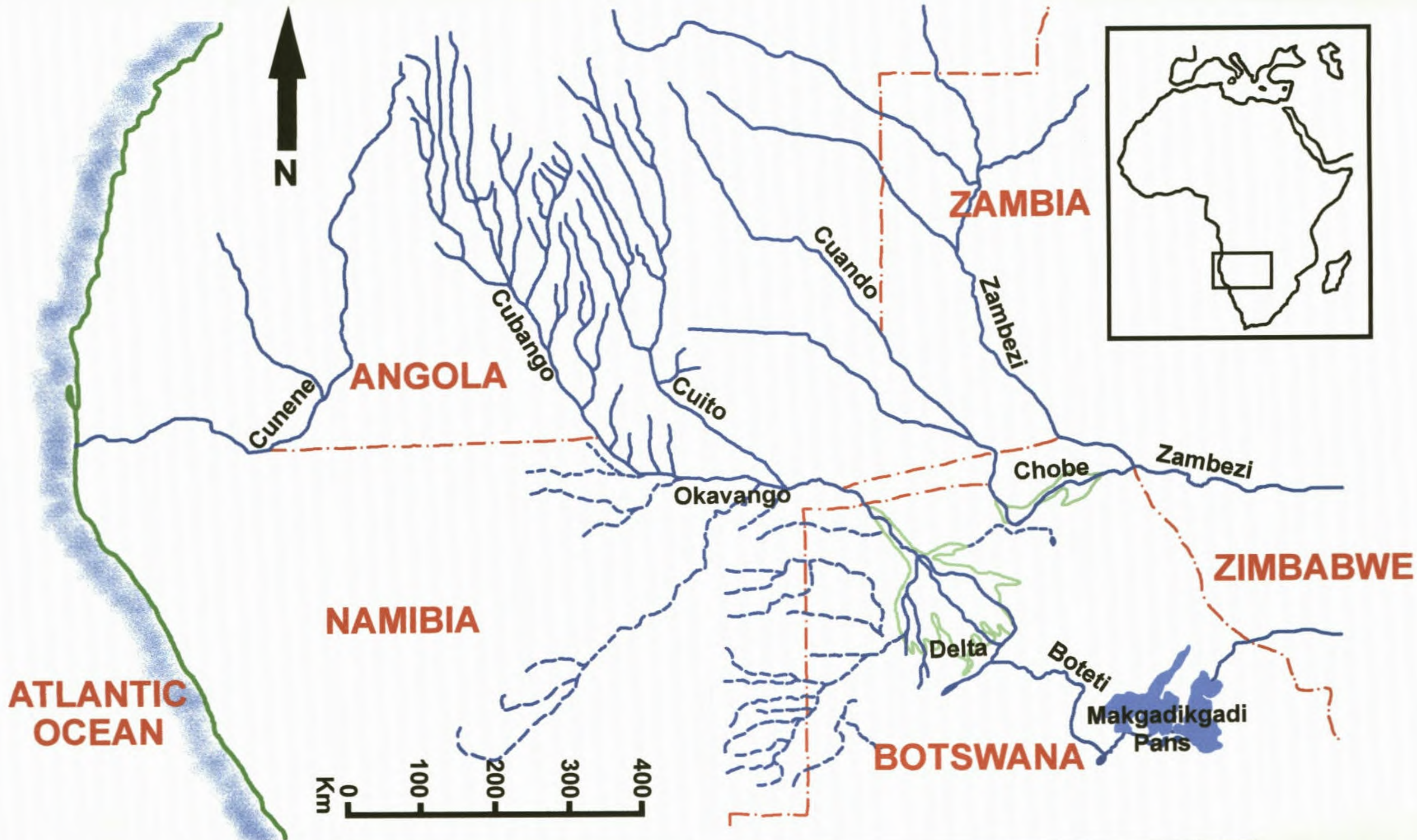


Figure 3.3: The Okavango Drainage system, with the Cunene River in the west and in the east by the Upper Zambezi system. [Redrawn from the JLB Smith Institute of Ichthyology Investigational Report (1988)].

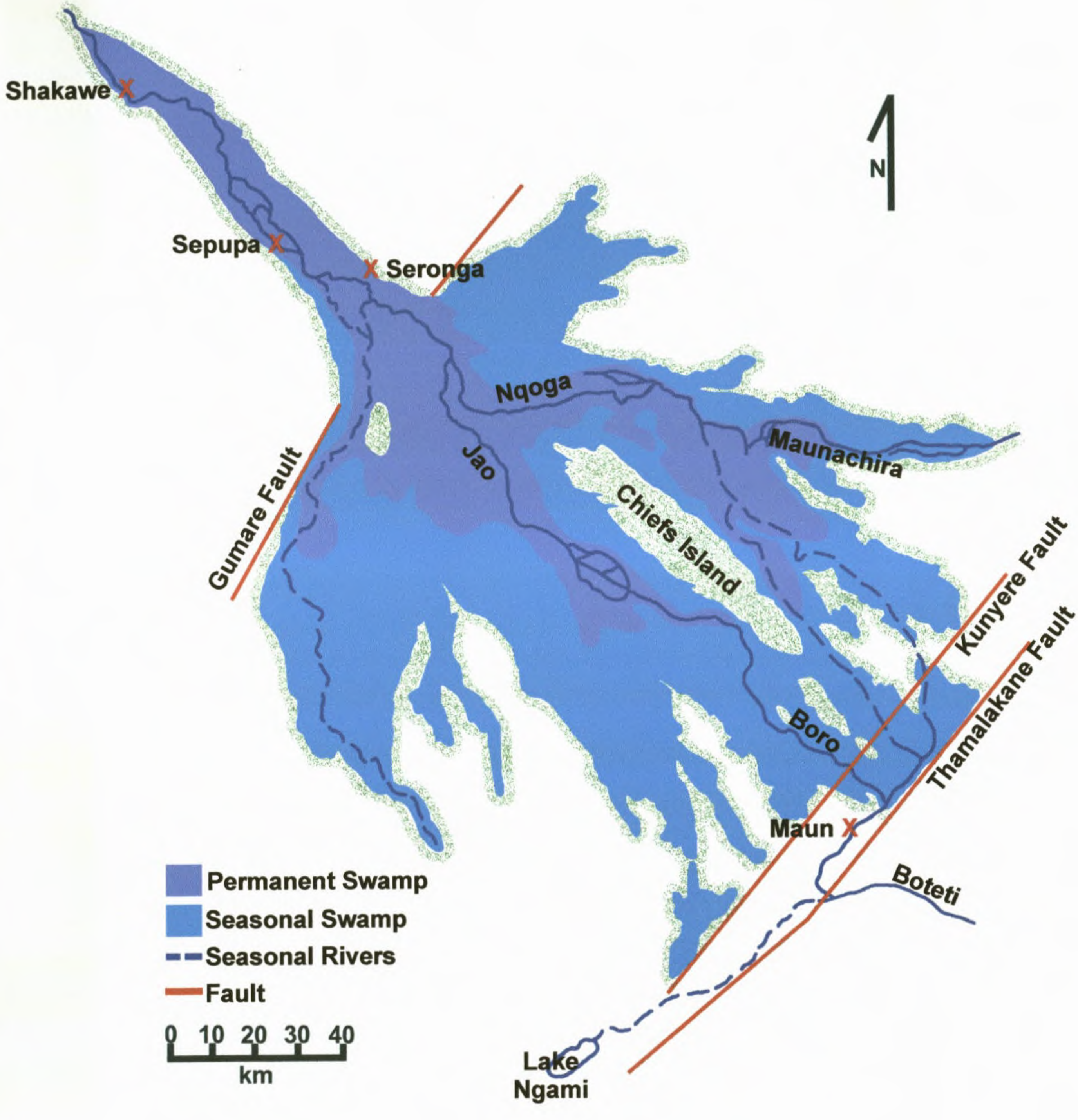


Figure 3.4: Map of the Okavango Delta drainage area [Redrawn from McCarthy *et al.* (1997)]

Figure 3.5

Photographs of the habitat and wildlife of the Okavango River and Delta.

- **A.** Floodplain neighboring the Shakawe camp
- **B.** Tree covered island, bordered by papyrus
- **C.** Channel bordered by papyrus and lily plants
- **D.** An oxbow lagoon off the main channel
- **E.** Meandering channels
- **F.** Swampland
- **G.** Fish eagle *Haliaeetus vocifer* one of the Delta's top predators
- **H.** Hippopotamus *Hippopotamus amphibius* Linnaeus, 1758 one of the Delta's keystone species

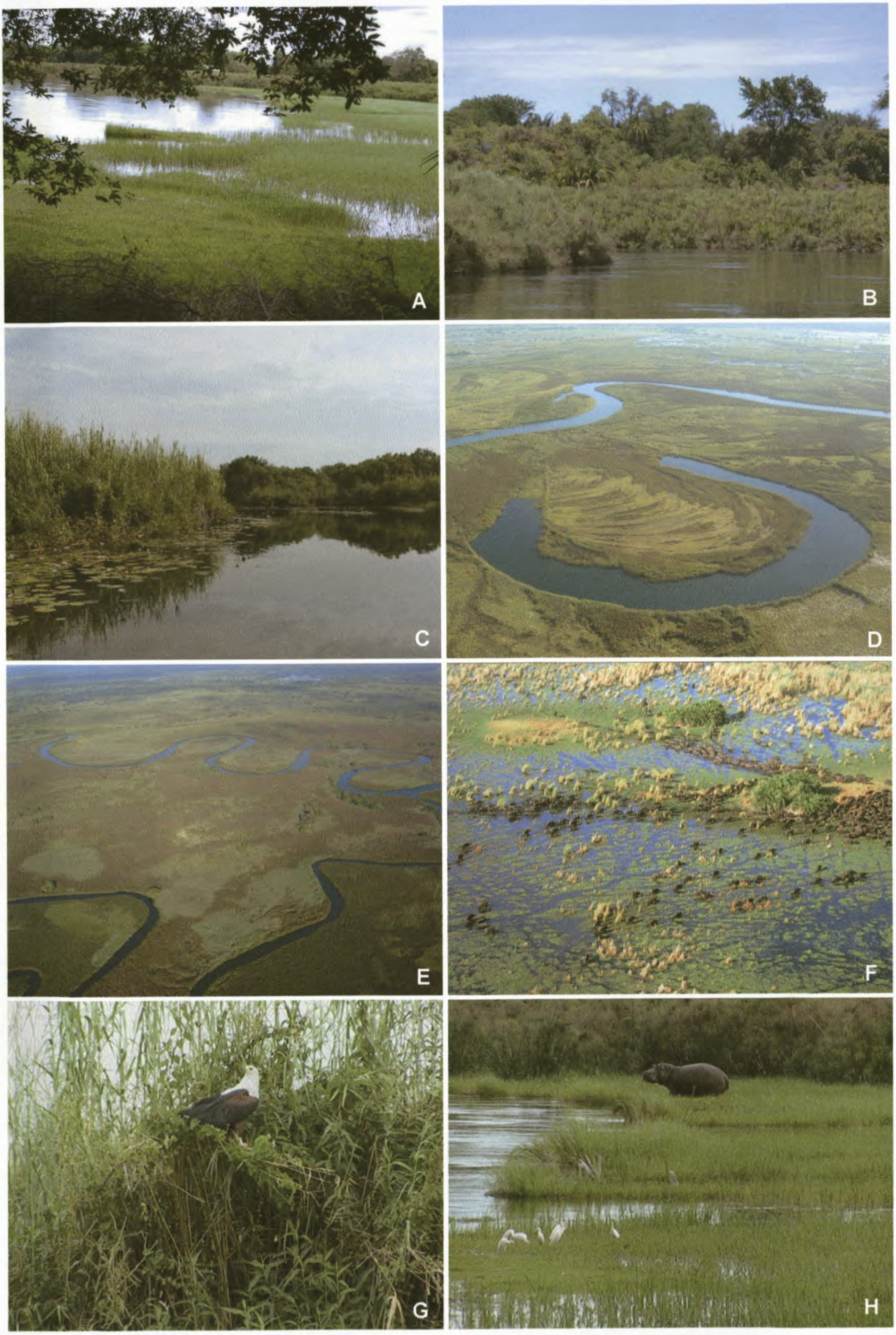

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Table 3.1: List of all the fish species and families found in the entire Okavango River and Delta [Compiled using Skelton (2001)].

FISH SPECIES AND FAMILIES
Mormyridae
Hippopotamyrus ansorgii (Boulenger, 1905)
Cyphomyrus discorhynchus (Peters, 1852)
Marcusenius macrolepidotus (Peters, 1852)
Mormyrus lacerda Castelnau, 1861
Petrocephalus catostoma (Günther, 1866)
Petrocephalus wesselsi (Kramer & van den Bank, 2000)
Pollimyrus castelnaui (Boulenger, 1911)
Kneriidae
Kneria polli Trewavas, 1936
Parakneria fortuita Penrith, 1973
Cyprinidae
Barbus afrovernayi Nichols & Boulton, 1927
Barbus barotseensis Pellegrin, 1920
Barbus barnardi Jubb, 1965
Barbus bifrenatus Fowler, 1935
Barbus brevidorsalis Boulenger, 1915
Barbus breviceps Trewavas, 1936
Barbus codringtoni Boulenger, 1908
Barbus eutaenia Boulenger, 1904
Barbus fasciolatus Günther, 1868
Barbus haaisianus David, 1936
Barbus kerstenii Peters, 1868
Barbus lineomaculatus Boulenger, 1903
Barbus miolepis Boulenger, 1902
Barbus multilineatus Worthington, 1933
Barbus paludinosus Peters, 1852
Barbus poechii Steindachner, 1911
? *Barbus puellus* Nichols & Boulton, 1927
Barbus radiatus Peters, 1853
? *Barbus tangandensis* Jubb, 1954
Barbus thamalakanensis Fowler, 1935
Barbus unitaeniatus Günther, 1866
Barbus sp.
Coptostomabarbus wittei David & Poll, 1937
Labeo cylindricus Peters, 1852
Labeo lunatus Jubb, 1963
Mesobola brevianalis (Boulenger, 1908)
Opsaridium zambezense (Peters, 1852)
Distichodontidae
Hemigrammocharax machadoi Poll, 1967
Hemigrammocharax multifasciatus Boulenger, 1923
Nannocharax macropterus Pellegrin, 1925

Table 3.1 (cont.): List of all the fish species and families found in the entire Okavango River and Delta [Compiled using Skelton (2001)].

FISH SPECIES AND FAMILIES
Characidae
Brycinus lateralis (Boulenger, 1900)
Hydrocynus vittatus Castelnau, 1861
Micralestes acutidens (Peters, 1852)
Rhabdalestes maunensis (Fowler, 1935)
Hepsetidae
Hepsetus odoe (Bloch, 1794)
Claroteidae
Parauchenoglanis ngamensis (Boulenger, 1911)
Amphiliidae
Leptoglanis rotundiceps (Hilgendorf, 1905)
Leptoglanis sp Boulenger, 1902
Amphilius uranoscopus (Pfeffer, 1889)
Schilbeidae
Schilbe intermedius Rüppell, 1832
Clariidae
? *Clarias dumerilii* Steindachner, 1866
Clarias gariepinus (Burchell, 1822)
Clarias liocephalus Boulenger, 1898
Clarias ngamensis Castelnau, 1861
Clarias stappersii Boulenger, 1915
Clarias theodorae Weber, 1897
Clariallabes platyprosopos Jubb, 1964
Mochokidae
Chiloglanis fasciatus Pellegrin, 1936
Synodontis leopardinus Pellegrin, 1914
Synodontis macrostigma Boulenger, 1911
Synodontis macrostoma Skelton & White, 1990
Synodontis nigromaculatus Boulenger, 1905
Synodontis thamalakanensis Fowler, 1935
Synodontis vanderwaali Skelton & White, 1990
Synodontis woosnami Boulenger, 1911
Cyprinodontidae
Aplocheilichthys hutereaui (Boulenger, 1913)
Aplocheilichthys johnstonii Günther, 1893
Aplocheilichthys katangae (Boulenger, 1912)
Aplocheilichthys sp. Bleeker, 1863
Cichlidae
Hemichromis elongatus (Guichenot, 1859)
Oreochromis andersonii (Castelnau, 1861)
Oreochromis macrochir (Boulenger, 1912)
Pharyngochromis acuticeps (Steindachner, 1866)
Pseudocrenilabrus philander (Weber, 1897)

Table 3.1 (cont.): List of all the fish species and families found in the entire Okavango River and Delta [Compiled using Skelton (2001)].

FISH SPECIES AND FAMILIES
Cichlidae (cont.)
Sargochromis carlottae (Boulenger, 1905)
Sargochromis codringtoni (Boulenger, 1908)
Sargochromis giardi (Pellegrin, 1903)
Sargochromis greenwoodi (Bell-Cross, 1975)
Serranochromis altus Winemiller & Kelso-Winemiller, 1990
Serranochromis angusticeps (Boulenger, 1907)
Serranochromis longimanus (Boulenger, 1911)
Serranochromis robustus (Günther, 1864)
Serranochromis macrocephalus (Boulenger, 1899)
Serranochromis thumbergi (Castelnau, 1861)
Tilapia rendalli rendalli (Boulenger, 1896)
Tilapia ruweti (Poll & Thys van den Audenaerde, 1965)
Tilapia sparrmanii A. Smith, 1840
Anabantidae
Microctenopoma intermedium (Pellegrin, 1920)
Ctenopoma multispine Peters, 1844
Mastacembelidae
Aethiomastacembelus frenatus (Boulenger, 1901)
Aethiomastacembelus vanderwaali (Skelton, 1976)

3.3 Lake Malawi

Lake Malawi is the southernmost lake on the Great Rift Valley, its shores lie on three different countries: Moçambique, Tanzania and Malawi (Fig. 3.6). The majority of it lies in Malawi taking up 24,400km^2 of the country's total area of 118,480km^2, this means that a large portion of the population relies on the lake in various ways.

Geographical Aspects

Lake Malawi is the ninth largest lake in the world and the third largest in Africa, with a total length of approximately 600km and an average width of 50km (Figs. 3.6 & 3.7). Certain regions of the lake can reach the depth of 700m; but this is not the deepest in Africa. The title of deepest lake is taken by Lake Tanganyika which reaches the depth of 1470m. Even though these lakes possess such a large volume of water, it does not mean that the entire water body is habitable. According to Grove (1998) the water below 200m is stagnant with a very low oxygen content, this renders the region below 200m virtually uninhabitable, the only organisms able to survive in this region are those which feed on the debris falling from above. The size of the lake makes it act more like an inland sea (Fig. 3.8D) than a lake, where waves reaching 3 to 4 metres have been measured during storms. There is no noticeable circulation between the different water layers in the lake, this causes the formation of the anoxic layers mentioned previously. It means that the water temperatures are greatly affected by atmospheric changes, causing four main climatic seasons to dominate the lake's temperature.

Climatological Aspects

Between June and August the windy and cold season prevails, this causes the water temperature in the shallower southern regions to drop to 20°C (Fig. 3.7). After this cold season there is a period of relatively calm weather between late August and mid-November, this means that the water temperature increases. The rainy season begins at the end of November and lasts until the end of February, with air temperatures ranging between 25°C to 40°C. The rains decrease until the end of May with high temperatures continuing throughout this time, once the rainy season is over the water level could have increased by over 2m (Konings 1990).

Ecological Aspects

There are many species of animals and birds that occur in and around the lake region and are affected by the climatic changes that occur annually. The large temperature changes discussed earlier influence the lifecycles of the fish species, most of the cichlid species tend to breed in the calmer periods between August and November, whereas the non-cichlids breed at the end of the rainy season, this is because many of the species have to migrate upriver in order to spawn (Konings 1990).

The following types of habitat occur in the lake: sandy open areas (Fig. 3.8B), rocky reefs (Figs. 3.8A,C&E), deep open water (Fig. 3.8D), swamplands and reed beds. All these factors combine together to ensure a large diversity of fish species (Table. 3.2). Currently approximately 56 genera and 344 species are known from the lake of which most are endemic, with new genera and species are being discovered almost every year. There are approximately 18 non-cichlid genera present in the lake, but the number of non-cichlid species is not known (Konings 1990). This is mainly because most studies on the fish of Lake Malawi have concentrated on the cichlids. The cichlids fall under four main groups: the large predatory ncheni, the smaller plankton feeding utaka, the brightly coloured algae eating mbuna and the chisawasawa which are bottom feeders (Briggs 1996).

The large number of habitats available to the fish has ensured that speciation occurs, an example of this are the species adapted to living on the rocky reefs. In the past they could have been different populations of a single species, with each populating different reefs separated by a large open sandy area. Most fish will not cross open sandy areas; this means that there would be no swapping of genes between the groups. If this separation continues for a long period of time a new species could form, this is known as adaptive radiation. If these fish are hosts to parasites this separation could inadvertently cause speciation in the parasites. The mbuna cichlids occur on the rocky regions of the lake and is the group which has experienced the greatest diversity in speciation.

Figure 3.6: Map of Lake Malawi and the surrounding areas [Redrawn from Konings (1990)]

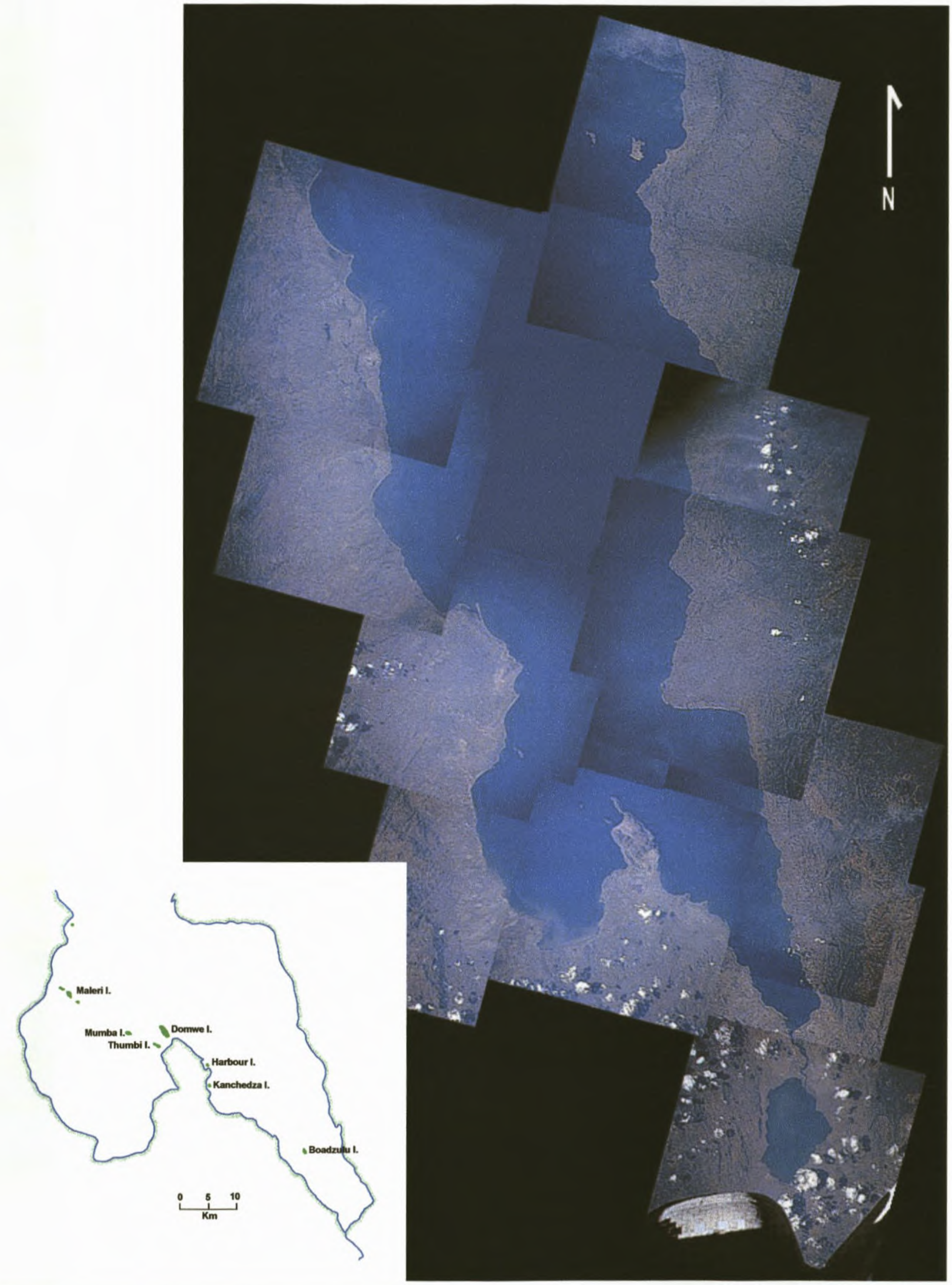


Figure 3.7: Satellite photograph of the southern half of Lake Malawi, with a map redrawn from Marsh (1983) of the same area

Figure 3.8

Photographs of Lake Malawi.

- **A.** Rocky shore
- **B.** Sandy shore with a view across the lake
- **C.** Rocky shore with local fishermen in the foreground
- **D.** View across the lake
- **E.** Rocky shore

[Photographs supplied by Prof. Sherman Hendrix]


A
B
C
D
E

Table 3.2: List of the fish genera and families found in Lake Malawi [Compiled using Ribbink *et al.* (1983) and Konings (1990)]

FISH FAMILIES AND GENERA
Cichlidae
Alticorpus Stauffer & McKaye, 1988
Aristochromis Trewavas, 1935
Astatotilapia Pellegrin, 1904
Aulonocara Regan, 1922
Buccochromis Eccles & Trewavas, 1989
Champsochromis Boulenger, 1915
Chilotilapia Boulenger, 1908
Copadichromis Eccles & Trewavas, 1989
Corematodus Boulenger, 1897
Cyathochromis Trewavas, 1935
Cynotilapia Regan, 1922
Cyrtocara Boulenger, 1902
Dimidiochromis Eccles & Trewavas, 1989
Diplotaxodon Trewavas, 1935
Docimodus Boulenger, 1897
Exochochromis Eccles & Trewavas, 1989
Fossorochromis Eccles & Trewavas, 1989
Genyochromis Trewavas, 1935
Gephyrochromis Boulenger, 1901
Hemitilapia Boulenger, 1902
Iodotropheus Oliver & Loiselle, 1972
Labidochromis Trewavas, 1935
Labeotropheus Ahl, 1926
Lethrinops Regan 1922
Lichnochromis Trewavas, 1935
Maravichromis Eccles & Trewavas, 1989
Melanochromis Trewavas, 1935
Nimbochromis Eccles & Trewavas, 1989
Nyassachromis Eccles & Trewavas, 1989
Otopharynx Regan, 1920
Oreochromis Günther, 1889
Petrotilapia Trewavas, 1935
Placidochromis Eccles & Trewavas, 1989
Protomelas Eccles & Trewavas, 1989
Pseudotropheus Regan, 1922
Rhamphochromis Regan, 1922
Serranochromis Regan, 1920
Sciaenochromis Eccles & Trewavas, 1989
Stigmatochromis Eccles & Trewavas, 1989
Taeniochromis Eccles & Trewavas, 1989
Taeniolethrinops Eccles & Trewavas, 1989
Tilapia Smith, 1840

Table 3.2 (cont.): List of the fish genera and families found in Lake Malawi [Compiled using Ribbink *et al.* (1983) and Konings (1990)]

FISH FAMILIES AND GENERA
Cichlidae
Tramitichromis Eccles & Trewavas, 1989
Trematocranus Trewavas, 1935
Tyrannochromis Eccles & Trewavas, 1989
Anguillidae
Anguilla Schrank, 1798
Aplocheilidae
Nothobranchius Peters, 1868
Bagridae
Bagrus Bosc, 1816
Characidae
Brycinus Valenciennes, 1849
Clariidae
Bathyclarias Jackson, 1959
Clarias Scopoli, 1777
Cyprinidae
Barbus Cuvier & Cloquet, 1861
Cheilobarbus Smith, 1841
Labeo Cuvier, 1817
Opsaridium Peters, 1854
Pseudobarbus Smith, 1841
Mochokidae
Chiloglanis Peters, 1868
Synodontis Cuvier, 1816
Mormyridae
Marcusenius Gill, 1862
Mormyrops Müller, 1843
Mormyrus Linnaeus, 1758
Petrocephalus Marcusen, 1854
Poeciliidae
Aplocheilichthys Bleeker, 1863

Chapter 4

The Morphology of the Ergasilids

In this chapter the morphology of the three main genera is discussed. The general morphology of the genus *Ergasilus* is discussed followed by short descriptions of the remaining two genera *Paraergasilus* and *Dermoergasilus*. The study of the ergasilids in Africa has been underway for over a hundred years, and though all the species discussed in this chapter are members of the same family, the terminology used at the time when each species was described differs. In order to ensure that there is no confusion when comparing the species, the author standardised the terminology mainly following the work of Ho *et al.* (1992), El-Rashidy & Boxshall (2001a) and Boxshall *et al.* (2002). This was done by grouping the different features into three main body regions, i.e. the cephalic, thoracic and abdominal regions.

4.1 The Cephalic Region

This region comprises the cephalothorax with the antennulae, antennae and mouthparts. The antennulae are reduced sensory structures, which in the free-living forms are larger and have a more functional role and are therefore more developed. The antennae are highly developed attachment organs, the presence of which is one of the main features of the representatives of the Ergasilidae. The mouthparts are very difficult to study without the adequate equipment. Because of this, the mouthparts of many of the African species have not been described.

Cephalothorax - The form of the cephalothorax differs between the various *Ergasilus* species, in all the species it consists of the cephalic and the first thoracic segment. The cephalic segment (Fig. 4.1) varies in shape and size, from a triangular form in *E. cunningtoni* Capart, 1944 to a quadrangular form in *E. megachier* (Sars, 1909) (Figs. 5.2A and 5.15A). The thoracic segment may be either separate (*E. cunningtoni*) or fused (*E. macrodactylus* (Sars, 1909) to the cephalic segment (Figs. 5.2A and 5.12A). The presence of a fusion between these segments suggests a more advanced body form. This is due to the fact that in the developing stages of most species the two segments are initially separate from each other becoming fused once reaching maturity (*E. macrodactylus*) as in Fig. 5.12A. It is generally the assumption that body forms present in larval stages are less developed than those in the mature stage, therefore if an adult shares characters with this 'less advanced' larval stage it is seen as a more primitive species. There are various forms of ornamentation to be found on the cephalothorax. Most are present in the region of the cephalic segment.

One of the most visible structures is the inverted T of chitinous material (Fig. 4.1). In all species with this structure the inverted T is situated in the centre of the cephalic segment. Anterior to the inverted T is a large circular cephalic structure (Fig. 4.1) and posterior to the inverted T is a oval cephalic structure (Fig. 4.1). When viewed laterally, using SEM technology, both of these structures seem to bulge outwards. Unlike the inverted T, which seems to have a supporting role, these markings do not appear to have a function. Both of these structures may be absent (*E. latus* Fryer, 1960), or only one present (*E. kandti* van Douwe, 1912) (Figs. 5.10A and 5.6A).

Some of the species described in this dissertation possess extra cephalic markings, two small slightly oval structures on the anterior margin of the cephalic segment. Unlike the previous structures these are not visible using light microscopy, they can only be viewed using the SEM. There are also many sensory setae and sensory pits present on the cephalothorax, these are tiny and can only be observed using SEM. Due to this fact they have only been described from *E. mirabilis* Oldewage & van As, 1987 (Fig. 5.18A) and from no other African species, so it is unknown whether the presence or absence of the sensory pits and setae differ between species. The final feature on the cephalothorax using light microscopy is the eyespot (Fig. 4.1). These are situated anterior to the circular cephalic structure and can be pigmented in various colours depending on the species. For example the eyespot in *Ergasilus* sp. A is a dark purple colour, and the eyespot from *Ergasilus* sp. B is a bright blue colour.

Figure 4.1

A line drawing of a generalised ergasilid

A. Antenna

AB. Abdomen

AN. Antennule

CC. Circular cephalic structure

CS. Cephalic segment

E. Eyespot

ES. Egg sac

FR. Furcal rami

FS. Furcal setae

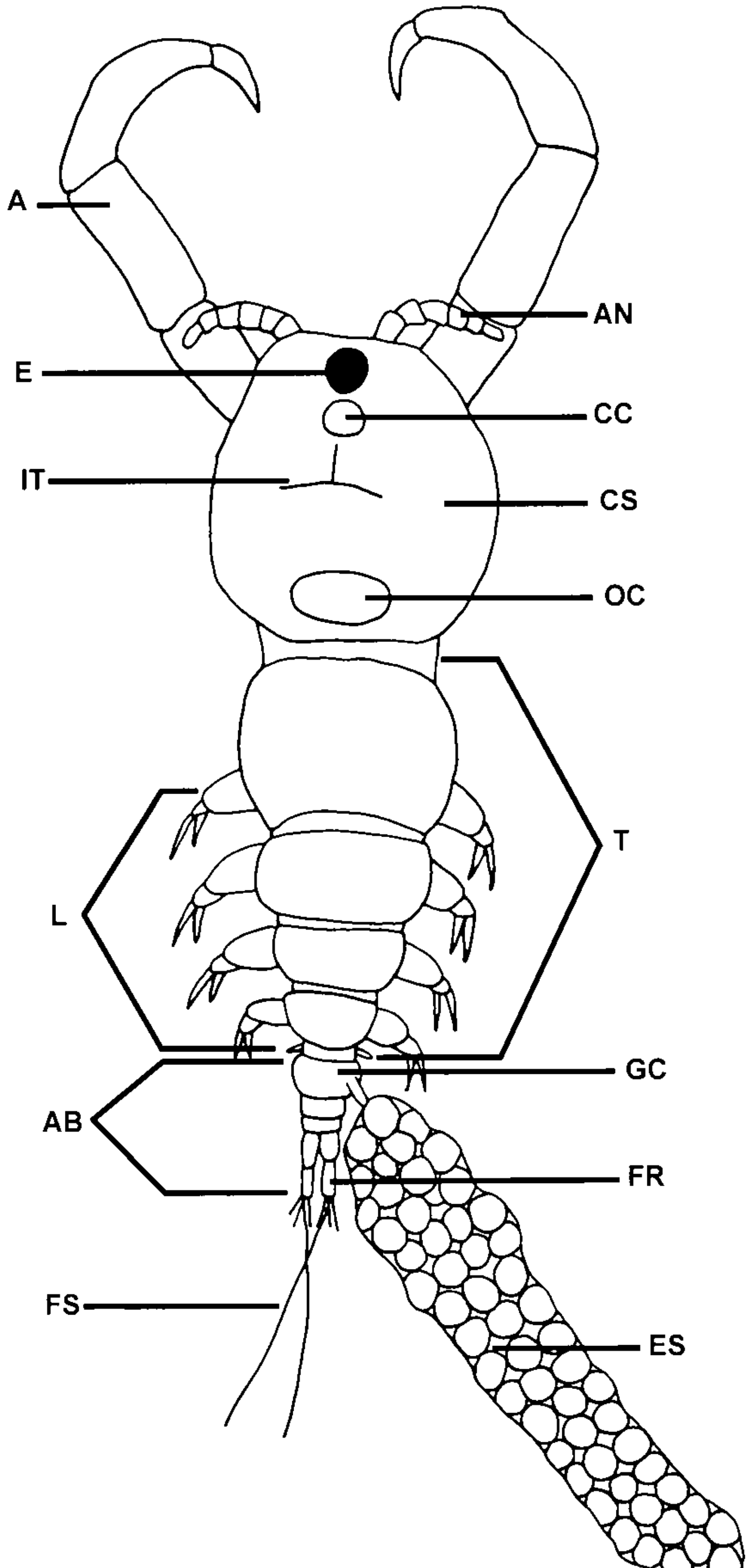
GC. Genital complex

IT. Inverted T-structure

L. Legs 1-5

OC. Oval cephalic structure

T. Thorax


A
AN
E
CC
IT
CS
OC
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GC
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FR
FS
ES

Antennule (Fig 4.1) – The primitive copepod antennule is uniramous and made up of twenty-eight segments, with each segment bearing different numbers of setae. Due to their parasitic life the ergasilids have extremely reduced antennulae, which have developed into small sensory appendages situated on the anterior margin of the cephalothorax. They can be either five-segmented (*E. kandti*) or six-segmented (*E. lamellifer* Fryer, 1961). Each segment possesses a certain number of setae depending on the species. In all the African species except *E. nodosus* Wilson, 1928 these setae are unadorned, whereas *E. nodosus* possesses two plumose setae on the fourth segment (Fig. 5.21C).

Antenna (Fig. 4.1) – The copepods generally possess a biramous antenna with a two-segmented protopod, comprising the coxa and basis, from which a ten-segmented exopod and a four-segmented endopod arise. Each of these segments possess different numbers of setae. The antennae of the *Ergasilus* species have lost many segments, becoming uniramous, four-segmented appendages. The antennae have evolved into highly developed attachment organs to keep the organism's position on the host's gill filaments. The basic form can be seen in *E. latus* where there are four unadorned segments (Fig. 5.10E), the final distal segment forming a sharp sclerotinised 'claw' to aid in clasping the gill filaments. Many species have developed characteristic additional features onto this basic form that can be used in species identification. Some of these additional features are blade-like lamellae (*E. lamellifer*), sharp spines (*E. kandti* and *E. megachier*) and swollen joints (*E. nodosus*) (Figs. 5.8C, 5.16A-C and 5.21A).

Mouthparts – The mouthparts are situated on the ventral side of the cephalothorax. These are not visible when viewed while the specimen is alive because they are covered by the large labrum, and consist of paired mandibles, maxillulae and maxillae. When viewed laterally the mouth opening is directed posteriorly. The mandibles are situated directly below the labrum on both sides of the mouth opening, and are reduced to a single segment. This terminates into a number of blades, armed with teeth along the anterior and posterior margins. The number of blades present is species specific.

The maxillulae are situated posterior to the mandibles and have been reduced to a single segment. Most species bear two distal setae and a small medial process. The positioning and armament of the setae and medial process is also species specific. The maxillae are two-segmented and are situated posterior to the maxillulae. The most proximal segment is the syncoxa; the second segment is called the basis, which is armed with many rows of sharp teeth and spinules.

4.2 The Thoracic Region

Thorax (Fig. 4.1) - The thorax comprises five segments with each segment gradually decreasing in width and length posteriorly. When viewed dorsally using SEM it can be seen that each segment possesses a number of sensory setae and pits. When viewed ventrally each segment has a group of spines and sensory setae situated anterior to the intercoxal bar. In many species the fifth segment is much reduced, is not visible dorsally and does not possess a visible chitinous segment.

Legs (Fig. 4.2) - Each thoracic segment possesses a pair of legs (Fig. 4.1). Each leg has two basal segments the coxa and basis (Fig. 4.2). The coxa attaches to the ventral side of the thorax. Legs one to four are biramous, with an exopodite and endopodite attached to the basis. In all the species the rami are three-segmented, except for the exopod of leg four which is two-segmented. The presence and distribution of spines and setae on the segments are species dependent, with differing numbers of each found on different species. The fifth leg is extremely reduced to a single-segmented appendage (*E. kandti*) or double-segmented appendage (*E. lamellifer*) see (Fig. 5.8B). The number of setae on either segment differs between the various species.

Figure 4.2

Line drawing of a generalised ergasilid leg.

B. Basis

C. Coxa

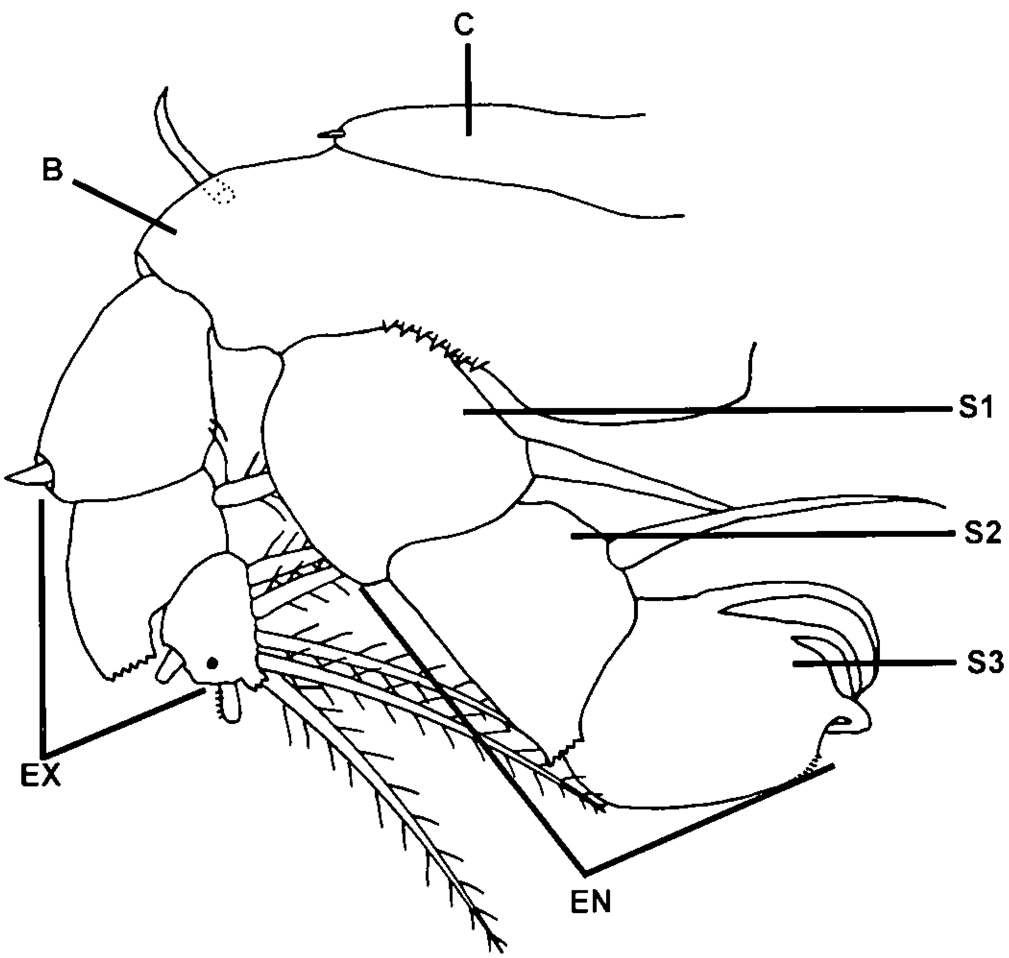
EN. Endopod

EX. Exopod

S1. Segment 1

S2. Segment 2

S3. Segment 3


C
B
S1
S2
S3
EX
EN

4.3 The Abdominal Region

This region comprises the abdominal segments and the furcal rami (Fig. 4.1). The most anterior abdominal segment has developed into the genital complex, which carries the egg sacs.

Genital complex (Fig. 4.1) - The genital complex is generally as large as the remaining abdominal segments combined, and is rather wider than long in most species. The egg sacs are situated on the dorsal side of the segment. Many species also possess a varying number of pectinate spines on the ventral side of this segment.

Egg Sacs (Fig. 4.1)- The shape and form of the egg sacs vary between the different species, they can be as long as the entire body (*E. flaccidus* Fryer, 1965) or only a fraction of the body length (*E. sarsi* Capart, 1944) (Fig. 5.23A). The number of eggs in each sac also differs between the species, with as many as 120 to 130 eggs in a sac (*E. nodosus*) (Fig. 5.21A). The pigmentation of the egg sacs differ between the various species, but seeing that many of the African species were described using preserved material, it has not been used as an indicative feature.

Free Abdominal Segments – The free abdominal segments decrease in width towards the posterior end, with the last segment being bi-lobed. The presence and positioning of the spines on the abdominal segments differs between the species.

Furcal rami (Fig. 4.1) – The furcal rami are simple structures. Some species possess spines and sensory pits on the posterior margin. All possess furcal setae (Fig. 4.1) numbering between three and five on each furcal rami, with the inner seta considerably longer than the others. Most of the African species have unadorned furcal setae with the exception of *E. nodosus* where the furcal setae are plumose (Fig. 5.21A).

4.4 Spines, Setae and Scale Varieties

In the past the definitions of the spines, setae and scales were very vague, with most studies ignoring the shape and form of these structures. The most reliable definitions were found in Watling (1989):

Seta: an articulated cuticular extension of practically any size and shape, the length can either be very small (10µm) or very large (1mm or more) and often possesses a very wide base.
Spine: a non-articulated cuticular extension with a base that is often not as wide as the spine length, spines do not possess sockets regardless of their size or shape.
Scale: a non-articulated cuticular extension with a base that is often very wide when compared to its length, the scales are often armed with tiny spine-like projections.

These definitions are probably very dependent on the type of crustacean being studied. Many of the spines and setae found on the specimens during this study do not necessarily fit these definitions with many spines originating from a socket. There were three major types of setae found during this study; the plumose setae (Fig. 4.3A) on the legs, unadorned setae with a socket (Fig. 4.3B) situated on the dorsal surface of the thorax and cephalothorax. The unadorned setae without a socket (Fig. 4.3C) are very fine and found in groups on the margins of the legs. Four different types of spine were found; an unadorned spine (Fig. 4.3D) situated on the legs and dorsal surface of the thorax and cephalothorax, the second type is the blade-like spine, with very small and sharp spines along its inner margin (Fig. 4.3E). There are two very similar types of spines, the only way to differentiate between the two is by the basal width and the spacing between each spine. The first (Fig. 4.3F) has a very narrow base and the spines are situated very close to each other, while the second (Fig. 4.3G) has a much wider base and the spaces between them are larger. There are three different types of scales; the first two are small and tooth-like. The first and smallest (Fig. 4.3H) is as wide as it is long and can be found on the dorsal surface of the legs, thorax and abdomen. The second (Fig. 4.3I) is longer than the previous and is only found on the dorsal surfaces of the thorax and abdomen. The third type of scale (Fig. 4.3J) is much larger than the previous, but is rounded with small spines on its posterior margin.

4.5 A Comparison between *Ergasilus* von Nordmann, 1832, *Paraergasilus* Markewitsch, 1937 and *Dermoergasilus* Ho & Do, 1982

As has been mentioned at the beginning of the chapter, the genus *Ergasilus* (Fig. 4.4A) was proposed by von Nordmann (1832). The next addition to the Ergasilidae was the genus *Paraergasilus* (Fig. 4.4C), which was established by Markewitsch (1937) to accommodate *Paraergasilus rylovi* Markevitsch, 1937, which was collected in the Caspian Sea. Then in 1982 the genus *Dermoergasilus* (Fig. 4.4B) was proposed by Ho & Do (1982) for *Ergasilus amplectans* Dogiel & Akhemerov, 1952. The males in all three genera are free living. The morphology of the parasitic female form of *Dermoergasilus* and *Paraergasilus* will be briefly discussed.

The general body form of species of *Paraergasilus* is similar to the members of the other two genera, but is much smaller in total body length. In many species the cephalothorax is very swollen and bulbous, comprising a fused cephalic segment as well as the first thoracic segment. The thoracic segments decrease in width posteriorly, with a very small fifth thoracic segment. The abdomen is three to four-segmented depending on the species. The furcal rami usually equals the length of the last abdominal segment, ending in varying numbers of setae, depending on the species. The antennulae are five-segmented, and the antennae are three or four segmented ending in three terminal claws which are used for attachment to the host. The mouthparts are similar to those of the members of *Ergasilus*. Legs one to four are of the same form as those of the *Ergasilus* species, biramous, all rami are three-segmented excluding the two-segmented exopod of leg four. Leg five is extremely small with a single segment bearing differing numbers of setae.

The body form of the *Dermoergasilus* species is similar to that of members of the genus *Ergasilus*, with an inflated cephalothorax, which covers the first leg-bearing thoracic segment as in the *Ergasilus* species. The thoracic segments are distinct, decreasing posteriorly in width; the fifth thoracic segment is extremely small and inconspicuous. The abdomen comprises two to three small segments (depending on the species). The furcal rami are small, with one terminal digitiform process, two short setae and one long seta. The antennulae are five- or six-segmented varying between the species. The antennae are four-segmented and are covered by a loose, hyaline cuticular membrane of various lengths depending on the species. The mouthparts of members of *Dermoergasilus* are similar to those of *Ergasilus* species. Legs one to four are of the same form as the *Ergasilus* species, i.e. biramous, all rami are three-segmented excluding the two-segmented exopod of leg four. Leg five is in the form of a single segment bearing three setae.

Figure 4.3

Line drawings of different forms of setae, spines and scales of ergasilids.

A. Plumose seta

B. Unadorned seta with a socket

C. Unadorned seta without a socket

D. Unadorned spine

E. Blade-like spine

F. Spines with a narrow base

G. Spines with a wider base

H. Small tooth-like scales, length equal to the basal width

I. Large tooth-like scales, length greater than the basal width

J. Large plate-like scales with small tooth-like projections on the projected end

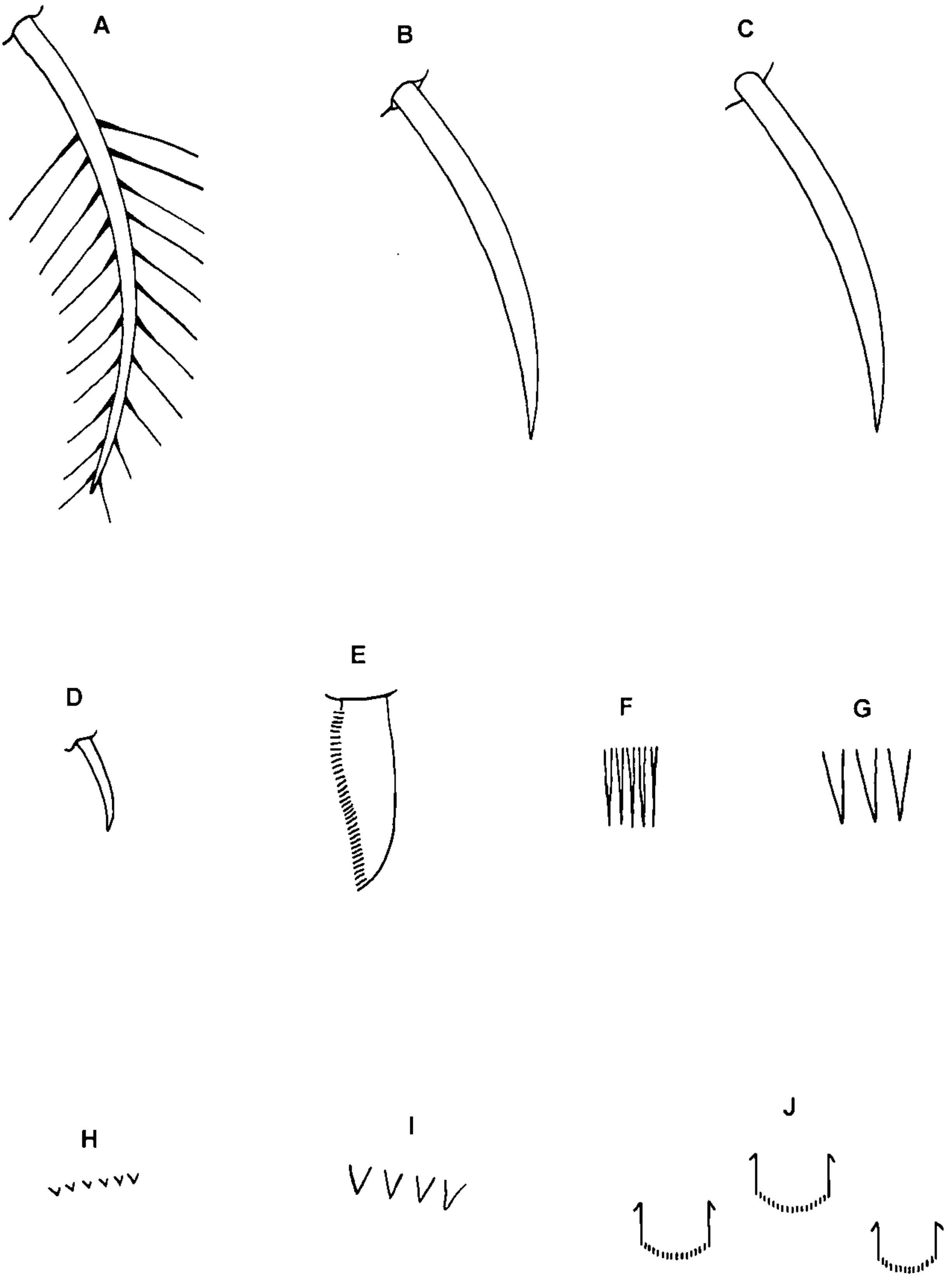

A
B
C
D
E
F
G
H
I
J

Figure 4.4

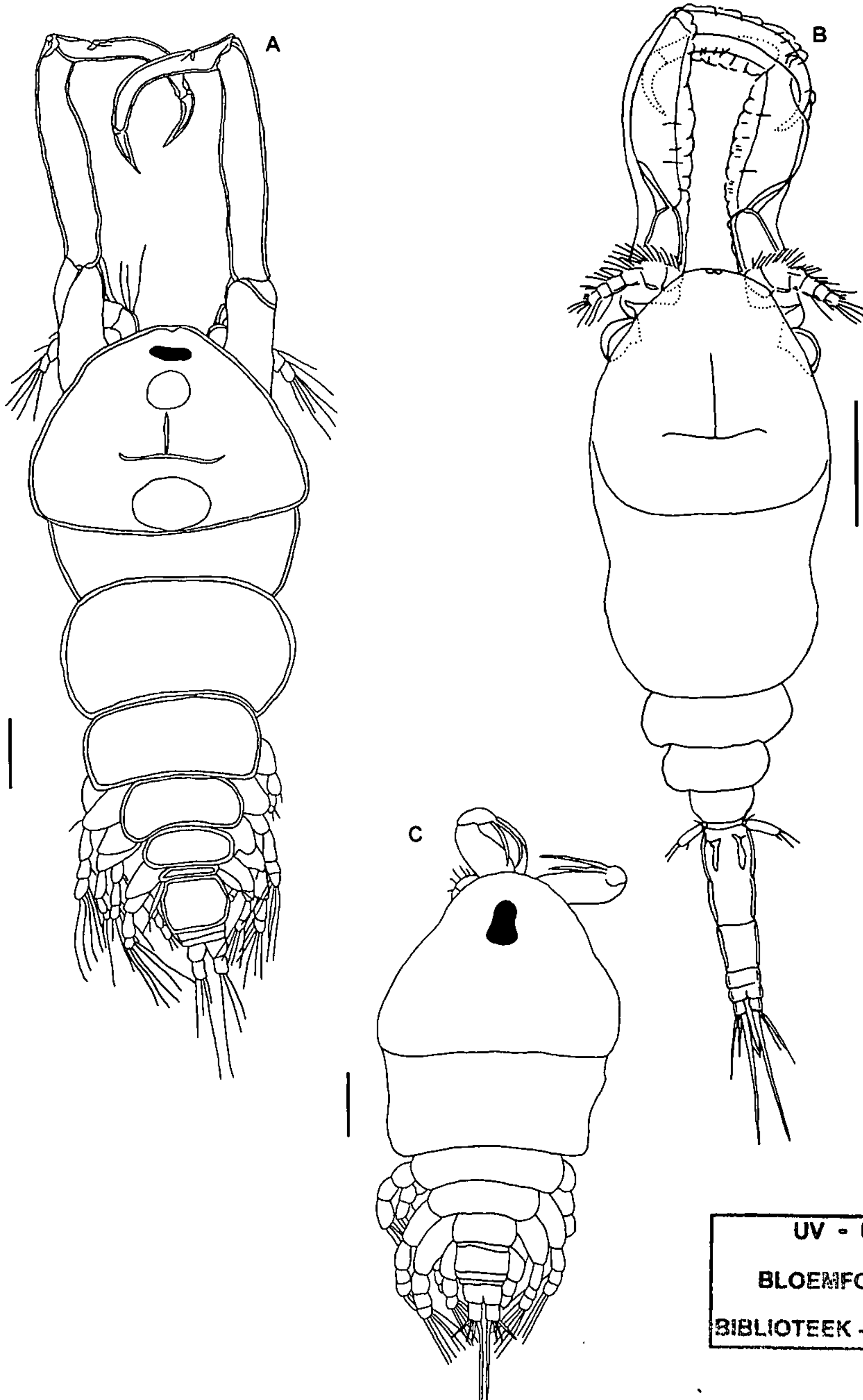
Line drawings of examples of the three African ergasilid genera dealt with in this study.

A. *Ergasilus cunningtoni* Capart, 1944

B. *Dermoergasilus semiamplectens* Ho & Do, 1982

C. *Paraergasilus minutus* (Fryer, 1956)

[A redrawn from Capart (1944), B from El-Rashidy & Boxshall (2001b) and C from Fryer (1956)] Scale bars – 100µm.


A
B
C

Chapter 5

Literature Study of the African Freshwater Ergasilids

5.1 The History of the Freshwater Ergasilids in Africa

During the 1800's the study of the free-living and parasitic crustaceans of the freshwater systems of Africa was largely ignored. Most of the studies conducted in the lakes and river systems of Africa were conducted as major expeditions funded by European museums. These specimens were given to different scientists to examine for copepod parasites. During these expeditions the main areas of study were the lakes of the rift valley, the Congo River and its tributaries, the Niger River, the Volta River and the Nile River.

The first studies were conducted between 1900 and 1928 in Lakes Tanganyika, Victoria, Malawi and Albert (Sars 1909, van Douwe 1912, Cunnington 1920 and Gurney 1928). These studies uncovered three new African species, i.e. *E. megacheir*, *E. macrodactylus* and *E. kandti*. Sars (1909) was the first to discover *Ergasilus* species in Africa; he placed these species into a new genus *Ergasiloides* (Sars, 1909). This genus was found invalid by Fryer (1968), because Sars described his two new species from the last free-living stage; these species now belong to the genus *Ergasilus*.

Over approximately 40 years between 1920 and the late 1960's, the emphasis of many scientific studies moved to the large river systems. Only one study was conducted on the copepods of the White Nile by Wilson (1928) where the fourth African species, *E. nodosus* was discovered. Being the largest African river the Congo River attracted a lot of attention, this is not surprising because the fish and their parasites of large regions of the system are yet undiscovered. The copepods of the Congo River were studied by Wilson (1920), Capart (1944) and Fryer (1963, 1964, 1967) where *E. cunningtoni* and *E. sarsi* were first described. The Niger River was the next major river system to be sampled, in which many known ergasilid species were found to occur (Capart 1956).

In the 1960's the emphasis shifted back to the lakes of the rift valley with studies being conducted in Lakes Albert, Edward, Kivu, Malawi, Rudolf, Tanganyika and Victoria (Fryer 1956, 1960, 1961, 1965). While collecting material from these lakes three new *Ergasilus* and one *Paraergasilus* species were discovered. The *Ergasilus* species were the following; *E. latus* from Lake Rudolf, *E. lamellifer* from the Victoria Nile and *E. flaccidus* from Lake Tanganyika. When Fryer discovered the *Paraergasilus* species from Lake Malawi he placed it under a new genus *Trigasilus* Fryer, 1956, which was later changed to *Paraergasilus* in Fryer (1968) and *P. minutus* (Fryer, 1956), which was also the first species of this genus to be found in Africa.

The last collections from West African rivers were undertaken in the late 60's and 70's. A study on the parasitic crustaceans of the Volta River Basin and southern Ghana unearthed the second *Paraergasilus* species, *P. lagoonaris* Paperna, 1969 (Paperna 1969). Shotter (1977) undertook the last study of the West African rivers by sampling the Niger River where he found many species of *Ergasilus* and a single *Paraergasilus* species in new localities and on new hosts.

The first *Ergasilus* species found in southern Africa is *E. mirabilis* which was collected from the Pongola River System (Oldewage & van As 1987). This species was collected again in 1994 during a sampling study in Lake Kariba, Zimbabwe by Douëllou & Erlwanger (1994).

The ergasilids are a group of parasites that occur throughout Africa, unfortunately because of the lack of interest in the study of these parasites over the last thirty years their true diversity has not yet been established. The African ergasilids are definitely not host specific, all the known host species, their localities and the ergasilids that parasitise them have been summarised in Table 5.1. The fish species that have experienced recent name changes have been included in Table 5.2.

Table 5.1: List of all the fish hosts, locations and freshwater ergasilid species by which they are parasitised

HOSTS	LOCATION													ERGASILID SPECIES											
	Congo System	Peshi Lagoon	Niger System	Pongola System	Volta System	Zambezi System	Nile River	Lake Albert	Lake Malawi	Lake Tanganyika	Lake Turkana	Lake Victoria	Lake Volta	*E. cunningtoni* Capart, 1944	*E. flaccidus* Fryer, 1965	*E. kandti* van Douwe, 1912	*E. lamellifer* Fryer, 1961	*E. latus* Fryer, 1960	*E. macrodactylus* (Sars, 1909)	*E. megachier* (Sars, 1909)	*E. mirabilis* Oldewage & van As, 1987	*E. nodosus* Wilson, 1928	*E. sarsi* Capart, 1944	*P. lagoonaris* Paperna 1969	*P. minutus* (Fryer, 1956)
Alestiidae																									
Brycinus imberi (Peters, 1852)									x										x						
B. leusiscus (Günther, 1867)			x										x	x											
B. nurse (Rüppel, 1832)			x										x	x											
Bagridae																									
Auchenoglanis occidentalis (Valenciennes, 1840)			x															x							
Bagrus bajad (Forsskål, 1775)							x	x								x						x			
Centropomidae																									
Lates niloticus (Linneaus, 1758)			x					x					x			x									
Characidae																									
Hydrocynus vittatus (Castelnau, 1861)			x											x											
Cichlidae																									
Astatoreochromis alluaudi Pellegrin, 1904												x					x								
Bathybates fasciatus Boulenger, 1901										x										x					
B. minor Boulenger, 1906										x										x					
Cyphotilapia frontosa (Boulenger, 1906)										x										x					
Haplochromis spp. Hilgendorf, 1888							x		x			x					x		x						
H. guiarti (Pellegrin, 1904)												x					x								
H. longirostris (Hilgendorf, 1888)												x					x								
H. moeruensis (Boulenger, 1899)	x																						x		
Cichlidae (cont.)																									
H. nuchisquamulatus (Hilgendorf, 1888)												x					x								
H. obesus (Boulenger, 1906)												x					x								
H. obliquidens (Hilgendorf, 1888)												x					x								
Haplotaxodon microlepis Boulenger, 1906										x										x					

Table 5.1 (cont.): List of all the fish hosts, locations and freshwater ergasilid species by which they are parasitised

HOSTS	LOCATION													ERGASILID SPECIES											
	Congo System	Peshi Lagoon	Niger System	Pongola System	Volta System	Zambezi System	Nile River	Lake Albert	Lake Malawi	Lake Tanganyika	Lake Turkana	Lake Victoria	Lake Volta	*E. cunningtoni* Capart, 1944	*E. flaccidus* Fryer, 1965	*E. kandti* van Douwe, 1912	*E. lamellifer* Fryer, 1961	*E. latus* Fryer, 1960	*E. macrodactylus* (Sars, 1909)	*E. megachier* (Sars, 1909)	*E. mirabilis* Oldewage & van As, 1987	*E. nodosus* Wilson, 1928	*E. sarsi* Capart, 1944	*P. lagoonaris* Paperna 1969	*P. minutus* (Fryer, 1956)
Cichlidae (cont.)																									
Hoplotilapia retrodens (Hilgendorf, 1888)												x					x								
Lamprologus lemairii Boulenger, 1899										x						x									
Lethrinops sp Regan, 1922									x										x						
Limnotilapia dardenii (Boulenger, 1899)										x						x				x					
Macropleurodus bicolor (Boulenger, 1906)												x					x								
Oreochromis niloticus niloticus (Linnaeus, 1758)			x															x							
O. tanganicae (Günther, 1894)										x					x	x									
Platytaeniodus degeni Boulenger, 1906												x					x								
Plecodus dardennei Anon.										x										x					
P. paradoxus Boulenger, 1898										x						x									
Petrotilapia tridentiger Trewavas, 1935									x																x
Pseudotropheus spp. Regan, 1922									x										x						
P. tropheops Regan, 1922									x																x
Pseudosimochromis curvifrons (Poll, 1942)										x						x				x					
Pterochromis congicus (Boulenger, 1897)	x													x		x				x					
Sarotherodon galilaeus galilaeus (Linnaeus, 1758)											x							x							
S. melanotheron nigripinnis (Gulchenot, 1861)			x															x							
S. melanotheron heudelotii (Duméril, 1861)		x																x							
Tilapia spp. Smith, 1840									x	x			x			x		x	x						
T. cabrae Boulenger, 1899	x																	x							
T. guineensis (Günther, 1862)		x																x							
T. zillii (Gervais, 1848)			x		x								x					x							
Tylochromis bangwuelensis Regan, 1920	x												x			x							x		

Table 5.1 (cont.): List of all the fish hosts, locations and freshwater ergasilid species by which they are parasitised

HOSTS	LOCATION													ERGASILID SPECIES											
	Congo System	Peshi Lagoon	Niger System	Pongola System	Volta System	Zambezi System	Nile River	Lake Albert	Lake Malawi	Lake Tanganyika	Lake Turkana	Lake Victoria	Lake Volta	*E. cunningtoni* Capart, 1944	*E. flaccidus* Fryer, 1965	*E. kandti* van Douwe, 1912	*E. lamellifer* Fryer, 1961	*E. latus* Fryer, 1960	*E. macrodactylus* (Sars, 1909)	*E. megachier* (Sars, 1909)	*E. mirabilis* Oldewage & van As, 1987	*E. nodosus* Wilson, 1928	*E. sarsi* Capart, 1944	*P. lagoonaris* Paperna 1969	*P. minutus* (Fryer, 1956)
Cichlidae (cont.)																									
T. microdon Regan, 1920	x													x											
T. mylodon Regan, 1920	x															x							x		
T. polylepis (Boulenger, 1900)	x															x									
Citharinidae																									
Citharinus citharus citharus (Geoffroy St. Hilaire, 1808 1809)													x			x									
Distichodus atroventralis Boulenger, 1898	x													x											
D. rostratus Günther, 1864													x	x											
Clariidae																									
Clarias anguillaris (Linnaeus, 1758)			x																				x		
C. gariepinus (Burchell, 1822)					x																		x		
C. ngamensis Castelnau, 1861	x																						x		
Heterobranchus bidorsalis Geoffroy St. Hilaire, 1809			x																				x		
Clupeidae																									
Pellonula leonensis Boulenger, 1916													x	x										x	
Sierrathrissa leonensis Thys van den Audenoerde, 1969			x																					x	
Cyprinidae																									
Barbus macrops Boulenger, 1911			x											x											
Raiamas senegalensis (Steindachner, 1870)			x											x											
Gobiidae																									
Awaous guineensis (Duméril, 1861)		x																						x	
Poeciliidae																									
Aplocheilichthys spp. Bleeker, 1863		x																						x	

Table 5.1 (cont.): List of all the fish hosts, locations and freshwater ergasilid species by which they are parasitised

HOSTS	LOCATION													ERGASILID SPECIES											
	Congo System	Peshi Lagoon	Niger System	Pongola System	Volta System	Zambezi System	Nile River	Lake Albert	Lake Malawi	Lake Tanganyika	Lake Turkana	Lake Victoria	Lake Volta	*E. cunningtoni* Capart, 1944	*E. flaccidus* Fryer, 1965	*E. kandti* van Douwe, 1912	*E. lamellifer* Fryer, 1961	*E. latus* Fryer, 1960	*E. macrodactylus* (Sars, 1909)	*E. megachier* (Sars, 1909)	*E. mirabilis* Oldewage & van As, 1987	*E. nodosus* Wilson, 1928	*E. sarsi* Capart, 1944	*P. lagoonaris* Paperna 1969	*P. minutus* (Fryer, 1956)
Mochokidae (cont.)																									
Hemisynodontis membranaceus (Geoffroy St. Hilaire, 1808-1809)													x			x									
Synodontis granulosus Boulenger, 1900										x										x					
S. leopardinus Pellegrin, 1914				x																	x				
S. multipunctatus Boulenger, 1898										x										x					
S. nigromaculatus Boulenger, 1905	x																						x		
S. nigriventris David, 1935	x													x											
Mormyridae																									
Campylomormyrus elephas (Boulenger, 1898)	x													x											
Hippopotamyrus psittacus (Boulenger, 1897)	x													x											
H. discorhynchus (Peters, 1852)						x															x				
Marcusenius greshoffii (Schilthaus, 1891)	x													x											
M. macrolepidotus (Peters, 1852)	x																						x		
M. moorii (Günther, 1867)	x													x											
Mormyrops anguilloides (Linneaus, 1758)			x											x											
M. nigricans Boulenger, 1899	x													x											
Mormyrus macrophthalmus Günther, 1866			x											x											
Petrocephalus grandoculus Boulenger, 1916	x													x											
Pollimyrus isidori (Valenciennes,1847)	x													x											
Schilbeidae																									
Parailia pellucida (Boulenger, 1901)													x				x								
Schilbe intermedius Rüppell, 1832													x			x									
Schilbe laticeps (Boulenger, 1899)	x													x											
S. mystus (Linnaeus, 1758)			x															x							
S. tumbanus (Pellegrin, 1926)	x													x											

Table 5.2: The invalid and valid names of fish species which have changed since they were referred to in the original papers.

OLD NAME	VALID NAME
Alestes imberi	*Brycinus imberi* (Peters, 1852)
Alestes leusiscus	*Brycinus leusiscus* (Günther, 1867)
Alestes nurse	*Brycinus nurse* (Rüppell, 1852)
Barilius senegalensis	*Raiamas senegalensis* (Steindachner, 1870)
Clarias mellandi	*Clarias ngamensis* Castelnau, 1861
Eutropius laticeps	*Schilbe laticeps* (Boulenger, 1899)
Eutropius tumbanus	*Schilbe tumbanus* (Pellegrin, 1926)
Gnathonemus elephas	*Campylomormyrus elephas* (Boulenger, 1898)
Gnathonemus greshoffi	*Marcusenius greshoffii* (Schilthaus, 1891)
Gnathonemus macrolepidotus	*M. macrolepidotus* (Peters, 1852)
Gnathonemus moorii	*M. moorii* (Günther, 1867)
Lates niloticus albertinus	*Lates niloticus* (Linnaeus, 1758)
Marcusenius isidori	*Pollimyrus isidori* (Valenciennes, 1847)
Marcusenius psittacus	*Hippopotamyrus psittacus* (Boulenger, 1897)
Mormyrops deliciosus	*Mormyrops anguilloides* (Linnaeus, 1758)
Pellonula afzeliusi	*Pellonula leonensis* Boulenger, 1912
Pelmatochromis congicus	*Pterochromis congicus* (Boulenger, 1897)
Simochromis curvifrons	*Pseudosimochromis curvifrons* (Poll, 1942)
Tilapia galilaea	*Sarotherodon galilaeus galilaeus* (Linnaeus, 1758)
Tilapia heudelotii dolloi	*Sarotherodon melanotheron nigripinnis* (Gulchenot, 1861)
Tilapia nilotica	*Oreochromis niloticus niloticus* (Linnaeus, 1758)
Tilapia tanganicae	*Oreochromis tanganicae* (Günther, 1894)
Tylochromis lateralis microdon	*Tylochromis microdon* Regan, 1920

5.2 Descriptions and Distribution Maps of the Known African Ergasilids

Each description is followed by the leg spine-setae formulae, presented in a table, as well as a table of all the known hosts and localities of each species.

Ergasilus cunningtoni Capart, 1944

Collected from three systems on 22 host species (Table 5.4 and Fig. 5.1).

Total Length	0.97mm (Figs. 5.2A&B).
Cephalothorax	Width – 0.42mm, length – 0.55mm. Triangular cephalic region with straight anterior border, arched lateral borders. Clearly marked thoracic region, narrower than cephalic region.
Ornamentation	Two lightly marked regions, anterior region circular, posterior region oval. Visible eyespot, lightly pigmented.
Pigmentation	Preserved material, pigmented yellowish-white.
Mouthparts	Not visible, posterior border of labrum slightly concave.
Thorax	Four well developed thoracic segments, decreasing in length and width. Fifth segment dorsally visible.
Legs	Legs 1-4 characteristic of *Ergasilus* sp (Figs. 5.2C-F), fifth pair reduced to single, long segment, with two setae; two terminal, one lateral (Fig. 5.2G). Spine-seta formulae provided in Table 5.3.
Abdomen	Four-segmented, genital complex wider than long.
Furcal Rami	Three terminal setae, one very long seta, two very short setae.
Antennulae	Six-segmented, with setae on anterior borders.
Antennae	First two segments as long as cephalothorax. Third segment indented on anterior border, indentation formed by two ridges crossing each other, embedded interiorly (Fig. 5.2H).
Egg Sacs	Long, thin, cylindrical.
Attachment to	Attached to distal end of gill filament, often covered by

host	hyperplastic epithelial tissue.
Relationships & Diagnostic features	General form similar to *E. monodi* Brian. Distinguished by antennae, which in *E. monodi* are very thin, short with third segment lacking indentations. Additional differences between *E. monodi* and *E. cunningtoni* are found in body dimensions, cephalothoracic shape, all five pairs of legs. *Ergasilus cunningtoni* with stocky shape, very long antenna with indentation on third segment, fifth thoracic segment visible dorsally, egg sacs cylindrical reaching half total body length.
Type Material	Syntypes: 6E Musée Royal d'Histoire Naturelle de Belgique I.G. No. 12.124.

Table 5.3: Spine-Seta Formula for *Ergasilus cunningtoni* Capart, 1944

	Coxa	Basis		Segment 1	Segment 2	Segment 3
Leg 1	0	1	Exopodite	I – 0	I – 1	II – 5
			Endopodite	0 - 1	0 - 1	II – 4
Leg 2	0	1	Exopodite	I - 0	0 - 1	0 – 6
			Endopodite	0 - 1	0 - 2	I – 4
Leg 3	0	0	Exopodite	I - 0	0 - 1	0 – 4
			Endopodite	0 - 1	0 - 2	1 – 4
Leg 4	0	0	Exopodite	0 - 0	0 - 5	-
			Endopodite	0 – 1	0 - 2	I - 3

Table 5.4: Hosts and Localities for *Ergasilus cunningtoni* Capart, 1944

Locality	Host	Reference
Lake Tumba, Congo System	*Campylomormyrus elephas* (Boulenger, 1898)[1]	Capart (1944)
	**Distichodus atroventralis* Boulenger, 1898	*Fryer (1964)
	**Marcusenius moorii* (Günther, 1867)[1]	°Fryer (1967)
	**M. greshoffi* (Schilthaus, 1891)[1]	
	**Mormyrops nigricans* Boulenger, 1899	
	**Pollimyrus isidori* (Valenciennes, 1847)	
	**Pterochromis congicus* (Boulenger, 1897)[1]	
	**Schilbe laticeps* (Boulenger, 1899)[1]	
	S. tumbanus (Pellegrin, 1926)[1]	
	*°*Tylochromis microdon* Regan, 1920[1]	
Congo System	*Hippopotamyrus psittacus* (Boulenger, 1897)[1]	Fryer (1964)
	Petrocephalus grandoculis Boulenger, 1916	
	Synodontis nigroventris David, 1935	
Galma River, N. Nigeria	*Barbus macrops* Boulenger, 1911	Shotter (1977)
	Brycinus nurse (Rüppel, 1832)[1]	
	Hydrocynus vittatus (Castelnau, 1861)	
	Mormyrops anguilloides (Linnaeus, 1758)[1]	
	Mormyrus macrothalmus Günther, 1866	
	Raiamas senegalensis (Steindachner, 1870)[1]	
Lake Volta, Ghana	*Brycinus leuciscus* (Günther, 1867)[1]	Paperna (1969)
	B. nurse (Rüppel, 1832)[1]	
	Distichodus rostratus Günther, 1864	
	Pellonula leonensis Boulenger, 1916[1]	

[1] Scientific names have changed since this species was recorded as a host (Table 5.2)

*° Indicate the specific papers in which the different host species were recorded

Figure 5.1: Distribution map for *Ergasilus cunningtoni* Capart, 1944. Arrows indicate the different collection sites [Map adapted from Grove (1998), distribution by author].

Figure 5.2

Line drawings of *Ergasilus cunningtoni* Capart, 1944

A. Dorsal view of adult female (100µm)

B. Lateral view of adult female (100µm)

C. Leg 1

D. Leg 2

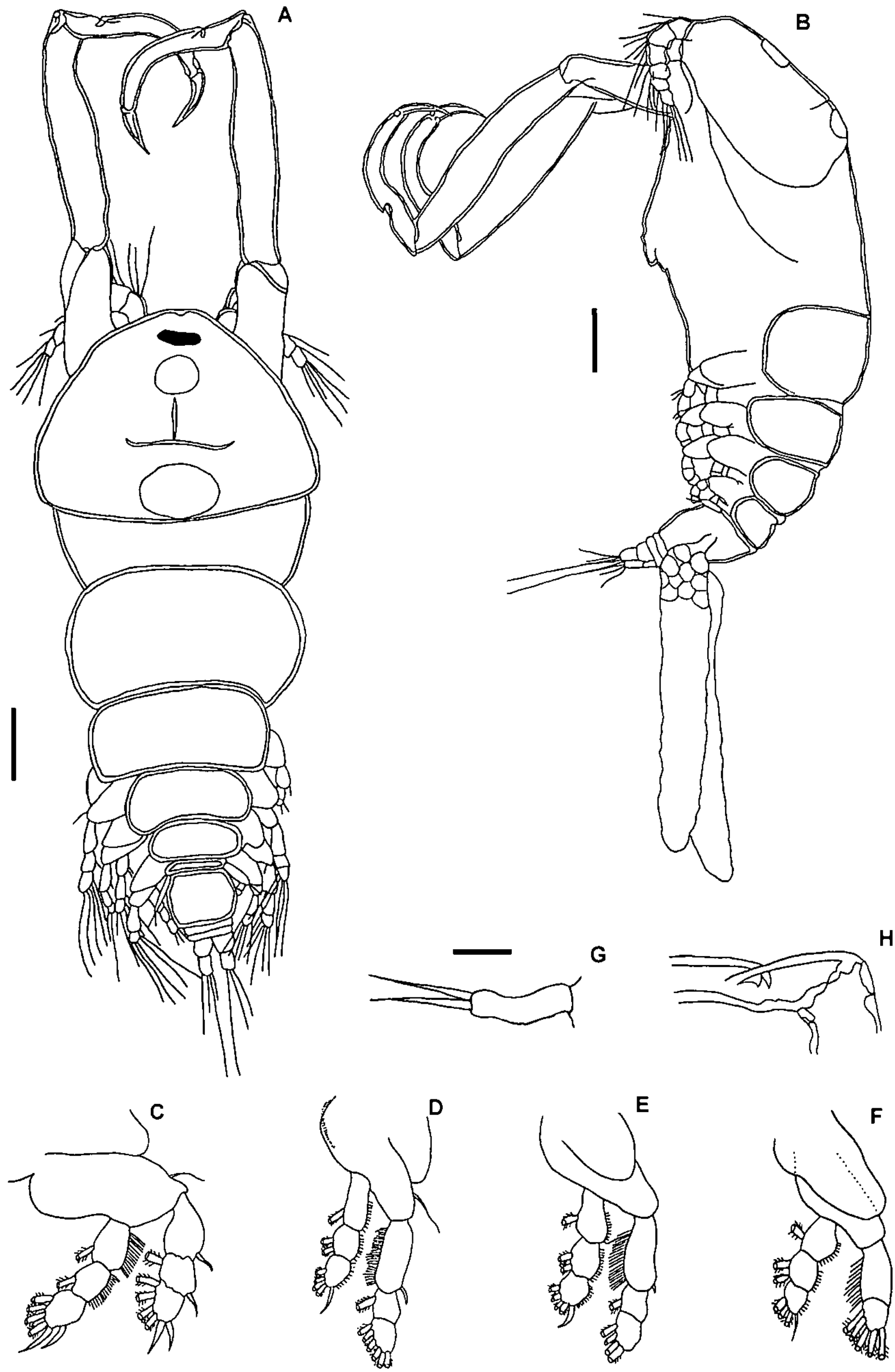
E. Leg 3

F. Leg 4

G. Leg 5 (25µm)

H. Antenna

[Redrawn from Capart (1944)]


A
B
C
D
E
F
G
H

Ergasilus flaccidus Fryer, 1965

Collected from one system on one host species (Table 5.6 and Fig. 5.3).

Total Length	900µm.
Cephalothorax	Longer than wide, bluntly rounded anteriorly.
Ornamentation	Inverted T structure of thickened chitin, medially situated on dorsal side of cephalothorax, anterior of inverted T is an ovoid area of thin cuticle.
Pigmentation	Unknown.
Mouthparts	Unknown.
Thorax	First four thoracic segments distinct, segment five very narrow with no distinctly visible segmented area.
Legs	Only one seta present on second segment of endopod of legs two and three. Leg five located dorsally, not visible ventrally. Two-segmented, very small basal segment with single seta, distal segment with two terminal setae. First terminal seta slender, longer than entire leg, second seta equals length of leg (Fig. 5.4B). Spine-seta formulae provided in Table 5.5.
Abdomen	Four-segmented, genital complex wider than long, bulged laterally, widest region in middle. Final segment with group of four to five spinules ventrally on each side, with minute lateral spine on each side (Fig. 5.4A).
Furcal Rami	Simple, as wide as long, each with arc of 12 fine spinules ventrally, one minute spinule situated laterally. Furcal rami with four terminal setae, innermost seta longest, swollen near proximal region, very indistinctly demarcated from furcal ramus (Fig. 5.4A).
Antennulae	Five-segmented.
Antennae	Prehensile, with small chitinous 'finger' near distal end of second segment. Terminal segment simply curved with thin walled cuticle (Fig. 5.4C).
Egg Sacs	Equals total body length.
Attachment to	Position on gill filaments unknown.

host	
Relationships & Diagnostic features	Characteristic features: five-segmented antennule (only *E. kandti* shares this feature), armature on second segment of antenna, ventral spines on abdomen and furcal rami, absence of a posterior area of thin cuticle on dorsal surface of cephalothorax, distinctive armature of legs two and three. Most African species of this genus possess two setae on these segments.
Type Material	Syntypes of this species are in collection of Institut royal des Sciences naturelles de Belgique, other specimens of the collection are in British Museum of Natural History.

Table 5.5: Spine-Seta Formula for *Ergasilus flaccidus* Fryer, 1965

	Coxa	Basis		Segment 1	Segment 2	Segment 3
Leg 1	-	-	Exopodite	I – 0	I – 1	II – 5
			Endopodite	0 – 1	0 – 1	II – 4
Leg 2	-	-	Exopodite	I – 0	0 – 1	0 – 6
			Endopodite	0 – 1	0 – 1	I – 4
Leg 3	-	-	Exopodite	I – 0	0 – 1	0 – 6
			Endopodite	0 – 1	0 – 1	I – 4
Leg 4	-	-	Exopodite	I – 0	0 - 5	-
			Endopodite	0 - 1	0 – 1	I - 3

Table 5.6: Host and Locality for *Ergasilus flaccidus* Fryer, 1965

Locality	Host	Reference
L. Tanganyika, Congo System	*Oreochromis tanganicae* (Günther, 1894) [1]	Fryer (1965)

[1] Scientific names have changed since this species was recorded as a host (Table 5.2)

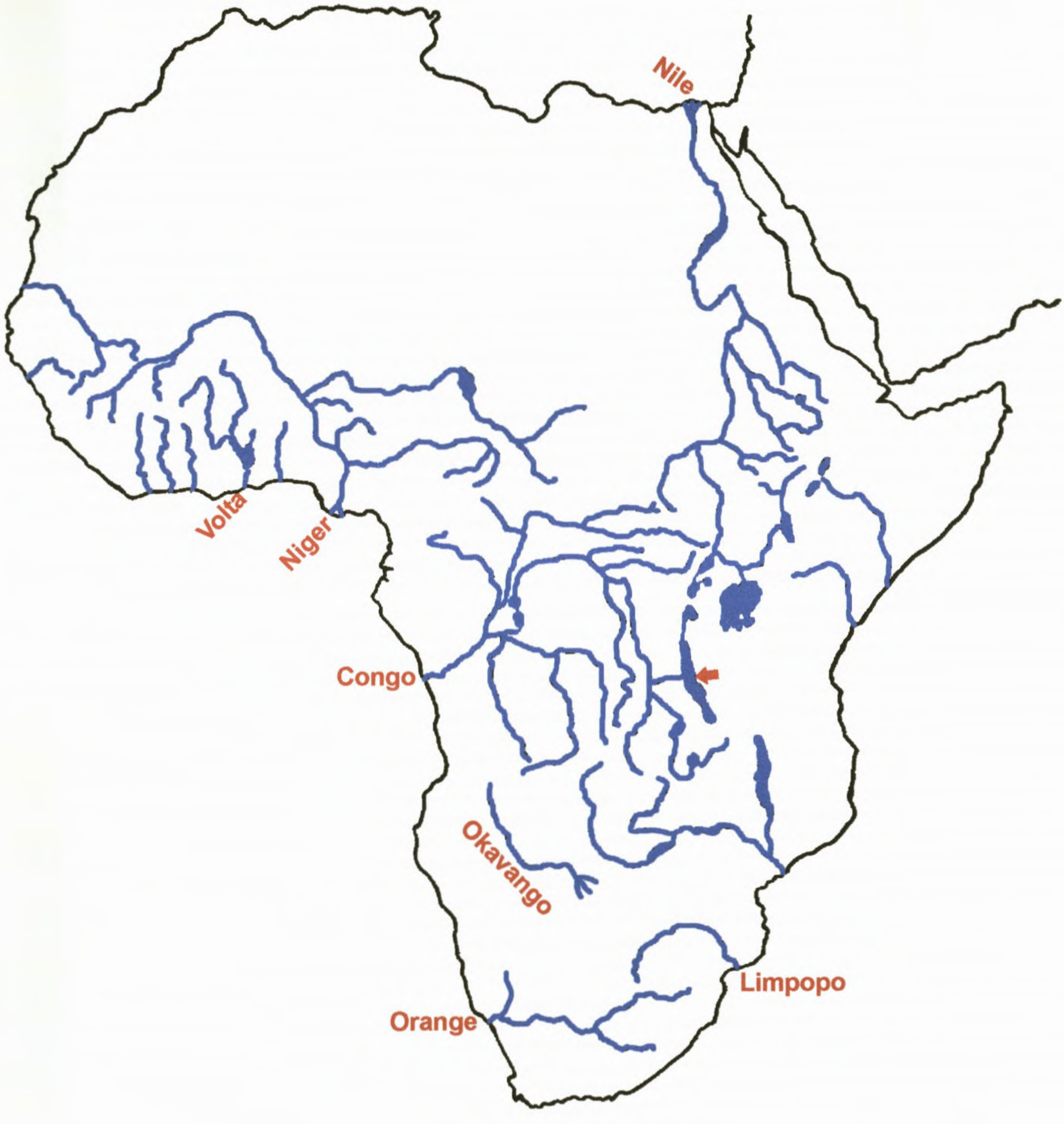


Figure 5.3 : Distribution map for *Ergasilus flaccidus* Fryer, 1965. Arrows indicate the different collection sites [Map adapted from Grove (1998), distribution by author].

Figure 5.4

Line drawings of *Ergasilus flaccidus* Fryer, 1965

A. Ventral view of abdomen (25μm)

B. Leg 5 (25μm)

C. Antenna (100μm)

[Redrawn from Fryer (1965)]


A
B
C

Ergasilus kandti van Douwe, 1912

Collected from five systems and 15 host species (Table 5.8 and Fig. 5.5).

Total Length	0.67mm (Fig. 5.6A).
Cephalothorax	Width – 0.37mm, length – 0.45mm. Elongated pentagon form. First thoracic segment more narrowly fused than cephalic segment. Frontal margin rounded, medially marked by narrow chitinous reinforcement.
Ornamentation	Circular cephalic structure situated anterior to inverted T, no posterior oval structure present.
Pigmentation	Eyespot unpigmented.
Mouthparts	Unknown.
Thorax	Segments two to four decreasing in size. Fifth segment not dorsally visible, fused to anterior margin of genital segment.
Legs	First four pairs well developed, fifth pair reduced, with single short segment. Spine-seta formulae provided in Table 5.7.
Abdomen	Four distinct abdominal segments. Posterior borders of genital and abdominal segments with fringes of fine short bristles (Fig. 5.6B).
Furcal Rami	Square, terminate in two very long setae and two to three short setae (Fig. 5.6B).
Antennulae	Five-segmented, each segment possessing long setae.
Antennae	Equals cephalothoracic length, third segment slightly arched with conical tooth-like projection on distal inner side.
Egg Sacs	Unknown.
Attachment to Host	Unknown placement on gill filament.
Relationships & Diagnostic features	Antennulae consist of five segments, antenna have a characteristic shape, ornamentation of genital and abdominal segments, and furcal bristles unique.

Table 5.7: Spine-Seta Formula for *Ergasilus kandti* van Douwe, 1912

	Coxa	Basis		Segment 1	Segment 2	Segment 3
Leg 1	-	-	Exopodite	I – 0	0 – 1	II – 5
			Endopodite	0 – 1	0 – 1	II – 4
Leg 2	-	-	Exopodite	I*- 0	0 – 1	0 – 6
			Endopodite	0 – 1	0 – 2	I – 4
Leg 3	-	-	Exopodite	0 – 0	0 – 1	0 – 6
			Endopodite	0 – 1	0 – 2	I – 4
Leg 4	-	-	Exopodite	0 – 0	0 – 5	-
			Endopodite	0 - 1	0 – 2	I - 3

* very small spinule

Table 5.8: Hosts and Localities for *Ergasilus kandti* van Douwe, 1912

Locality	Host	Reference
Lake Albert	°**Lates niloticus* (Linneaus, 1758)[1] **Bagrus bayad* (Forsskål, 1775)	°Fryer (1965) *Thurston (1970)
Lake Tumba, Congo System	*Pterochromis congicus* (Boulenger, 1897)[1]	Fryer (1959)
Lake Mweru, Congo System	*Tylochromis mylodon* Regan, 1920 *T. bangwelensis* Regan, 1920 *T. polylepis* (Boulenger, 1900)	Fryer (1967)
Lake volta, Ghana	*Citharinus citharus citharus* (Geoffroy St. Hilaire, 1808-1809) *Hemisynodontis membranaceus* (Geoffroy St. Hilaire, 1808-1809) *Lates niloticus* (Linneaus, 1758)[1] *Schilbe intermedius* Rüppell, 1832	Paperna (1969)
Lake Tanganyika	*Limnotilapia dardenii* (Boulenger, 1899) *Lamprologus lemairii* Boulenger, 1899 *Plecodus paradoxus* Boulenger, 1898 **Pseudosimochromis curvifrons* (Poll, 1942) *Tilapia* spp. Smith, 1840 *Oreochromis tanganicae* (Günther, 1894)[1]	*Capart (1944) Fryer (1965)
Niger River	*Lates niloticus* (Linnaeus, 1758)[1]	Capart (1956)

[1] Scientific names have changed since this species was recorded as a host (Table 5.2)

*° Indicates the specific papers in which the different host species were recorded

Figure 5.5: Distribution map for *Ergasilus kandti* van Douwe, 1912. Arrows indicate the different collection sites [Map adapted from Grove (1998), distribution by author].

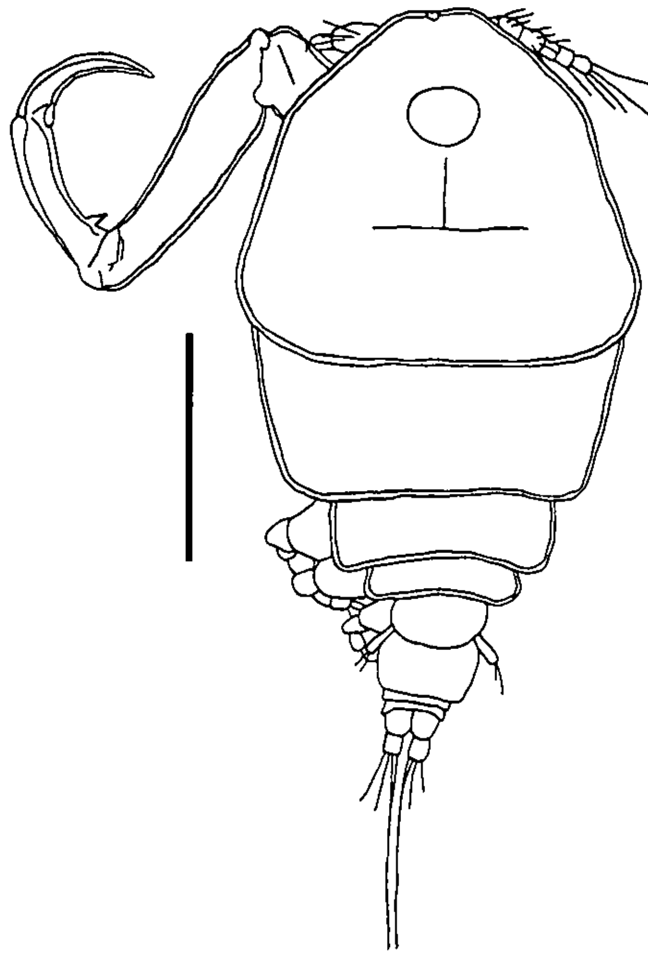
Figure 5.6

Line drawings of *Ergasilus kandti* van Douwe, 1912

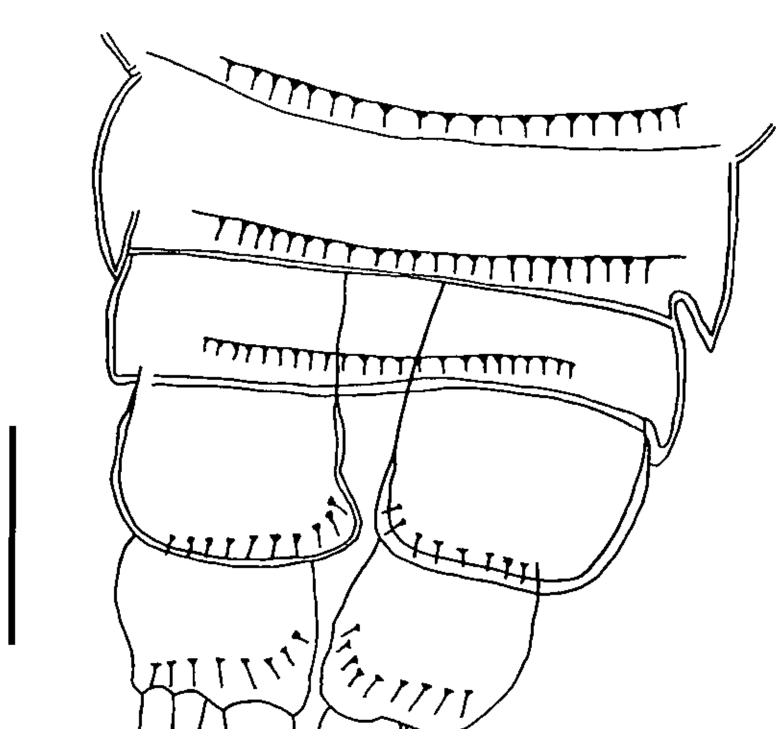
A. Dorsal view of adult female (200µm)

B. Ventral view of abdomen (50µm)

[Redrawn from Capart (1944)]



A



B

Ergasilus lamellifer Fryer, 1961

Collected from two systems and 11 host species (Table 5.10 and Fig. 5.7).

Total Length	850µm.
Cephalothorax	Cephalothorax fused to segment of leg one, longer than wide, bluntly rounded anteriorly, shallowly indented in posterior third.
Ornamentation	Inverted T, anterior to ovoid structure, posterior to circular structure present.
Pigmentation	White in colour, with patches of blue pigment.
Mouthparts	Unknown.
Thorax	Unknown.
Legs	Segments of legs one to five distinct, leg five two-segmented, with minute basal segment. Distal segment with two terminal setae, longest is 1 ½ x length of shortest seta. Basal segment with one small seta (Fig. 5.8B). Spine-seta formulae provided in Table 5.9.
Abdomen	Four-segmented, genital complex wider than long bulged laterally, widest anterior to midsection. Remaining abdominal segments very short (Fig. 5.8A).
Furcal Rami	Simple, 1 ½ x as long as wide with four unjointed terminal setae. Innermost seta longest more than 2 ½ x as long as next seta. Longest seta swollen with a 'kink' near proximal end (Fig. 5.8A).
Antennulae	Six-segmented.
Antennae	Prehensile, four-segmented. Inner margin of segment two with thin, blade-like chitinous lamella (Fig. 5.8C).
Egg Sacs	Long, 75% of body length.
Attachment & Host	Placement on gill filaments unknown.
Relationships & Diagnostic features	Closely related to *E. macrodactylus, E. sarsi, E. kandti* and *E. cunningtoni*. Distinguished by chitinous lamella on segment two of antenna.

Table 5.9: Spine-Seta Formula for *Ergasilus lamellifer* Fryer, 1961

	Coxa	**Basis**		**Segment 1**	**Segment 2**	**Segment 3**
Leg 1	-	-	Exopodite	I - 0	I – 1	II - 5
			Endopodite	0 – 1	0 – 1	II – 4
Leg 2	-	-	Exopodite	0 – 0	0 – 1	0 – 6
			Endopodite	0 – 1	0 – 2	I – 4
Leg 3	-	-	Exopodite	0 – 0	0 – 1	0 – 6
			Endopodite	0 – 1	0 – 2	I – 4
Leg 4	-	-	Exopodite	I*- 0	0 – 5	-
			Endopodite	0 – 1	0 – 2	I – 3

* very small spinule

Table 5.10: Hosts and Localities for *Ergasilus lamellifer* Fryer, 1961

Locality	**Host**	**Reference**
Lake Volta, Ghana	*Parailia pellucida* (Boulenger, 1901)	Paperna (1969)
Lake Victoria & the Victoria Nile	*Astatoreochromis alluaudi* Pellegrin, 1904 **Haplochromis* spp. Hilgendorf, 1888 *H. guiarti* (Pellegrin, 1904) *H. longirostris* (Hilgendorf, 1888) *H. nuchisquamulatus* (Hilgendorf, 1888) *H. obesus* (Boulenger, 1906) *H. obliquidens* (Hilgendorf, 1888) *Haplotilapia retrodens* (Hilgendorf, 1888) *Macropleurodus bicolor* (Boulenger, 1906) *Platytaeniodus degeni* Boulenger, 1906	*Fryer (1961) Thurston (1970)

*° Indicates the specific papers in which the different host species were recorded

Figure 5.7: Distribution map for *Ergasilus lamellifer* Fryer, 1961. Arrows indicate the different collection sites [Map adapted from Grove (1998), distribution by author].

Figure 5.8

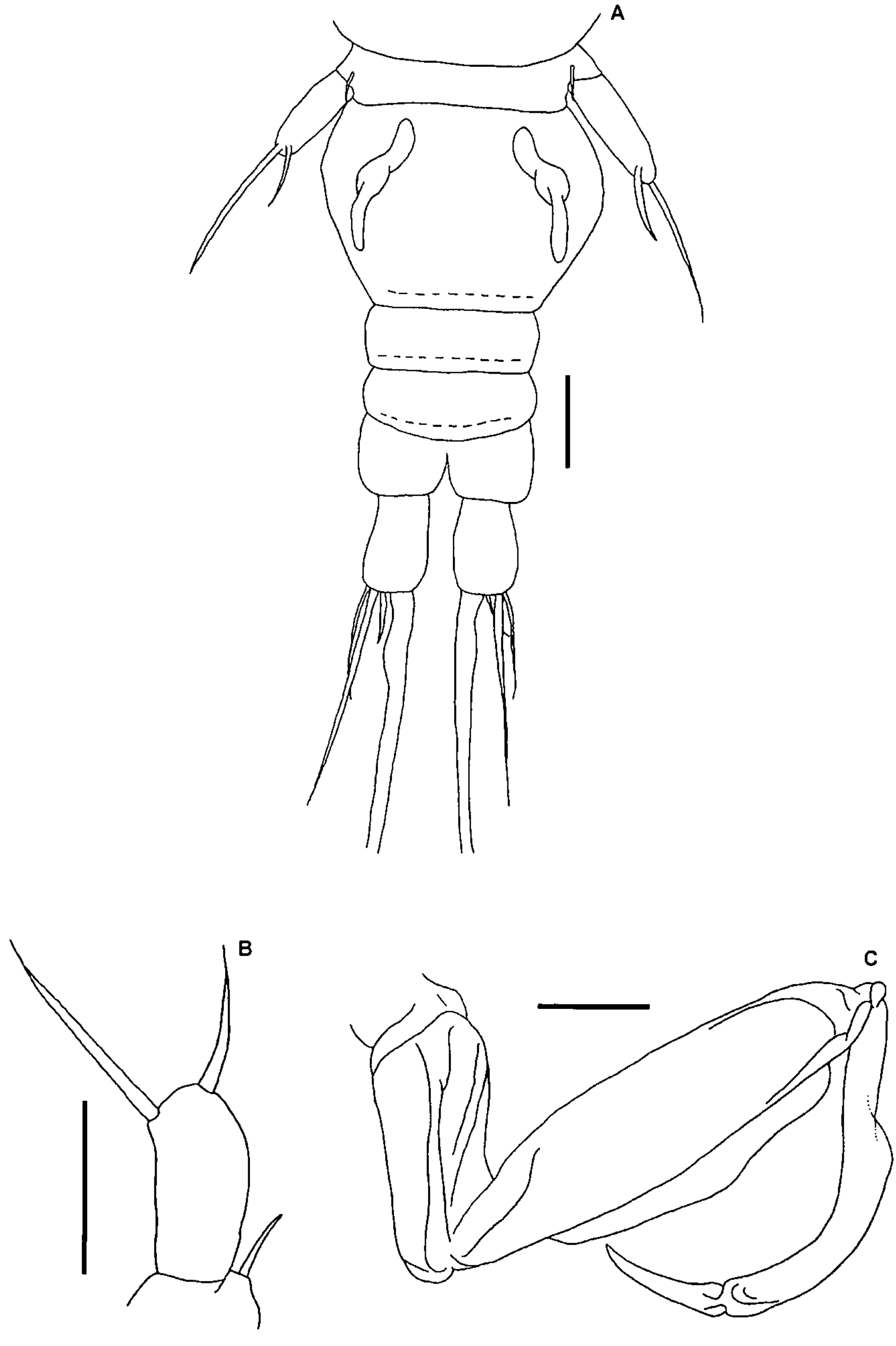
Line drawings of *Ergasilus lamellifer* Fryer, 1961

A. Ventral view of abdomen (25µm)

B. Leg 5 (25µm)

C. Antenna (50µm)

[Redrawn from Fryer (1961)]


A
B
C

Ergasilus latus Fryer, 1960

Collected from four systems and 10 host species (Table 5.12 and Fig. 5.9).

Total Length	900µm (Fig. 5.10A).
Cephalothorax	Cephalothorax fused to segment of leg one, longer than wide, bluntly rounded anteriorly, bulged laterally, shallowly indented in posterior third.
Ornamentation	Inverted T structure present, no other chitinous head structures present.
Pigmentation	Brown colour, with traces of purple pigment present ventrally in cephalothorax.
Mouthparts	Unknown.
Thorax	Unknown.
Legs	Segments of leg one to five distinct, typical of members of genus. Leg five very broad with three setae, two terminal setae as long as entire leg, one shorter lateral seta (Figs. 5.10B&C). Spine-seta formulae provided in Table 5.11.
Abdomen	Four-segmented, genital complex wider than long, bulged laterally, widest in midsection. Remaining abdominal segments very short (Fig. 5.10D).
Furcal Rami	Simple, longer than wide, with five terminal setae, innermost longest. Longest seta with characteristic bend near proximal end.
Antennulae	Six-segmented.
Antennae	Prehensile, long, slender with swollen region on proximal end of third segment (Fig. 5.10E).
Egg Sacs	Long, reaches past longest furcal seta.
Attachment to host	Position on gill filaments unknown.
Relationships & Diagnostic features	Swollen area on proximal end of third antennal segment is similar to *E. nodosus*, but swelling less conspicuous in *E. latus*. Characteristic features: fusion of first segment of leg onewith cephalothorax, arrangement of furcal setae, and very broad fifth leg.

Table 5.11: Spine-Seta Formula for *Ergasilus latus* Fryer, 1960

	Coxa	Basis		Segment 1	Segment 2	Segment 3
Leg 1	-	-	Exopodite	0 – 0	I – 1	II – 5
			Endopodite	0 – 1	0 – 1	II – 4
Leg 2	-	-	Exopodite	0 – 0	0 – 1	0 – 6
			Endopodite	0 – 1	0 – 2	I – 4
Leg 3	-	-	Exopodite	0 – 0	0 – 1	0 – 6
			Endopodite	0 – 1	0 – 2	I – 4
Leg 4	-	-	Exopodite	I – 0	0 – 5	-
			Endopodite	0 - 1	0 - 2	I – 3

Table 5.12: Hosts and Localities for *Ergasilus latus* Fryer, 1960

Locality	Host	Reference
Lake Turkana, Kenya	*Oreochromis niloticus niloticus* (Linnaeus, 1758) [1] *Sarotherodon galilaeus galilaeus* (Linnaeus, 1758)[1]	Fryer (1960)
Volta Basin, Ghana	*Tilapia* spp. Smith, 1840 *T. zillii* (Gervais, 1848) *Oreochromis niloticus niloticus* (Linnaeus, 1758) [1]	Paperna (1969)
Peshi Lagoon, Ghana	*Sarotheradon melanotheron heudelotii* (Duméril, 1861) *Tilapia guineensis* (Günther, 1862)	Paperna (1969)
Galma River, Nigeria	*Auchenoglanis occidentalis* (Valenciennes, 1840) *Oreochromis niloticus niloticus* (Linnaeus, 1758) [1] *Sarotherodon galilaeus galilaeus*(Linnaeus, 1758) [1] *Schilbe mystus* (Linnaeus, 1758) *Tilapia zillii* (Gervais, 1848)	Shotter (1977)
Congo Basin	*Sarotheradon melanotheron nigripinnis* (Gulchenot, 1861) [1] **Tilapia cabrae* Boulenger, 1899	*Fryer (1963) Fryer (1967)

[1] Scientific names have changed since this species was recorded as a host (Table 5.2)
* Indicates the specific papers in which the different host species were recorded

Figure 5.9: Distribution map for *Ergasilus latus* Fryer, 1960. Arrows indicate the different collection sites [Map adapted from Grove (1998), distribution by author].

Figure 5.10

Line drawings of *Ergasilus latus* Fryer, 1960

A. Lateral view of adult female (100µm)

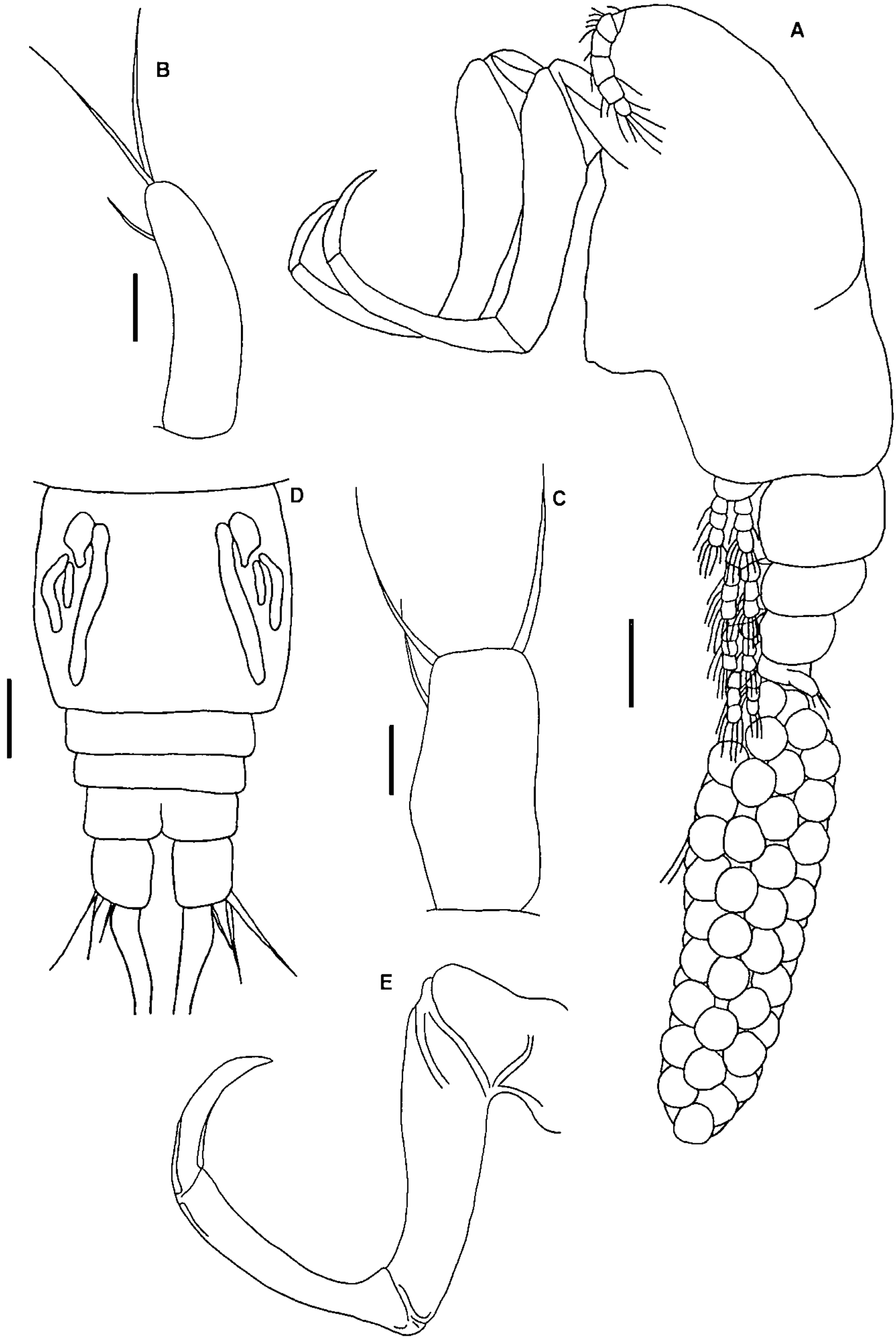
B. Lateral view of Leg 5 (10µm)

C. Dorsal view of Leg 5 (10µm)

D. Ventral view of abdomen (25µm)

E. Antenna

[Redrawn from Fryer (1960)]


A
B
C
D
E

Ergasilus macrodactylus (Sars, 1909)

Collected from one system and five host species (Table 5.14 Fig. 5.11).

Total Length	0.97 –1.0mm (Fig. 5.12A).
Cephalothorax	Cephalothorax fused to first segment of leg one (in adults). Much longer than wide, bluntly rounded anteriorly. Bulged laterally, shallowly indented in posterior third (Figs. 5.12B&C).
Ornamentation	Possesses well-developed eye. Circular cephalic structure anterior to inverted T, with ovoid cephalic structure posterior.
Pigmentation	White with patches of purple ventrally in cephalothorax region.
Mouthparts	Unknown.
Thorax	Segments two to five distinct, evenly rounded at lateral margins. Segment five narrow, but distinct.
Legs	Legs one to four typical of genus. Leg five simple, cylindrical, with two terminal setae (Fig. 5.13B). Spine-seta formula provided in Table 5.13.
Abdomen	Four-segmented, anterior region of genital complex bulged laterally (Fig. 5.13A).
Furcal Rami	Simple, slightly longer than wide, slightly wider posteriorly with four unjointed setae. Innermost furcal seta more than 5x longer than others, directed obliquely outwards, swollen near base (Fig. 5.13A).
Antennulae	Six-segmented.
Antennae	Prehensile, long, slender (Fig. 5.12D).
Egg Sacs	Long, reach beyond furcal setae.
Attachment to Host	Placement on gill filaments unknown.
Relationships & Diagnostic features	*Ergasilus macrodactylus* shares many features with *E. megacheir*, general body form very similar; abdomen of *E. megacheir* more compact. Antenna of *E. megacheir* with terminal spine while antenna of *E. macrodactylus* is unadorned. Leg spine-seta formula differs between species.

Table 5.13: Spine-Seta Formula for *Ergasilus macrodactylus* (Sars, 1909)

	Coxa	Basis		Segment 1	Segment 2	Segment 3
Leg 1	-	-	Exopodite	I - 0	I - 1	II - 5
			Endopodite	0 – 1	0 – 1	II – 4
Leg 2	-	-	Exopodite	1*– 0	0 – 1	0 – 6
			Endopodite	0 – 1	0 – 2	I – 4
Leg 3	-	-	Exopodite	0°– 0	0 – 2	I – 4
			Endopodite	0 – 1	0 – 2	I – 4
Leg 4	-	-	Exopodite	0 - 0	0 – 5	-
			Endopodite	0 – 1	0 - 1	I – 3

* very small spinule ° tiniest of spinules on some specimens

Table 5.14: Hosts and Localities for *Ergasilus macrodactylus* (Sars, 1909)

Locality	Host	Reference
Lake Malawi	*Brycinus imberi* (Peters, 1852)[1] *Haplochromis* spp. Hilgendorf, 1888 *Lethrinops* spp. Regan, 1922 *Pseudotropheus* spp. Regan, 1922 *Tilapia* spp. Smith, 1840	Fryer (1956)

[1] Scientific names have changed since this species was recorded as a host (Table 5.2)

Figure 5.11: Distribution map for *Ergasilus macrodactylus* (Sars, 1909). Arrows indicate the different collection sites [Map adapted from Grove (1998), distribution by author].

Figure 5.12

Line drawings of *Ergasilus macrodactylus* (Sars, 1909)

A. Dorsal view of adult female (100μm)

B. Ventral view of immature cephalothorax

C. Ventral view of mature cephalothorax

D. Antenna (50μm)

[Redrawn from Sars (1909) and Fryer (1956)]

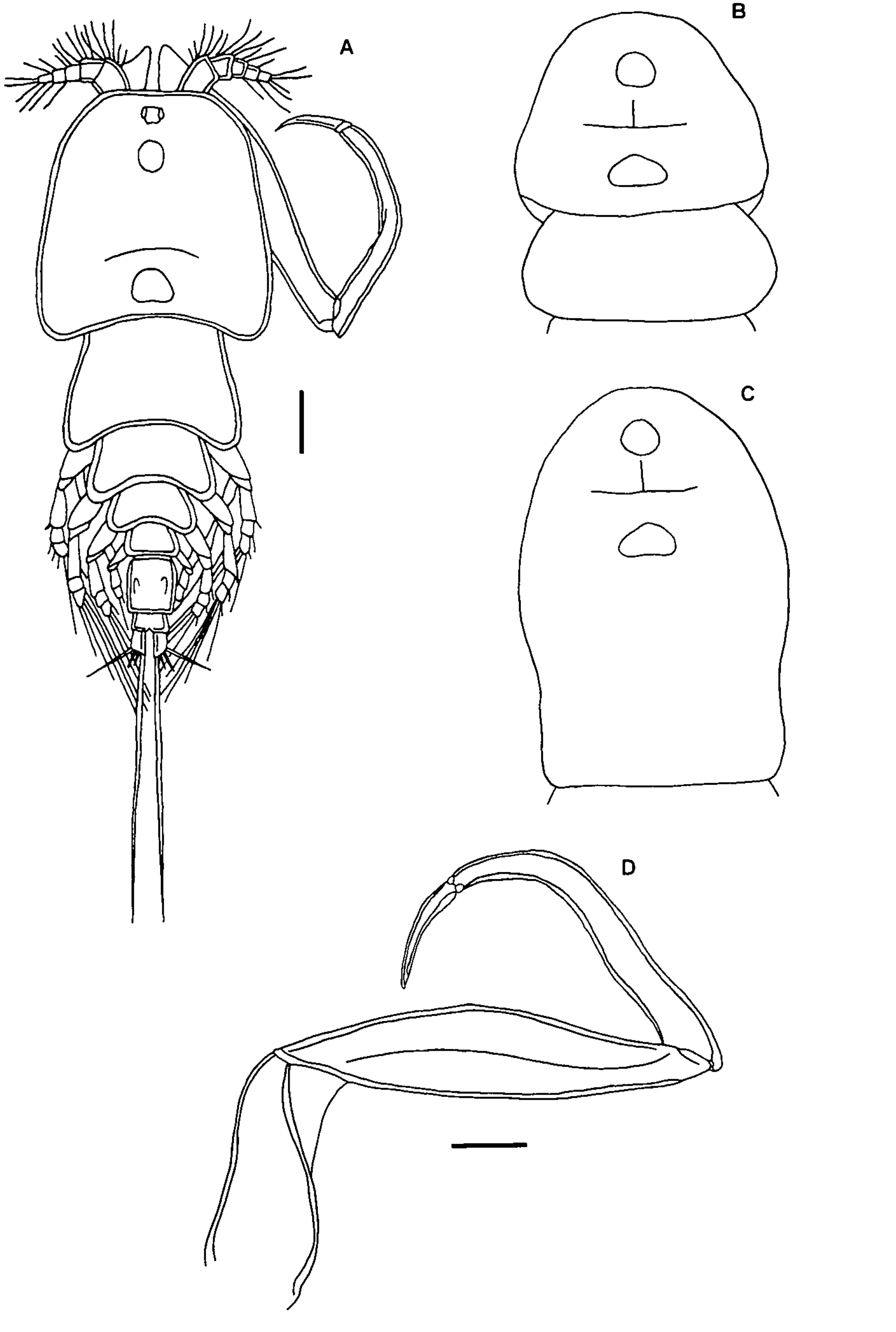

A
B
C
D

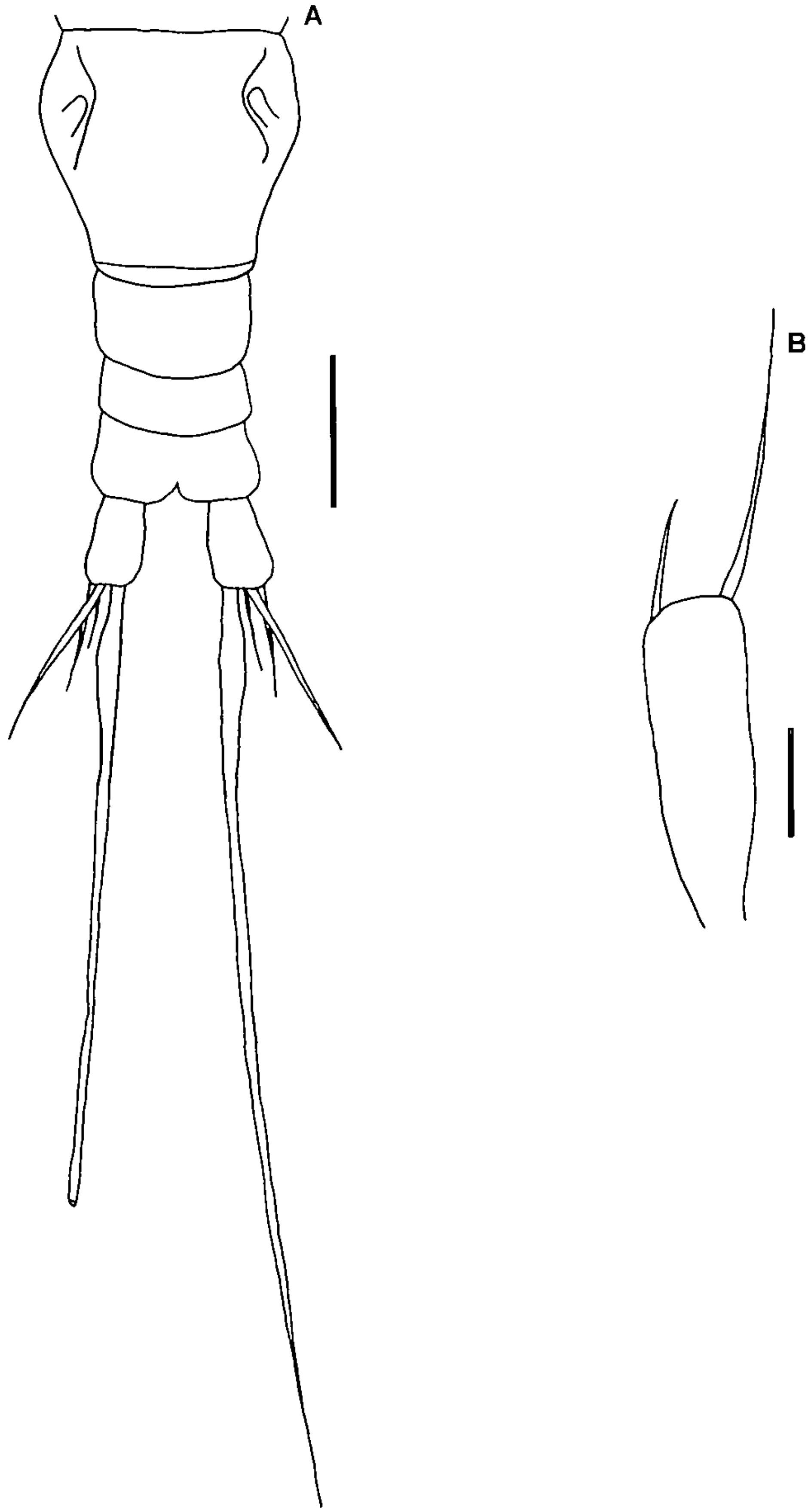
Figure 5.13

Line drawings of *Ergasilus macrodactylus* (Sars, 1909)

A. Ventral view of abdomen (50µm)

B. Leg 5 (10µm)

[Redrawn from Sars (1909) and Fryer (1956)]


A
B

Ergasilus megacheir (Sars, 1909)

Collected from two systems and nine host species (Table 5.16 and Fig. 5.14).

Total Length	0.62mm (Figs. 5.15A&B). Body short, subpyriform in outline when viewed dorsally.
Cephalothorax	Cephalothorax very large, quadrangular in form.
Ornamentation	Inverted T structure present. Both circular and oval cephalic structures present. Frontal margin of cephalic segment transversely truncated, postero-lateral corners only slightly prominent, round.
Pigmentation	Unknown.
Mouthparts	Characteristic of members of genus (Figs. 5.16F-I).
Thorax	First four thoracic segments with lateral regions pointing backwards, obtusely rounded at end. Fifth segment almost entirely concealed.
Legs	Legs one to four with both rami three-segmented, except for two-segmented exopod of fourth pair. Fifth pair extremely small (Figs. 5.15C-F). Spine-seta formula provided in Table 5.15.
Abdomen	1/3 of total body length, genital complex dilated, rounded, oval in form (Fig. 5.16E).
Furcal Rami	Equal length of last abdominal segment, with setae on inner corner simple, pointing straight behind.
Antennulae	Six-segmented (Fig. 5.16D).
Antennae	Very large, second segment twice as long as basal segment, oblong in form. Anterior margin with thin hyaline border, not fully extending to base. Third segment length half of second segment, slightly twisted, terminal claw short with recurved denticle on inner margin (Figs. 5.16A-C).
Egg Sacs	Unknown.
Attachment on Host	Placement on gill filaments unknown.
Relationships & Diagnostic	*Ergasilus megacheir* shares many features with *E. macrodactylus*, general body form very similar, abdomen more

features	elongated in *E. macrodactylus*, antenna of *E. megacheir* with terminal spine while antenna of *E. macrodactylus* is unadorned. Leg spine-seta formula differs between species.

Table 5.15: Spine-Seta Formula for *Ergasilus megacheir* (Sars, 1909)

	Coxa	Basis		Segment 1	Segment 2	Segment 3
Leg 1	-	-	Exopodite	I - 0	I - 1	II - 5
			Endopodite	0 – 1	0 – 1	II – 4
Leg 2	-	-	Exopodite	0 – 0	0 – 1	0 – 6
			Endopodite	0 – 1	0 – 1	I – 4
Leg 3	-	-	Exopodite	0 – 0	0 – 1	0 – 6
			Endopodite	0 – 1	0 – 1	I – 4
Leg 4	-	-	Exopodite	0 - 0	0 – 5	-
			Endopodite	0 – 1	0 - 1	I – 3

Table 5.16: Hosts and Localities for *Ergasilus megacheir* (Sars, 1909)

Locality	Host	Reference
Lake Tumba, Congo System	*Pterochromis congicus* (Boulenger, 1897)	Fryer (1964)
Lake Tanganyika, Congo System	*Bathybates minor* Boulenger, 1906 *B. fasciatus* Boulenger, 1901 *Cyphotilapia frontosa* (Boulenger, 1906) *Haplotaxodon microlepis* Boulenger, 1906 *Limnotilapia dardennii* (Boulenger, 1899) **Pseudosimochromis curvifrons* (Poll, 1942) *Synodontis multipunctatus* Boulenger, 1898 *S. granulosus* Boulenger, 1900	*Capart (1944) Fryer (1965)

* Indicates the specific papers in which the different host species were recorded

Figure 5.14: Distribution map for *Ergasilus megacheir* (Sars, 1909). Arrows indicate the different collection sites [Map adapted from Grove (1998), distribution by author].

Figure 5.15

Line drawings of *Ergasilus megacheir* (Sars, 1909)

- **A.** Dorsal view of adult female (100μm)
- **B.** Lateral view of adult female (100μm)
- **C.** Leg 1
- **D.** Leg 3
- **E.** Leg 4
- **F.** Leg 5

[Redrawn from Sars (1909) and Fryer (1965)]

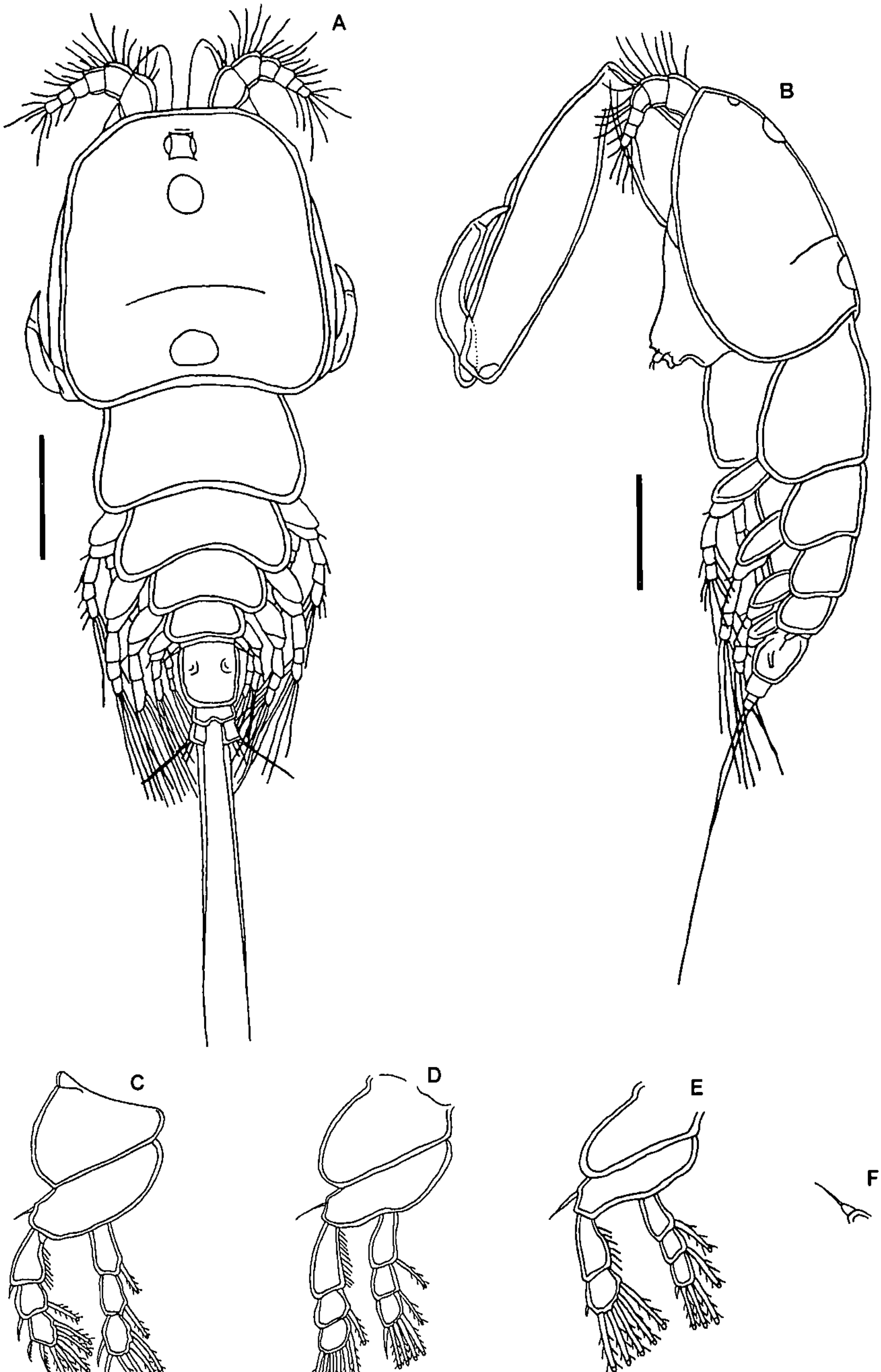

A
B
C
D
E
F

Figure 5.16

Line drawings of *Ergasilus megacheir* (Sars, 1909)

A – C. Antenna (C – 50µm)

D. Antennule (50µm)

E. Ventral view of abdomen (50µm)

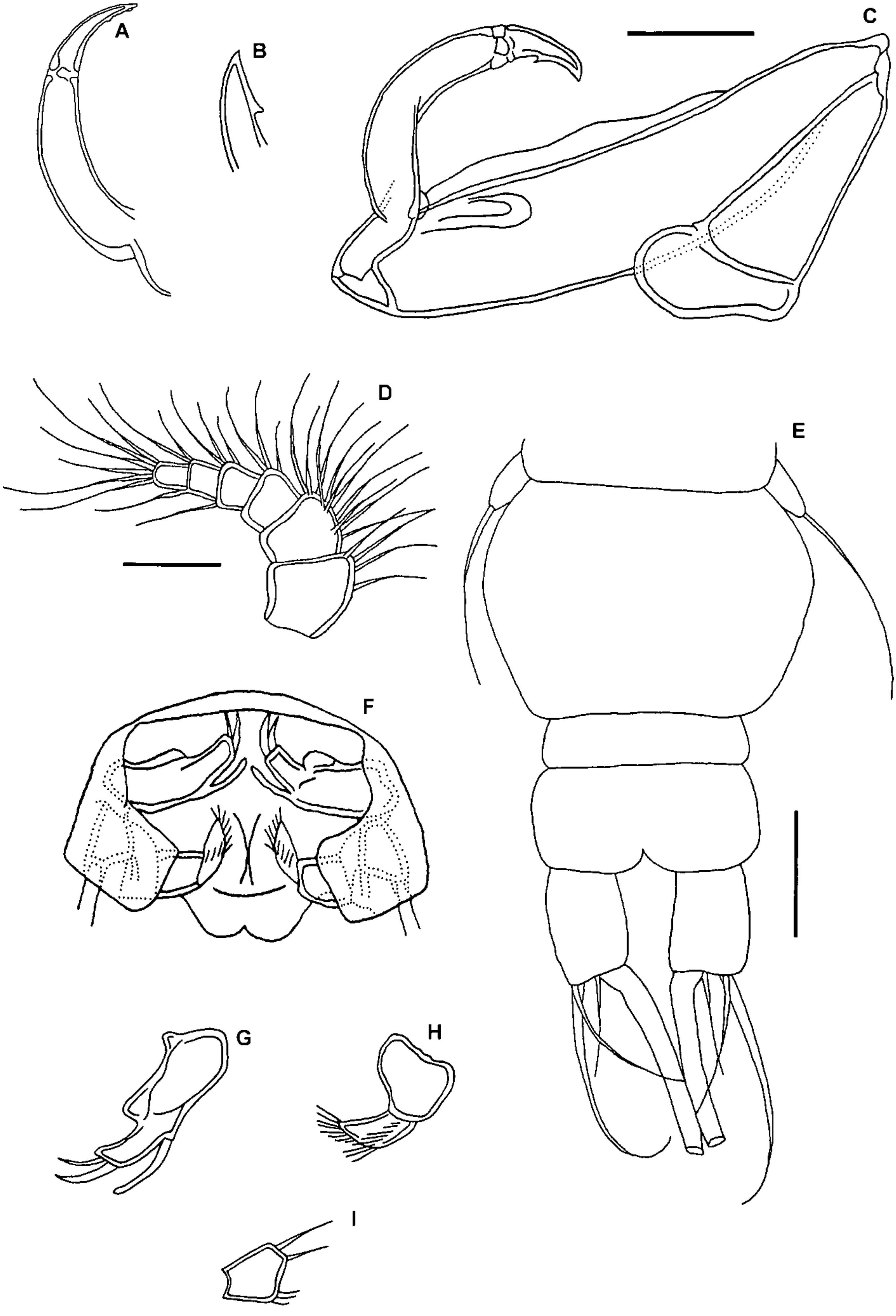
F. Mouthparts

G. Mandible

H. Maxilla

I. Maxillule

[Redrawn from Sars (1909) and Fryer (1965)]


A
B
C
D
E
F
G
H
I

Ergasilus mirabilis Oldewage & van As, 1987

Collected from two systems and two host species (Table 5.18 and Fig. 5.17).

Total Length	930µm (Fig. 5.18A&B).
Cephalothorax	Cephalothoracic segment largest, as long as wide.
Ornamentation	Two dorsal oval structures, anterior and posterior to inverted T pattern. Eyespot situated anteriorly to anterior oval structure. Two sensory pits medially situated between inverted T and anterior structure.
Pigmentation	Unknown.
Mouthparts	Mouth opens posteriorly under ventrally projected, denticulate-edged labrum. Mandible with two spines, stout, 'feathered' terminal spine and similar sub-terminal spine ½ its length. Endopodite single palp 'feathered' ventrally. First maxilla typical for genus. Exopodite with two setae, few bristles, endopodite bearing single seta. Second maxilla three-segmented, with terminal process of spiny bristles, basal bristles, large, single seta. Mouth opens horizontally between first maxillae. Short stout spines present below labrum, between first and second maxilla on basal segments of second maxilla. Mandible and second maxilla oppose each other in buccal cavity. Labium with two lateral glandular projections (Fig. 5.19D).
Thorax	First four thoracic segments progressively smaller and wider than long. Paired sensory setae occur dorsally on segments two to four. Single sensory pits on second and third segments directly anterior to sensory setae. Single row of bristles on posterior ventral edge of segments two to four. Fifth thoracic segment compressed, lacks sensory apparatus.
Legs	Fifth leg single-segmented with two terminal setae (Fig. 5.18C-G). Spine-seta formula provided in Table 5.17.
Abdomen	Four-segmented, segments short. First and second abdominal segments with posterior row of ventral bristles.

	Third segment splits dorso-ventrally with two rows of bristles on posterior, ventral surface of both sides (Fig. 5.19A).
Furcal Rami	Twice as long as wide, with long, stout, median seta, single shorter dorso-lateral seta and two even shorter ventro-lateral setae (Fig. 5.19A).
Antennulae	Six-segmented, originate on anterior periphery of cephalic segment, dorsal to antennae. Seta formula - 0-7-4-2-2-4, terminal segment with tuft of short, fine setules (Fig. 5.19B).
Antennae	Slender, smooth and four-segmented, terminal segment short, curved, pointed, scleritonised (Fig. 5.19C).
Egg Sacs	Egg sacs long, slender.
Attachment to host	Unknown placement on gill filaments.
Relationships & Diagnostic features	Similar in general body form to *Ergasilus* sp. A. Differs from this species by form of antennae, fifth leg and spine-setae formula of legs one to four.
Type Material	Holotype No E86/2/12-1 & 2 Paratypes No E86/2/12-2 & E86/2/12-3 in the collection of the Department of Zoology, Rand Afrikaans University, Johannesburg, South Africa.

Table 5.17: Spine-Seta Formula for *Ergasilus mirabilis* Oldewage & van As, 1987

	Coxa	Basis		Segment 1	Segment 2	Segment 3
Leg 1	-	-	Exopodite	I – 0*	I – 1*	0 – 6*
			Endopodite	0 – 1	0 – 1*	II – 4
Leg 2	-	-	Exopodite	0 – 0*	0 – 1*	0 – 4*
			Endopodite	0 – 1*	0 – 1*	0 – 6*
Leg 3	-	-	Exopodite	I – 0*	I – 1*	0 – 6*
			Endopodite	0 – 1*	0 – 2*	0 – 5*
Leg 4	-	-	Exopodite	I – 0	0 – 5*	
			Endopodite	0 – 0*	0 – 0*	0 – 6*

* very small spinule

Table 5.18: Hosts and Localities for *Ergasilus mirabilis* Oldewage & van As, 1987

Locality	Host	Reference
Pongola System	*Synodontis leopardinus* Pellegrin, 1914	Oldewage & van As (1987)
Lake Kariba, Zambezi System	*Hippopotamyrus discorhynchus* (Peters, 1852)	Douëllou & Erlwanger (1994)

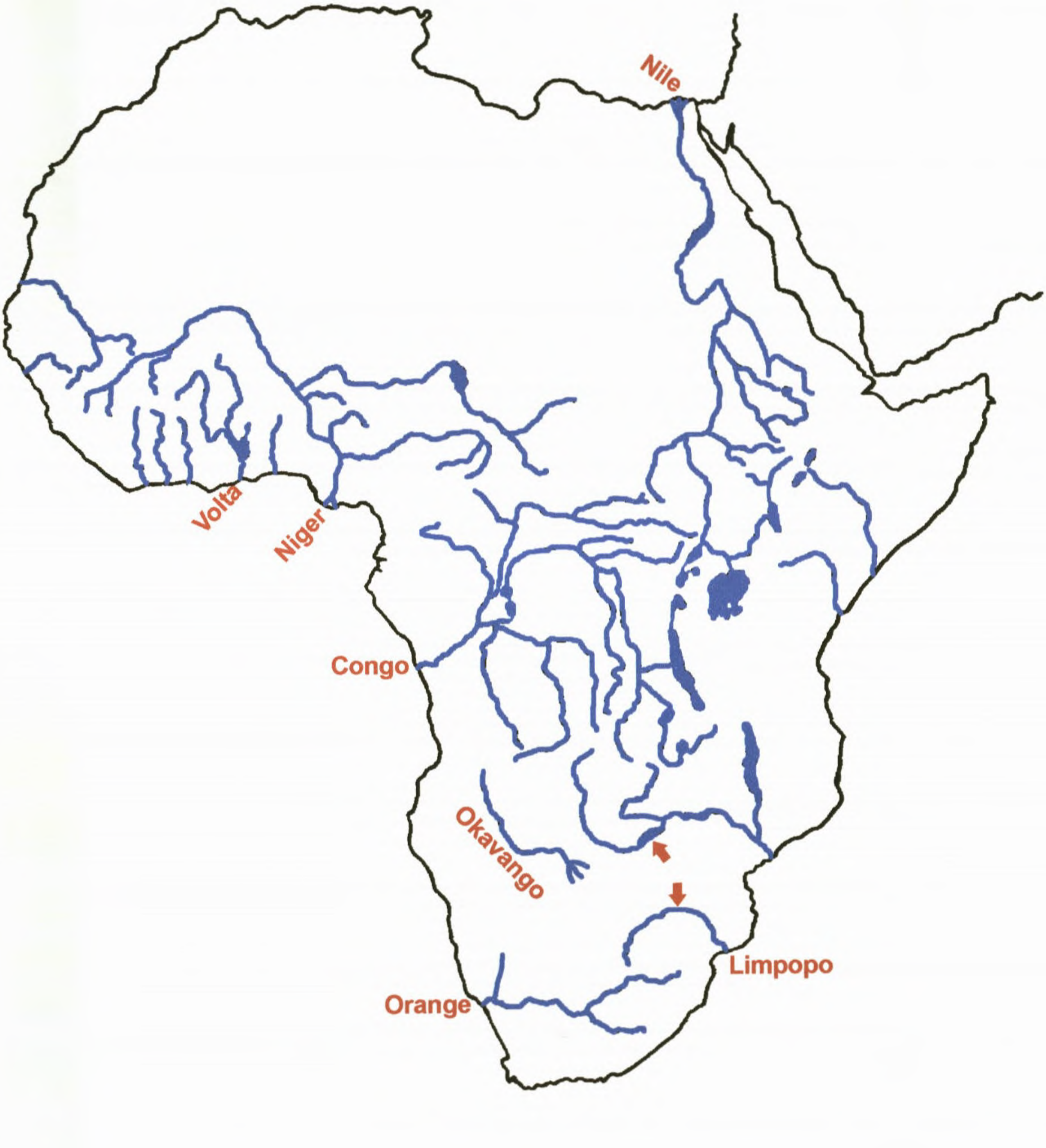


Figure 5.17: Distribution map for *Ergasilus mirabilis* Oldewage & Van As, 1987. Arrows indicate the different collection sites [Map adapted from Grove (1998), distribution by author].

Figure 5.18

Line drawings of *Ergasilus mirabilis* Oldewage & van As, 1987

A. Dorsal view of adult female (100µm)

B. Lateral view of adult female (100µm)

C. Leg 1 (50µm)

D. Leg 2 (50µm)

E. Leg 3 (50µm)

F. Leg 4 (50µm)

G. Leg 5 (25µm)

[Redrawn from Oldewage & van As (1987)]

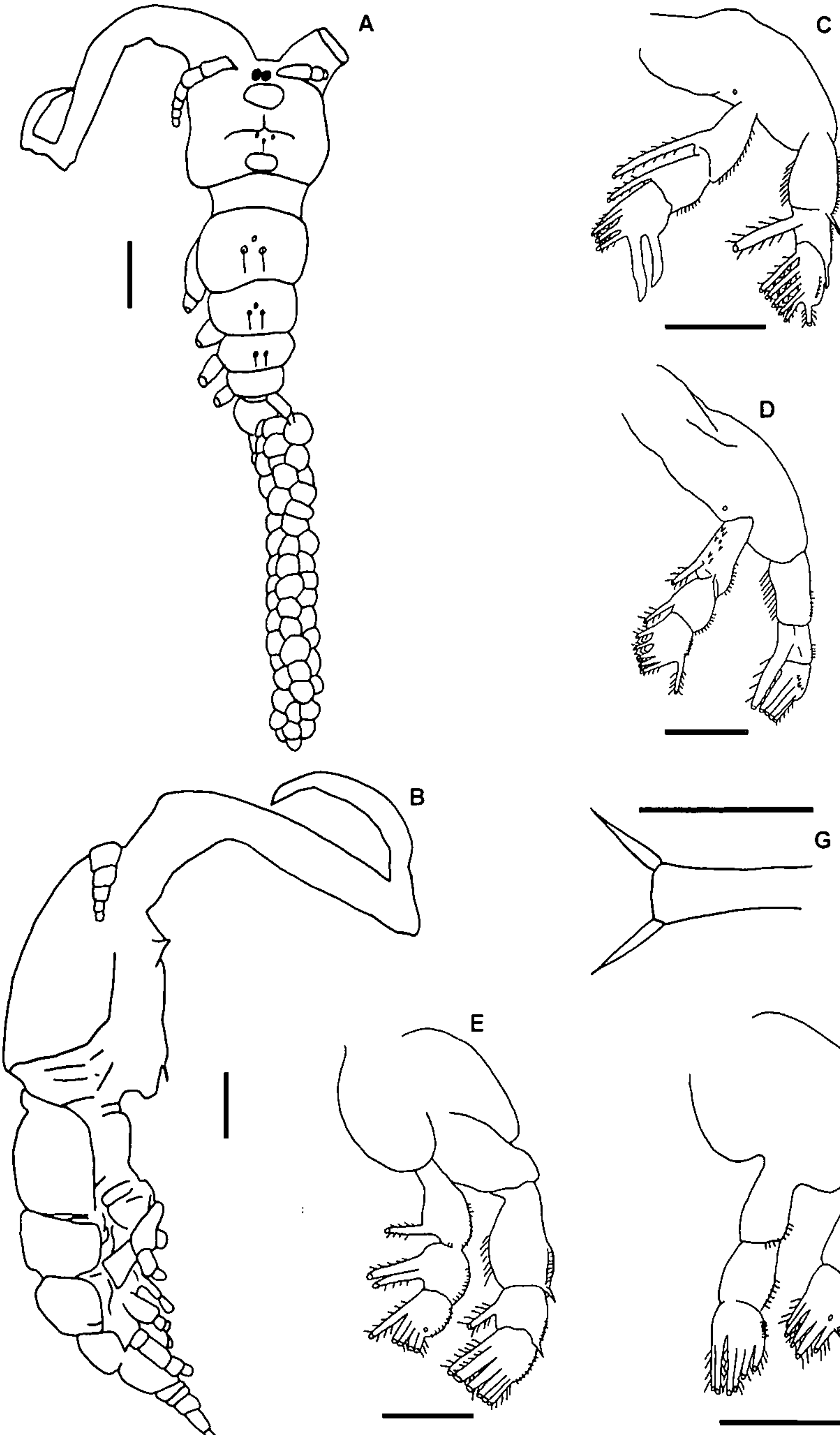

A
B
C
D
E
F
G

Figure 5.19

Line drawings of *Ergasilus mirabilis* Oldewage & van As, 1987

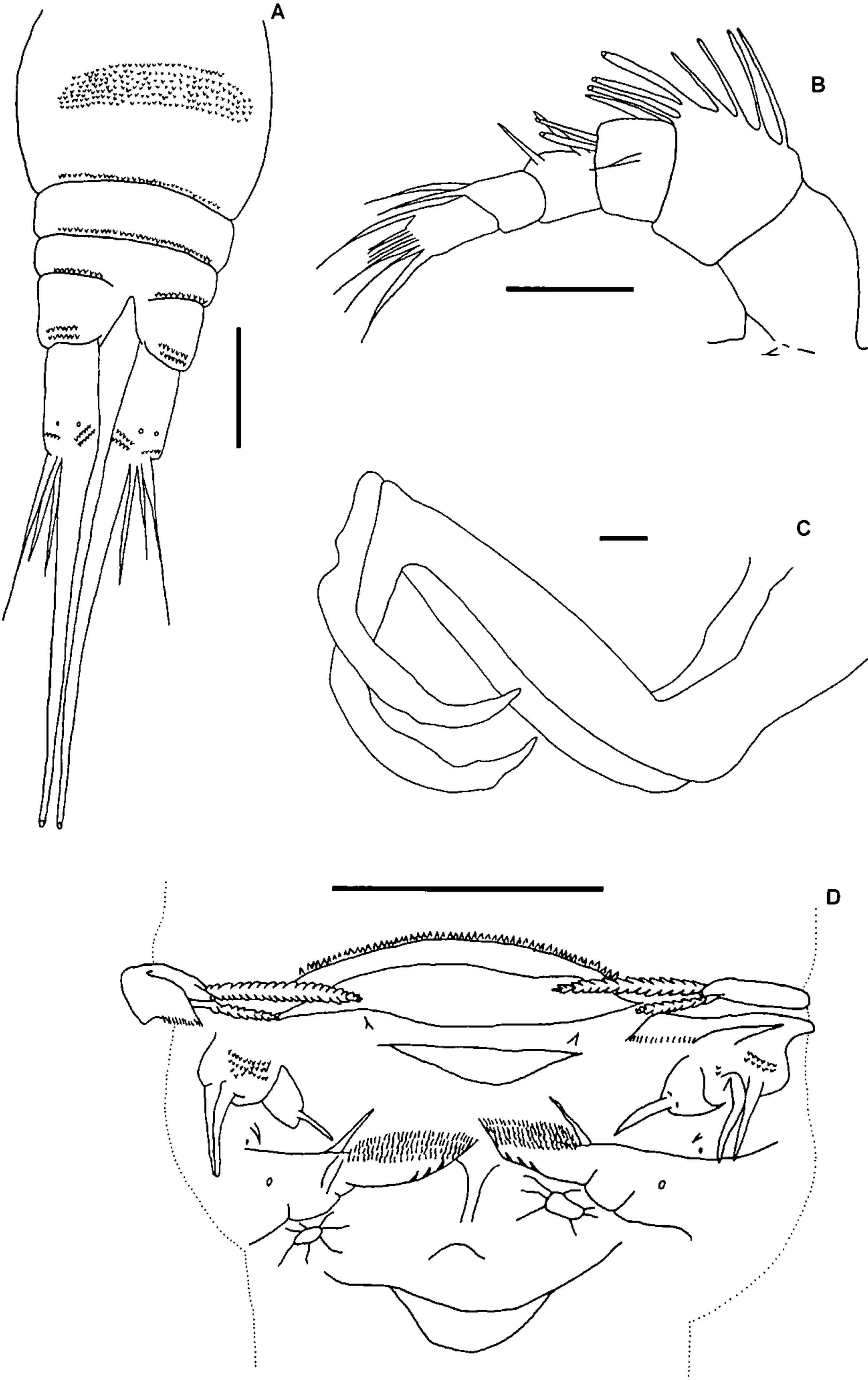
A. Ventral view of abdomen (50µm)

B. Antennule (50µm)

C. Antenna (50µm)

D. Mouthparts (50µm)

[Redrawn from Oldewage & van As (1987)]


A
B
C
D

Ergasilus nodosus Wilson, 1928

Collected from one system and one host species (Table 5.20 and Fig. 5.20).

Total Length	1mm (Figs. 5.21A&B).
Cephalothorax	Width-0.5mm, length-0.4mm. Body elongate-obovate, broadest anteriorly, decreasing regularly posteriorly. Cephalic segment distinctly separated from first thoracic segment. Cephalic segment short, ¼ wider than long, round margin.
Ornamentation	Unknown.
Pigmentation	Preserved material, uniform yellowish-gray, egg strings orange.
Mouthparts	Viewed laterally, project from ventral surface of cephalothorax, with maxillae at outermost tip of projection. Labrum fused to cephalothorax, with outlines indistinguishable. Mandibles stout, basal segment long, allows mandible to shut forward beneath upper lip, cutting blade elongate-triangular, curved sharply forward, with row of long sharp spines around margin. Palp attaches to posterior margin of basal segment, projects behind base of cutting blade. Entire posterior margin scalloped, length and width of scallops diminishing proximally. First maxillae of usual pattern – knobs armed with setae. Second maxillae similar to mandibles, without palps, basal segment stout, as wide as long. Terminal blade curves forward, armed along anterior margin with row of short spines (Fig. 5.21D).
Thorax	Free thoracic segments diminishing regularly in width, posterior margins of first three slightly invaginate, fourth segment semicircular. Fifth segment entirely concealed in dorsal view.
Legs	Rami of first four pairs of legs three-segmented, except two-segmented exopod of fourth pair, basal longer than terminal. Fifth leg entirely lacking (Figs. 5.21E&F). Spine-seta formula provided in Table 5.19.
Abdomen	Four-segmented. Genital complex ¼ narrower than fourth

	thoracic segment, slightly longer than wide with nearly straight sides. Remaining abdominal segments much narrower than genital complex, all segments of equal width and length.
Furcal Rami	Oblong, equaling last two abdominal segments in length, each with three plumose furcal setae, inner seta longer and stouter than others.
Antennulae	Five-segmented, basal segment longer than others, anterior margins of all segments, tip of terminal segment armed with long setae. Fourth segment with two long, stout setae on posterior margin (Fig. 5.21C).
Antennae	Enormous, 1.25mm long when straightened, four distinct segments. Second and third segments longer than others, joint between segment two and three swollen to 2x diameter of segments. All segments curved, last two forming half circle.
Egg Sacs	1mm long, spindle-shaped, equals body length, 5x as long as wide. Eggs arranged in six to seven longitudinal rows, approximately 20 eggs in a row.
Attachment to host	Attach near to base of gill filament, buries tip of antennae in filament tissue, as far as swollen joints. Buried portions turned at right angles to basal portions, long enough to overlap each other.
Relationships & Diagnostic features	Distinguishing characteristics: large antennae, with prominent swollen second joints, antennulae, plumose furcal setae, fourth pair of legs and absence of leg five.
Material	Type specimens in Naturhistoriska Riksmuseum in Stockholm and in Museum of Gothenburg.

Table 5.19: Spine-Seta Formula for *Ergasilus nodosus* Wilson, 1928

	Coxa	Basis		Segment 1	Segment 2	Segment 3
Leg 1	-	-	Exopodite	-	-	-
			Endopodite	-	-	-
Leg 2	-	-	Exopodite	-	-	-
			Endopodite	-	-	-
Leg 3	0	0	Exopodite	I - 0	0 - 1	0 – 5
			Endopodite	0 - 1	0 - 2	0 – 5
Leg 4	0	1	Exopodite	I - 0	0 - 4	-
			Endopodite	0 - 0	0 - 0	I – 2

Table 5.20: Hosts and Localities for *Ergasilus nodosus* Wilson, 1928

Locality	Host	Reference
White Nile, Omdurman	Bagrus bajad (Forsskål, 1775)	Wilson (1928)

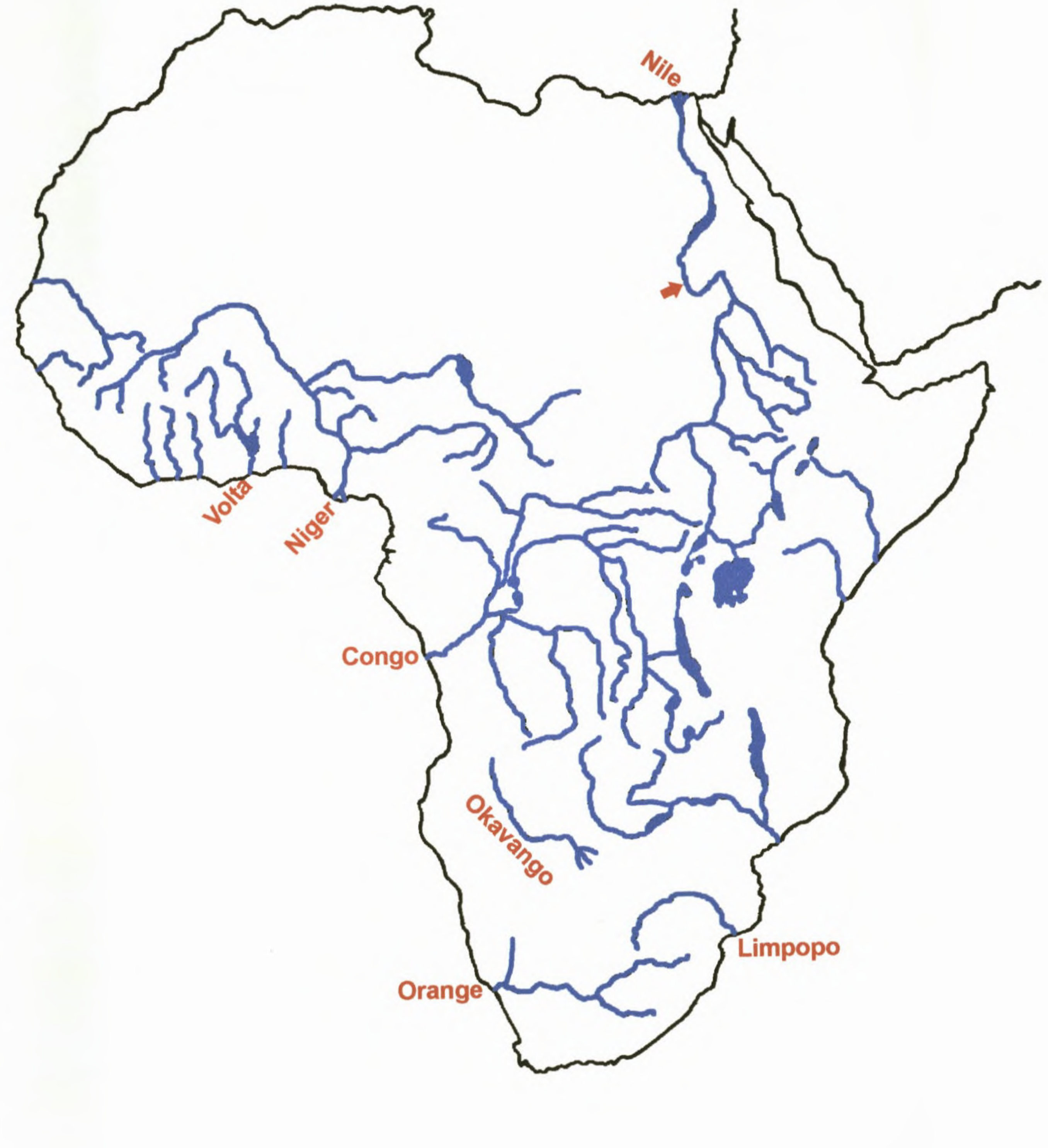


Figure 5.20: Distribution map for *Ergasilus nodosus* Wilson, 1928. Arrows indicate the different collection sites [Map adapted from Grove (1998), distribution by author].

Figure 5.21

Line drawings of *Ergasilus nodosus* Wilson, 1928

A. Dorsal view of adult female (200µm)

B. Lateral view of adult female (200µm)

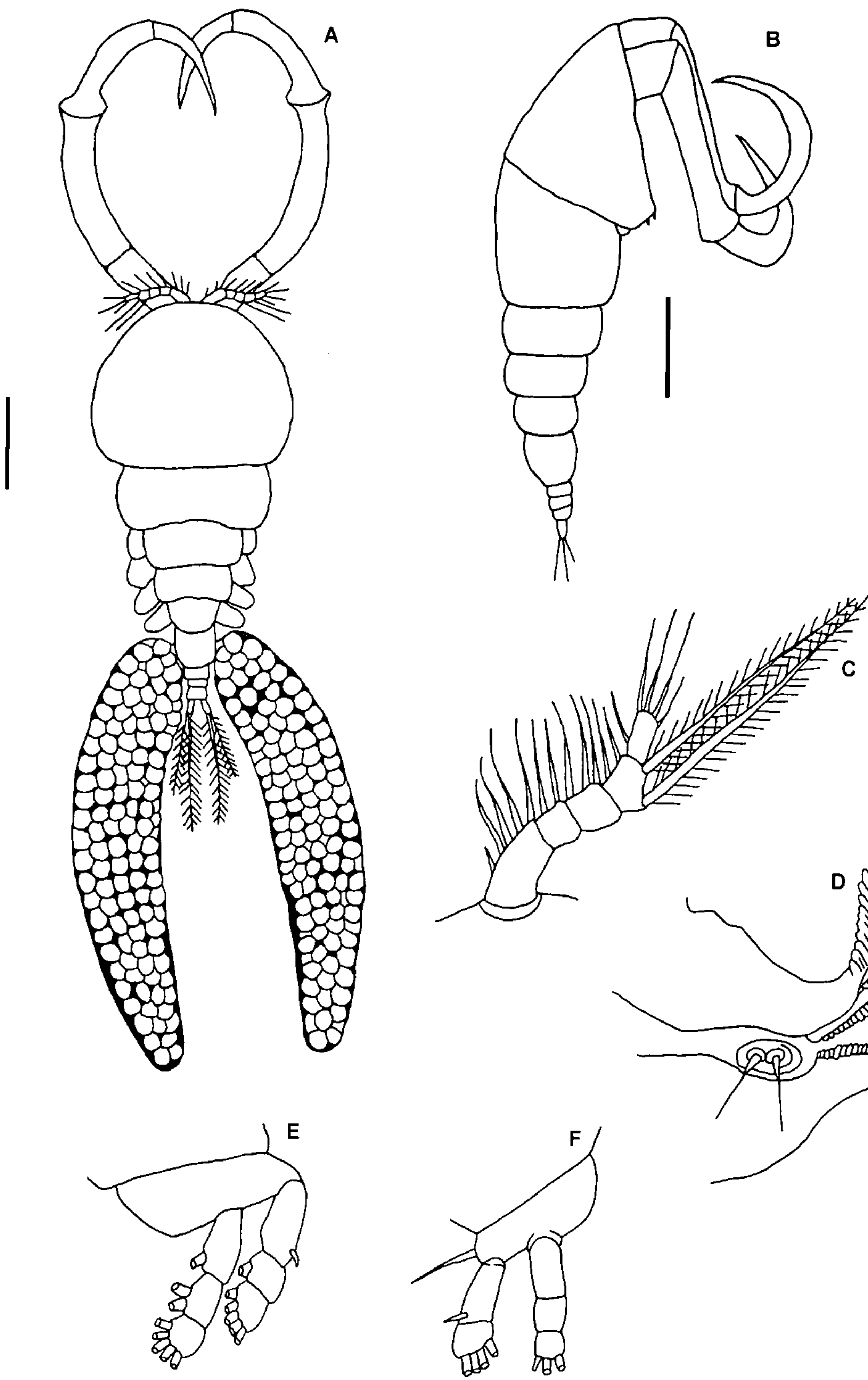
C. Antennule

D. Mouthparts

E. Leg 3

F. Leg 4

[Redrawn from Wilson (1928)]


A
B
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E
F

Ergasilus sarsi Capart, 1944

Collected from three systems and nine host species (Table 5.21 and Fig. 5.22).

Total Length	0.65mm (Figs. 5.23A&B).
Cephalothorax	Width – 0.33mm, length – 0.39mm. Anterior border evenly rounded, posterior border straight. Gap between cephalic segment and first thoracic segment clearly marked.
Ornamentation	Cephalic segment with distinct pattern. Eyespot visible.
Pigmentation	Unknown.
Mouthparts	Unknown.
Thorax	First four segments well-developed, decreasing in length and width posteriorly. Fifth segment dorsally visible.
Legs	First four pairs of legs typical of genus. Fifth pair reduced to single segment, with three setae. Two short terminal setae, one short postero-lateral seta. Spine-seta formula not provided by original author.
Abdomen	Four-segmented.
Furcal Rami	Longer than final abdominal segment, each ramus bearing three setae, one longer than others.
Antennulae	Six-segmented, with long setae on anterior border. Antennule setae formula: 2-8-2-2-2-6 (Fig. 5.23D).
Antennae	Long and robust, second segment much longer than third. Anterior border of third segment marked by slight but wide depression (Fig. 5.23C).
Egg Sacs	Length – 0.22mm, cylindrical, short.
Attachment on host	Unknown placement on gill filaments.
Relationships & Diagnostic characteristics	General form similar to *E. nodosus*, distinguished by structure of antennae and antennulae. Resembles *E. macrodactylus*, but *E. macrodactylus* has antennule with five segments, very thin antennae and abdomen with two segments and much reduced fifth pair of legs. Characteristic features: six-segmented antennulae, robust antennae, four segmented abdomen.

Type Material	Syntypes: 6E de Lubunduj, Musée Royal d'Histoire Naturelle de Belgique I.G. No. 13.057.

Table 5.21: Hosts and Localities for *Ergasilus sarsi* Capart, 1944

Locality	Host	Reference
Lake Mweru, Congo Basin	**Haplochromis moeruensis* (Boulenger, 1899) °**Tylochromis mylodon* Regan, 1920 **T. bangwuelensis* Regan, 1920	°Capart (1944) *Fryer (1967)
Lake Bangweula, Congo Basin	*Clarias ngamensis* Castelnau, 1861 *Marcusenius macrolepidatus* (Peters, 1852)[1] *Synodontis nigromaculatus* Boulenger, 1905	Fryer (1959)
Volta Basin, Ghana	*Clarias gariepinus* (Burchell, 1822)	Paperna (1969)
Galma River, Northern Nigeria	*Clarias anguillaris* (Linnaeus, 1758) *Heterobranchus bidorsalis* Geoffroy Saint-Hilaire, 1809	Shotter (1977)

[1] Scientific names have changed since this species was recorded as a host (Table 5.2)
*° Indicate the specific papers in which the different host species were recorded

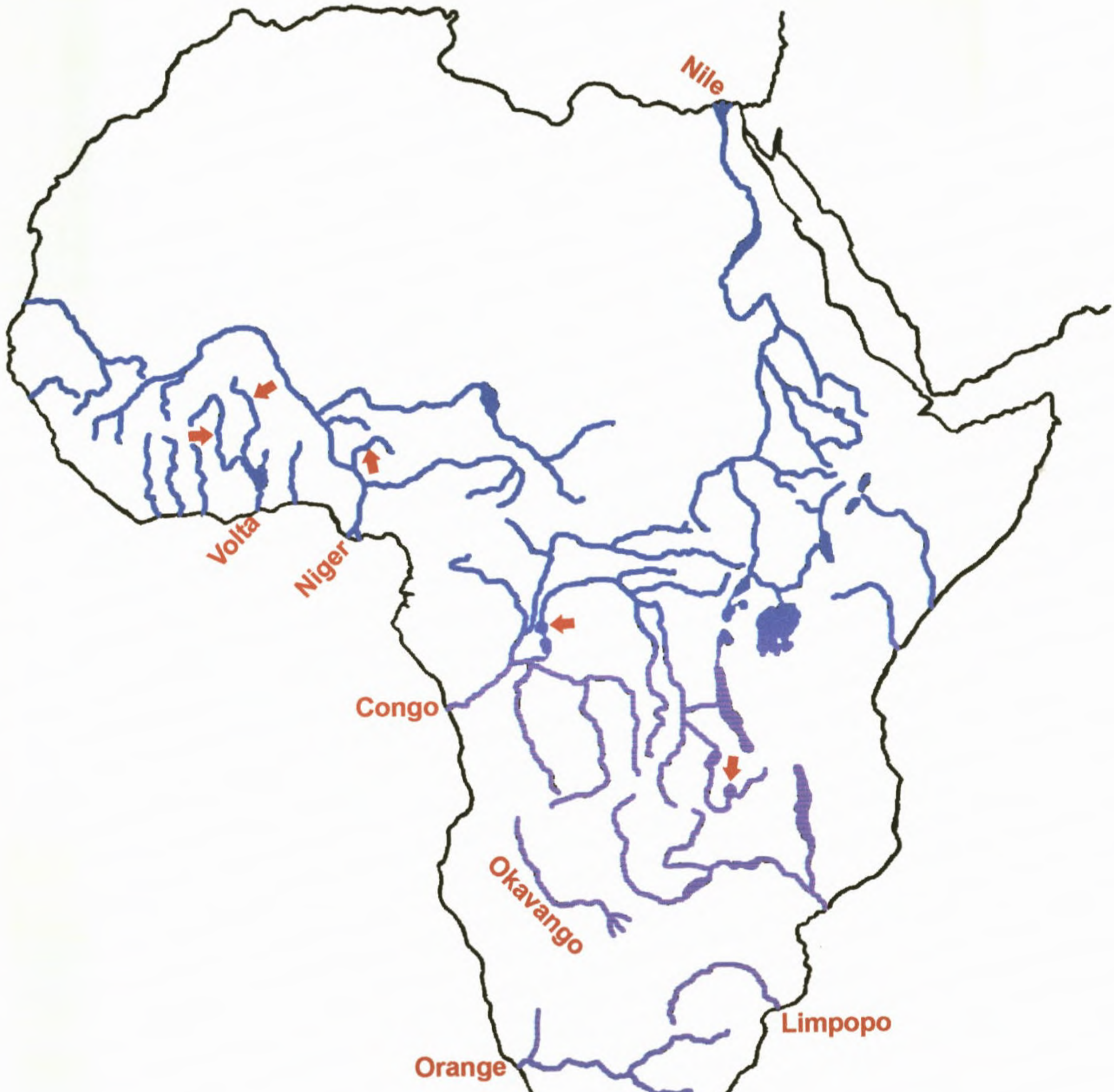


Figure 5.22: Distribution map for *Ergasilus sarsi* Capart, 1944. Arrows indicate the different Collection sites [Map adapted from Grove (1998), distribution by author].

Figure 5.23

Line drawings of *Ergasilus sarsi* Capart, 1944

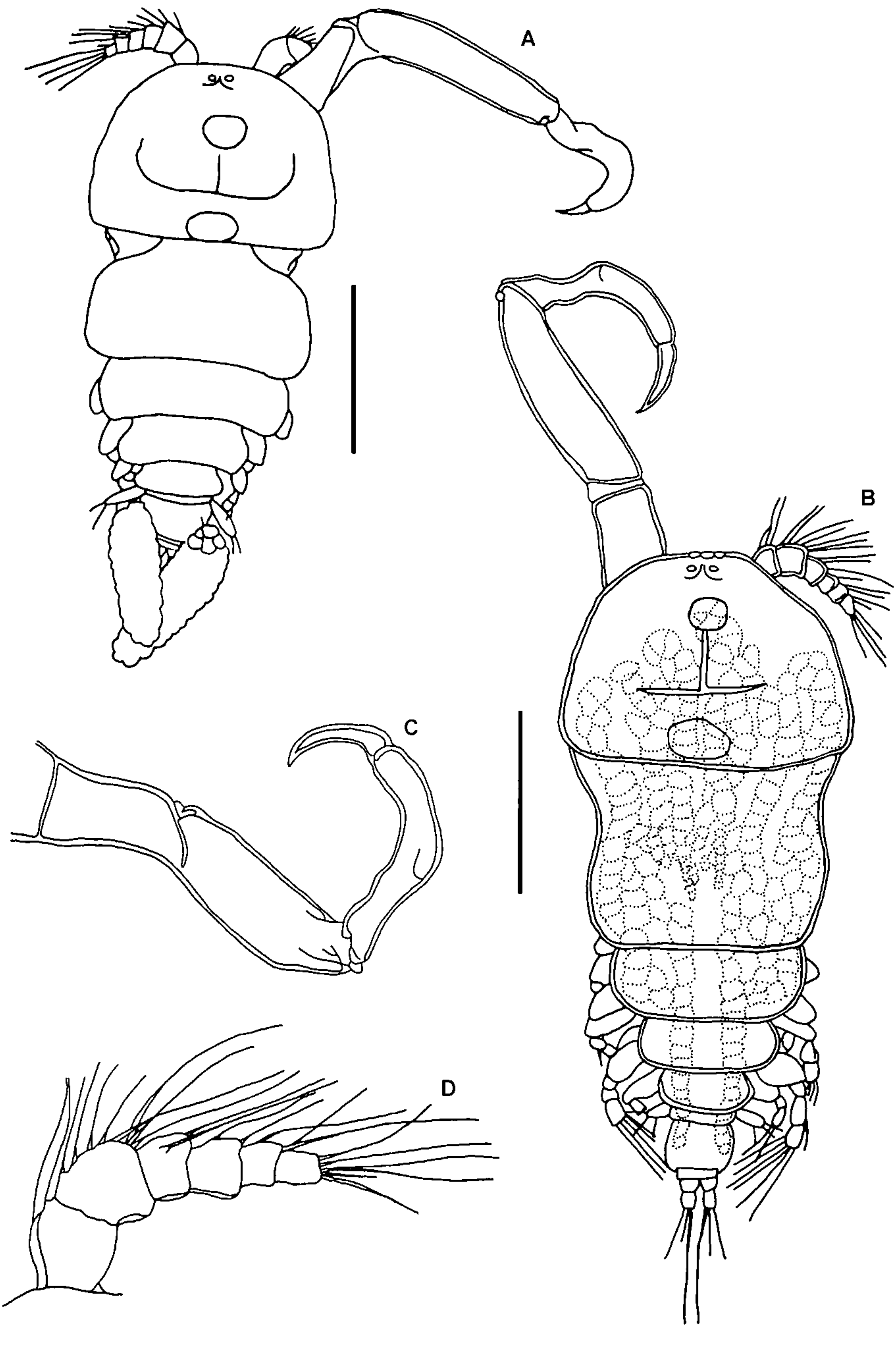
A. Dorsal view of adult female (200μm)

B. Dorsal view of adult female with eggs present in the cephalothoracic region (200μm)

C. Antenna

D. Antennule

[Redrawn from Capart (1944)]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Paraergasilus lagoonaris Paperna, 1969

Collected from two systems and five host species (Table 5.23 and Fig. 5.24).

Total Length	0.3 – 0.45mm (Fig. 5.25A).
Cephalothorax	Width 0.15-0.25mm.
Ornamentation	Unknown.
Pigmentation	Unknown.
Mouthparts	Unknown.
Thorax	Unknown.
Legs	Setation of first leg endopodite consists of single elongated spine on each segment, distal segment with few additional minute spines (Figs. 5.25D-G). Spine-seta formula provided in Table 5.22.
Abdomen	Unknown.
Furcal Rami	0.15-0.2mm long, exceeds length of egg sacs.
Antennulae	Five-segmented, as long as first two segments of antenna (Fig. 5.25C).
Antennae	Small, second segment very small, 1/2 width of cephalothorax, three distal spiniform claws shorter than length of second proximal segment (Fig. 5.25B).
Egg Sacs	Short, 0.15-0.2mm, ½ length of furcal setae.
Attachment on host	Found on walls of gill cavity.
Relationships & Diagnostic features	Differs from *P. minutus* in having considerably shorter claws on antennae, these do not exceed in length second proximal segment whereas in *P. minutus* they do so. Setation of first exopodite different in two species. In *P. lagoonaris* egg sacs are much shorter than furcal setae, in *P. minutus* they are longer.

Table 5.22: Spine-Seta Formula for *Paraergasilus lagoonaris* Paperna, 1969

	Coxa	Basis		Segment 1	Segment 2	Segment 3
Leg 1	-	-	Exopodite	I - 0	0 - 1	II – 6
			Endopodite	I - 0	I - 0	I(II)- 0
Leg 2	-	-	Exopodite	I - 0	0 - 1	0 – 6
			Endopodite	0 - 1	0 - 2	I – 4
Leg 3	-	-	Exopodite	I - 0	0 - 1	0 – 6
			Endopodite	0 - 1	0 - 2	I – 4
Leg 4	-	-	Exopodite	0 - 0	0 - 5	-
			Endopodite	0 - 1	0 - 2	I – 3

Table 5.23: Hosts and Localities for *Paraergasilus lagoonaris* Paperna, 1969

Locality	Host	Reference
Peshi Lagoon, Ghana	*Aplocheilichthys* spp. Bleeker, 1863 *Awaous guineensis* (Duméril, 1861) *Tilapia guineensis* (Günther, 1862)	Paperna (1969)
Lake Volta, Ghana	*Pellonula leonensis* Boulenger, 1916[1]	Paperna (1969)
Niger River, Nigeria	*Sierrathrissa leonensis* Thys van den Audenoerde, 1969	Thurston (1970)

[1] Scientific names have changed since this species was recorded as a host (Table 5.2)

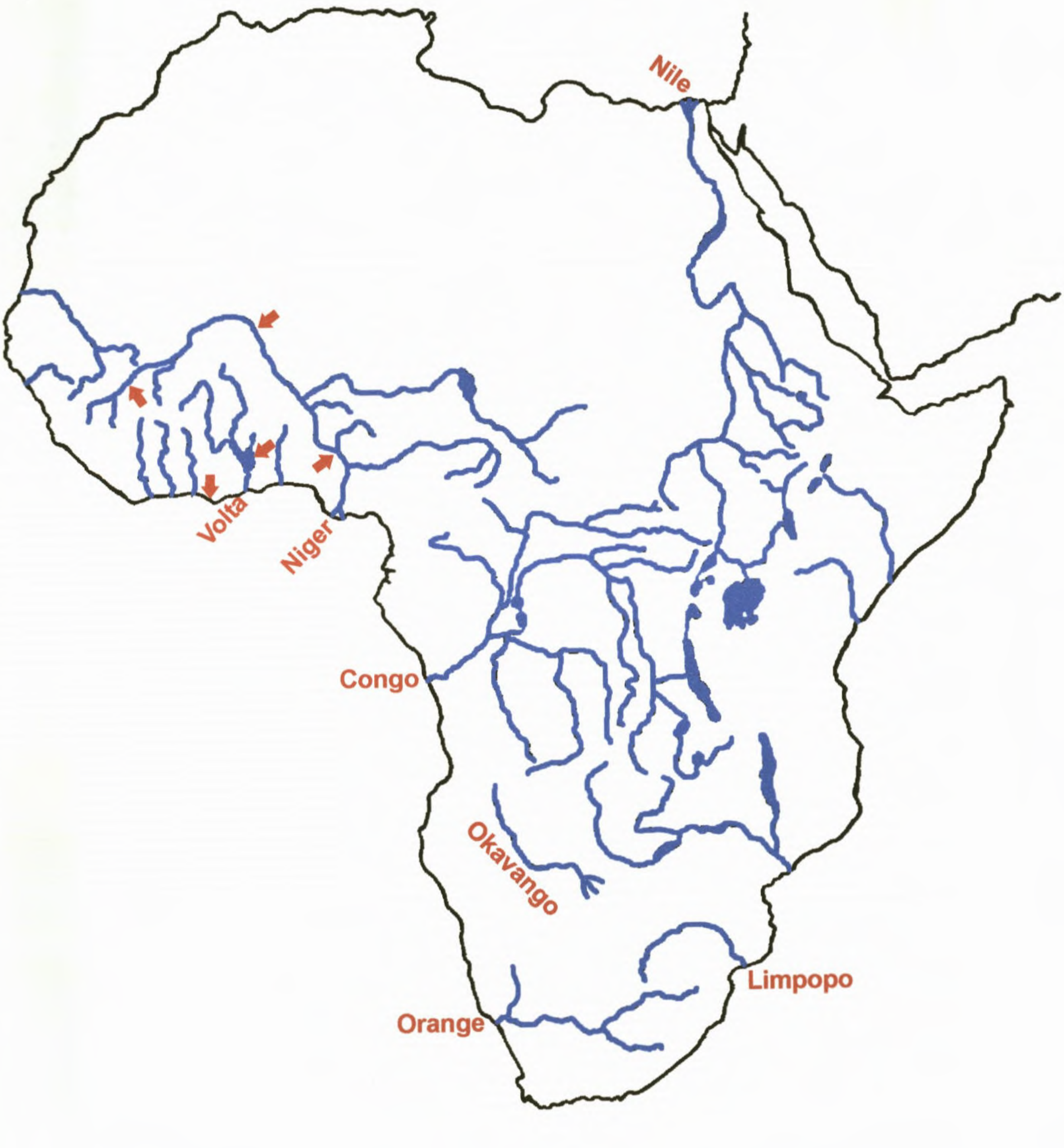


Figure 5.24 : Distribution map for *Paraergasilus lagoonaris* Paperna, 1969. Arrows indicate the different collection sites [Map adapted from Grove (1998), distribution by author].

Figure 5.25

Line drawings of *Paraergasilus lagoonaris* Paperna, 1969

A. Dorsal view of adult female (100µm)

B. Antenna (10µm)

C. Antennule (10µm)

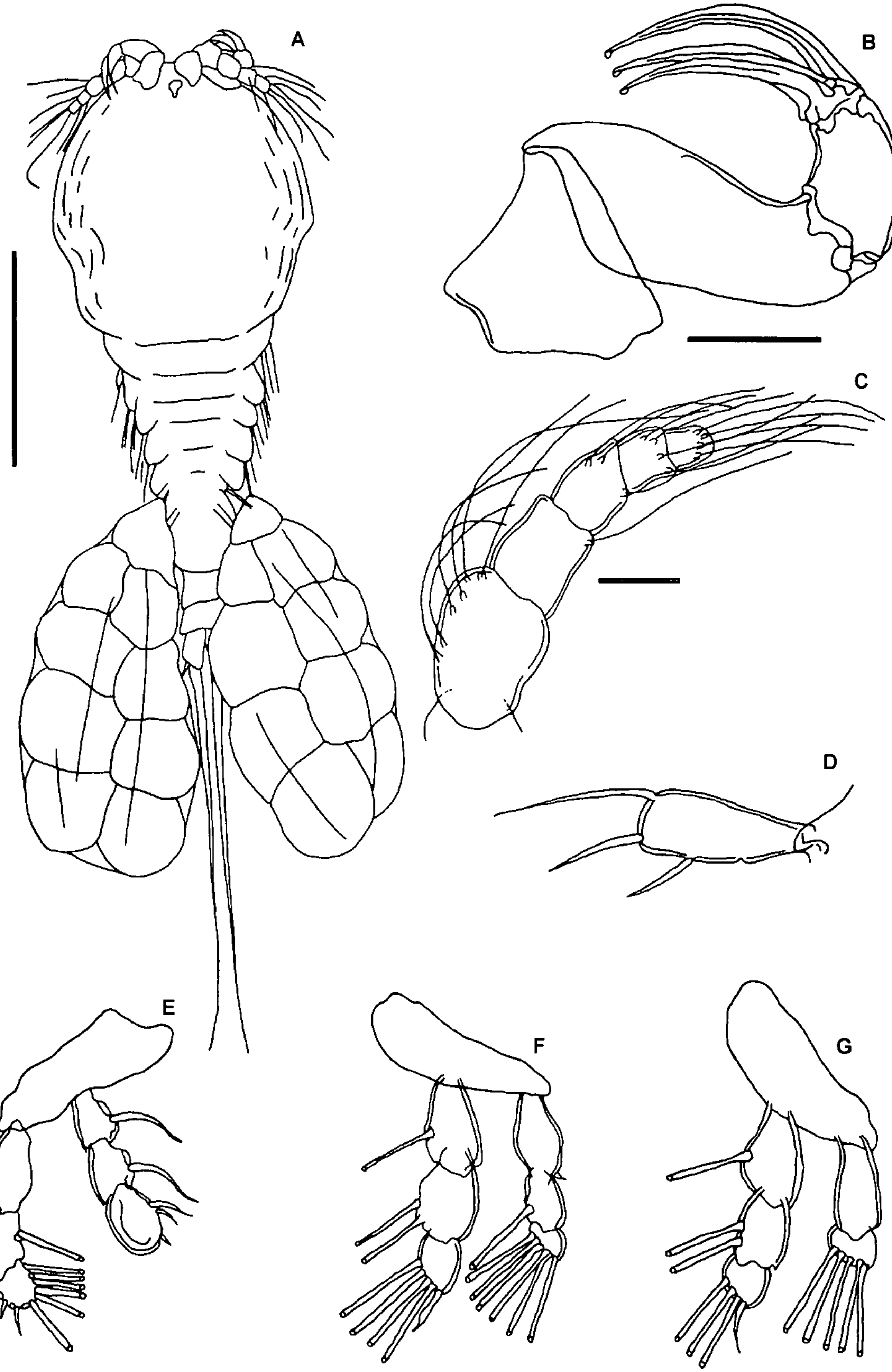
D. Leg 5

E. Leg 1

F. Leg 2

G. Leg 4

[Redrawn from Paperna (1969)]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G

Paraergasilus minutus (Fryer, 1956)

Collected from one system and two host species (Table 5.25 and Fig. 5.26).

Total Length	0.344mm (Fig. 5.27A).
Cephalothorax	Body cyclopiform, dorso-ventrally flattened, shortened posteriorly. First thoracic segment fused with cephalic segment forming enormous pentagonal cephalothorax, comprising 60% of total length. Cephalic segment isosceles triangle, with bluntly rounded corners.
Ornamentation	Eyespot very large, roughly rectangular in shape, deep purple in colour.
Pigmentation	Colourless, with small flecks of purple pigment dorsally in cephalothorax.
Mouthparts	Similar to *Ergasilus* species.
Thorax	Thoracic segments two to four, gradually decreasing in size, second segment much smaller than first. Fifth segment very narrow, incipiently separated from genital segment.
Legs	First four pairs biramous. All rami three-segmented, except two-segmented exopodite of leg four. Leg five minute, platelike with two terminal setae and slightly sub-terminal seta on posterior margin (Fig. 5.27B). Spine-seta formulae provided in Table 5.24, formulae for endopodites not included by original author.
Abdomen	Very short, three-segmented. Genital segment slightly swollen, broader than long. Abdominal segments two and three very short.
Furcal Rami	Short, as long as wide with four terminal setae. Innermost seta longest, swollen near base. Outermost seta directed 45° outwards.
Antennulae	Well developed, 63µm in length, five-segmented. Anterior border with many setae. Terminal segment with long terminal setae, two longest setae 80% length of entire antennule.
Antennae	Stout and prehensile, three-segmented, distal segment with

	three recurved and subequal spines. Shortest 1/2 length of antenna (Fig. 5.27C).
Egg Sacs	Long, 321µm in length, approximately 30 eggs/sac. Eggs white in colour.
Attachment on host	Unknown.
Relationships & Diagnostic features	Differs from *P. lagoonaris* in having longer claws on antennae, exceeding second proximal segment in length. Setation of first exopodite is different in two species. In *P. minutus* egg sacs are longer than furcal setae, whereas in *P. lagoonaris* they are shorter.

Table 5.24: Spine-Seta Formula for *Paraergasilus minutus* Fryer, 1956

	Coxa	Basis		Segment 1	Segment 2	Segment 3
Leg 1	-	-	Exopodite	I –0	0 – 0	I – 5
			Endopodite	-	-	-
Leg 2	-	-	Exopodite	0 – 0	0 – 1	0 – 6
			Endopodite	-	-	-
Leg 3	-	-	Exopodite	0 – 0	0 – 1	0 – 6
			Endopodite	-	-	-
Leg 4	-	-	Exopodite	0 - 0	0 – 5	
			Endopodite	-	-	-

Table 5.25: Hosts and Localities for *Paraergasilus minutus* Fryer, 1956

Locality	Host	Reference
Lake Malawi	*Petrotilapia tridentiger* Trewavas, 1935 *Pseudotropheus tropheops* Regan, 1922	Fryer (1956)

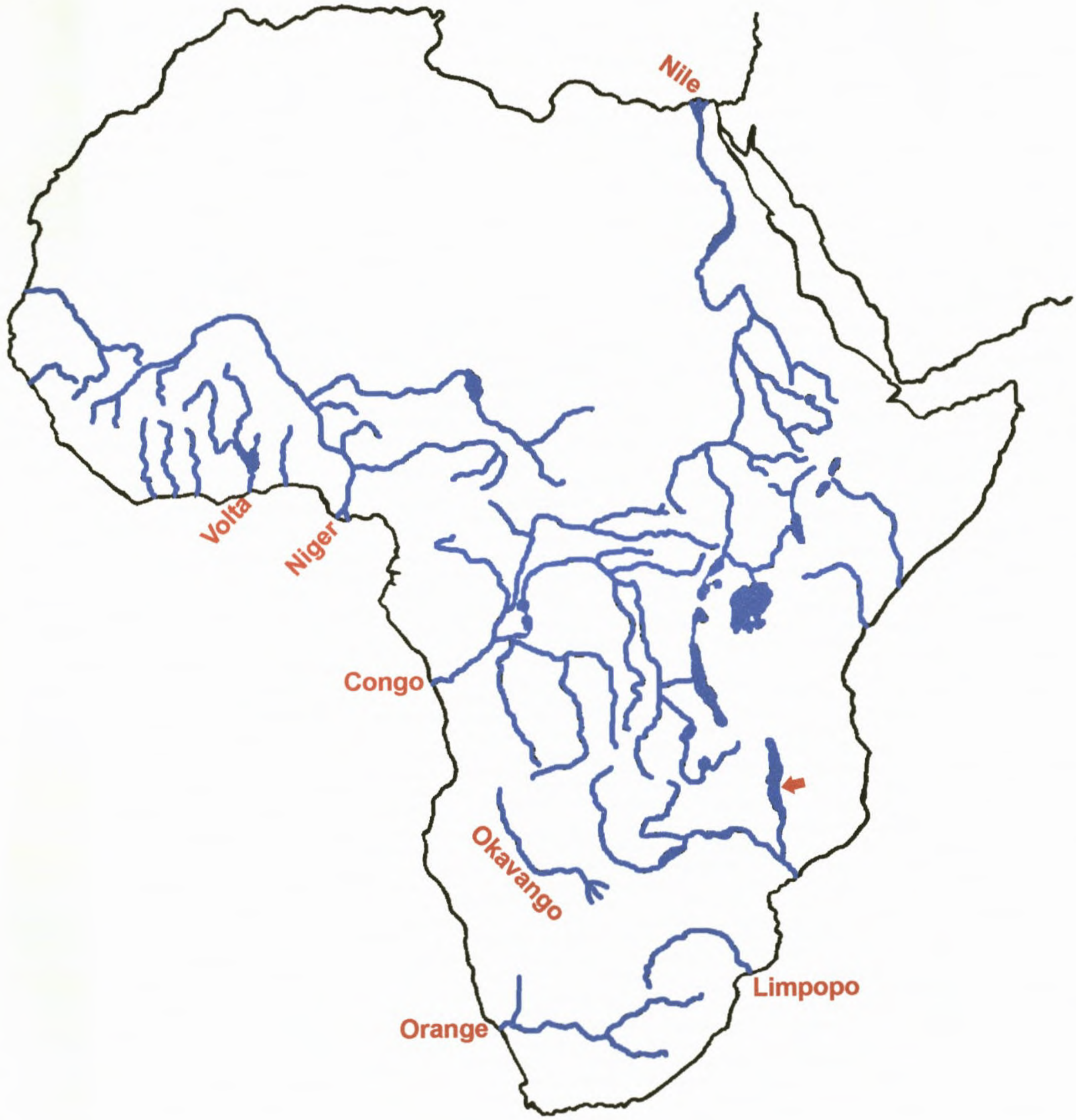


Figure 5.26: Distribution map for *Paraergasilus minutus* Fryer, 1956. Arrows indicate the different collection sites [Map adapted from Grove (1998), distribution by author].

Figure 5.27

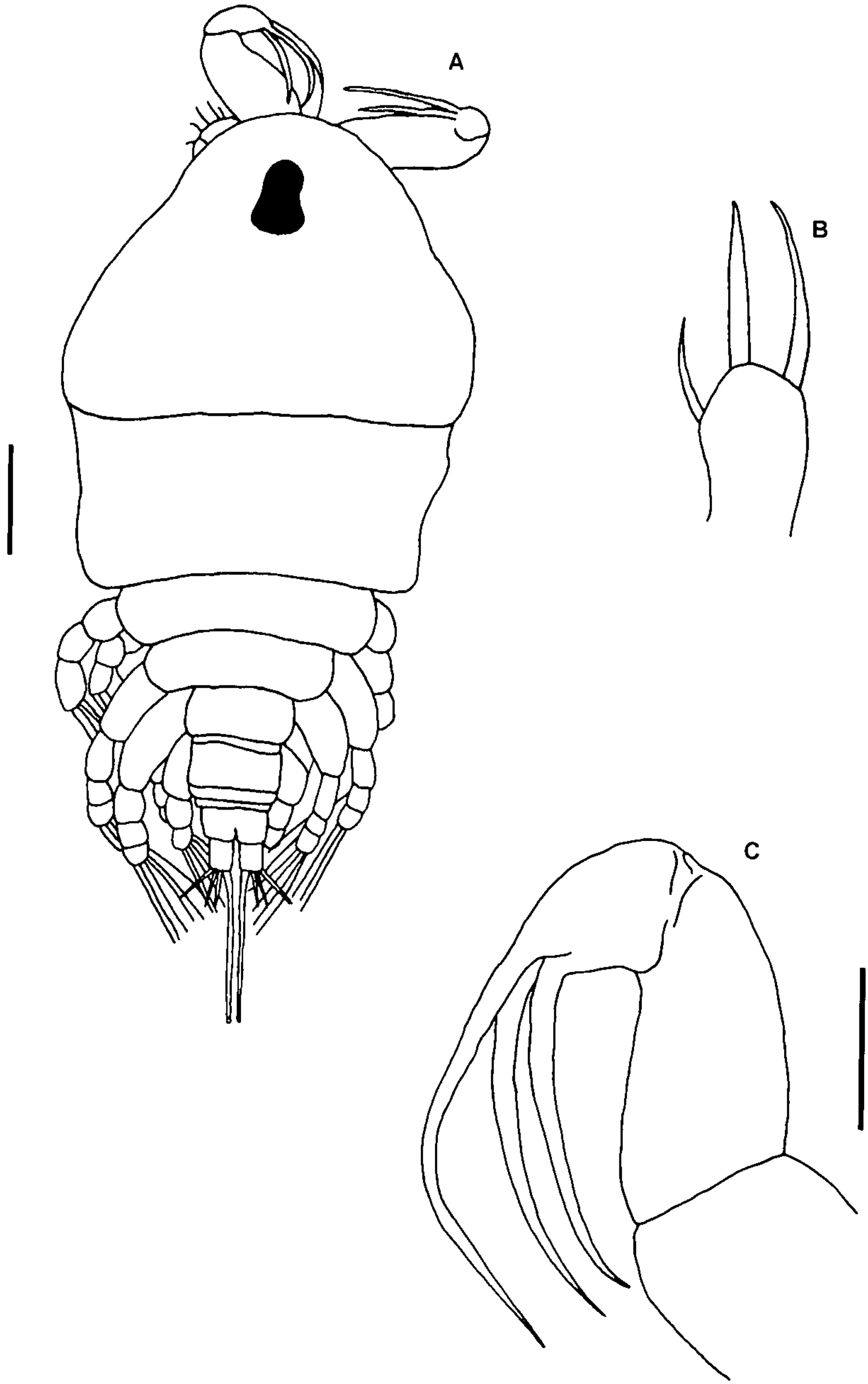
Line drawings of *Paraergasilus minutus* (Fryer, 1956)

A. Dorsal view of adult female (100µm)

B. Leg 5

C. Antenna (25µm)

[Redrawn from Fryer (1956)]


A
B
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Chapter 6

Results

6.1 Results from the Okavango River and Delta

Descriptions of the Species Collected

All four of the following species descriptions were done following the general framework of El-Rashidy & Boxshall (2001a).

***Ergasilus* sp. A**

Type Host

Synodontis nigromaculatus Boulenger, 1905

Type Locality

Okavango Delta, Upper Panhandle Region (S18°26'05.0" ; E021°54'23.0")

Other Hosts

Schilbeidae:

Schilbe intermedius Rüppell, 1832

Cichlidae:

Serranochromis angusticeps (Boulenger, 1907)

S. macrocephalus (Boulenger, 1899)

Mochokidae:

Synodontis vanderwaali Skelton & White, 1990

S. thamalakenensis Fowler, 1935

S. leopardinus Pellegrin, 1914

S. macrostigma Boulenger, 1911

Species Description (based on 25 specimens).

Total Length: Mean length 1.44mm (1.3-1.52mm range) excluding furcal setae (Figs. 6.1A & 6.4F).

Cephalothorax: Body gradually narrowing posteriorly, cephalic segment as wide as long, distinctly separated from first thoracic segment. Distinct distribution of sensory setae and pits on dorsal surface of cephalic segment (Fig. 6.2A).

Ornamentation: Circular cephalic structure anterior to inverted T, oval cephalic structure posterior to inverted T. Two small oval cephalic structures situated anterior to circular cephalic structure (Fig. 6.2A). Inverted T only visible using light microscopy.

Pigmentation: Eyespot anterior to inverted T, dark purple pigmented. Dark purple pigmentation in cephalothoracic region.

Mouthparts: Maxilla with seta medially situated on upper margin, second segment ending in two spinulose areas. Sensory pit situated posterior to seta (Figs. 6.2E & 6.4A&B).

Thorax: Thoracic segments decrease in size, with less sclerotinised regions between segments. Dorsal surface with distinct distribution of sensory setae and pits (Fig. 6.2B). Intercoxal plate with row of comb-like setae situated medially extending from left to right, plate with sensory pits at each end (Fig. 6.2D). Ventral surface of fifth thoracic segment with group of spines and row of short bristles.

Legs: Legs one to four, typical of genus, all setae plumose (Figs. 6.3A-C). Coxa of leg one with two groups of tooth-like scales, first consisting of larger tooth-like scales, second consisting of smaller tooth-like scales. Leg one, large group of long fine setae on outer margin of first endopodal segment, small group of short fine setae on inner margin of first exopodal segment. All spines on leg one unadorned. Basis of leg two with line of comb-like spines on inner edge. Large group of fine setae on first exopodal segment of leg two. Two lines of comb-like spines on ventral surface of first segment of endopod of leg two, endopod also with row of long fine setae and row of short toothlike spines on inner margin. Third endopodal segment of leg two with sensory pit at distal end. All spines of leg two unadorned. Leg three similar to leg two, except for second and third endopodal segments, each possesses row of tiny spines along outer edge. Two rows of spines on first endopodal segment of leg four. Leg five two-segmented, basal segment with a single seta, distal segment with two terminal and one lateral setae (Figs. 6.2C & 6.4E). Spine-seta formulae provided in Table 6.1.

Table 6.1: Spine-seta formulae for *Ergasilus* von Nordmann, 1832 sp. A collected from *Synodontis nigromaculatus* Boulenger, 1905 from the Okavango River and Delta

	Coxa	Basis		Segment 1	Segment 2	Segment 3
Leg 1	o	1	Exopodite	I – 0	I – 1	II – 5
			Endopodite	0 – 1	0 – 1	II – 4
Leg 2	0	1	Exopodite	I – 0	0 – 1	0 – 6
			Endopodite	0 – 1	0 – 2	I – 4
Leg 3	0	1	Exopodite	I – 0	0 – 1	0 – 6
			Endopodite	0 – 1	0 – 2	I – 4
Leg 4	0	1	Exopodite	I – 0	0 - 5	-
			Endopodite	0 – 1	0 - 2	I - 3

Abdomen: Abdomen four-segmented. Genital complex with three rows of tooth-like scales on ventral surface, middle row consists of larger scales. Genital complex with row of comb-like spines along posterior margin. Posterior margin of first free abdominal segment bordered by row of comb-like spines. Posterior margin of second free abdominal segment bordered by row of tooth-like spines. Third free abdominal segment bi-lobed, with group of approximately seven tooth-like spines on both lobes (Fig. 6.1B).

Furcal Rami: Furcal rami longer than third abdominal segment. Two sensory pits near base of each ramus, four tooth-like spines posterior to each sensory pit. Four furcal setae present on each ramus, innermost longest, longer than abdomen (Fig. 6.1B).

Antennulae: Six-segmented.

Antennae: Mean length 1.03mm (0.95-1.12mm range) Four-segmented, all segments slender, unadorned. Very large, average length 0.98mm. Third segment with large twisted area near centre (Figs. 6.1C&D & 6.4C&D).

Egg Sacs: Egg sacs very long, mean length 1.07mm (1.0-1.2mm range). In certain specimens the egg sacs equalled the total body length. Each sac with approximately 45-50 eggs (Figs. 6.1A & 6.4F).

Attachment to Host: Attach to tip of gill filament, with abdomen and egg sacs protruding.

Remarks: *Ergasilus* sp. A differs from *E. flaccidus* and *E. lamellifer* by having a fifth leg with two terminal setae and one lateral seta, while these two species have no lateral setae. *Ergasilus cunningtoni, E. nodosus* and *E. sarsi* have three furcal setae whilst *Ergasilus* sp. A has four furcal setae. *Ergasilus macrodactylus, E. megacheir, E. mirabilis, E. latus* and *E. kandti* have single-segmented fifth legs and *Ergasilus* sp. A has a two segmented fifth leg.

Based on the above description and the differences between *Ergasilus* sp. A and the known species there is little doubt that *Ergasilus* sp. A is a new species. The combination of the following characteristics distinguish this species from the others:

- Two-segmented fifth leg, with a seta on the basal segment, two terminal setae and one lateral seta on the distal segment.
- Antennal third segment with a large twisted area near its centre.
- Abdomen four-segmented with a distinct pattern of spines on the ventral surface.
- The pattern of comb-like spines on the ventral surface of legs one to four.

Figure 6.1

Line drawings of *Ergasilus* von Nordmann, 1832 sp. A collected from *Synodontis nigromaculatus* Boulenger, 1905 from the Okavango River and Delta

A. Dorsal view of whole specimen (100µm)

B. Ventral view of abdomen (10µm)

C. Third segment of the antenna (100µm)

D. Lateral view of antenna. (100µm)

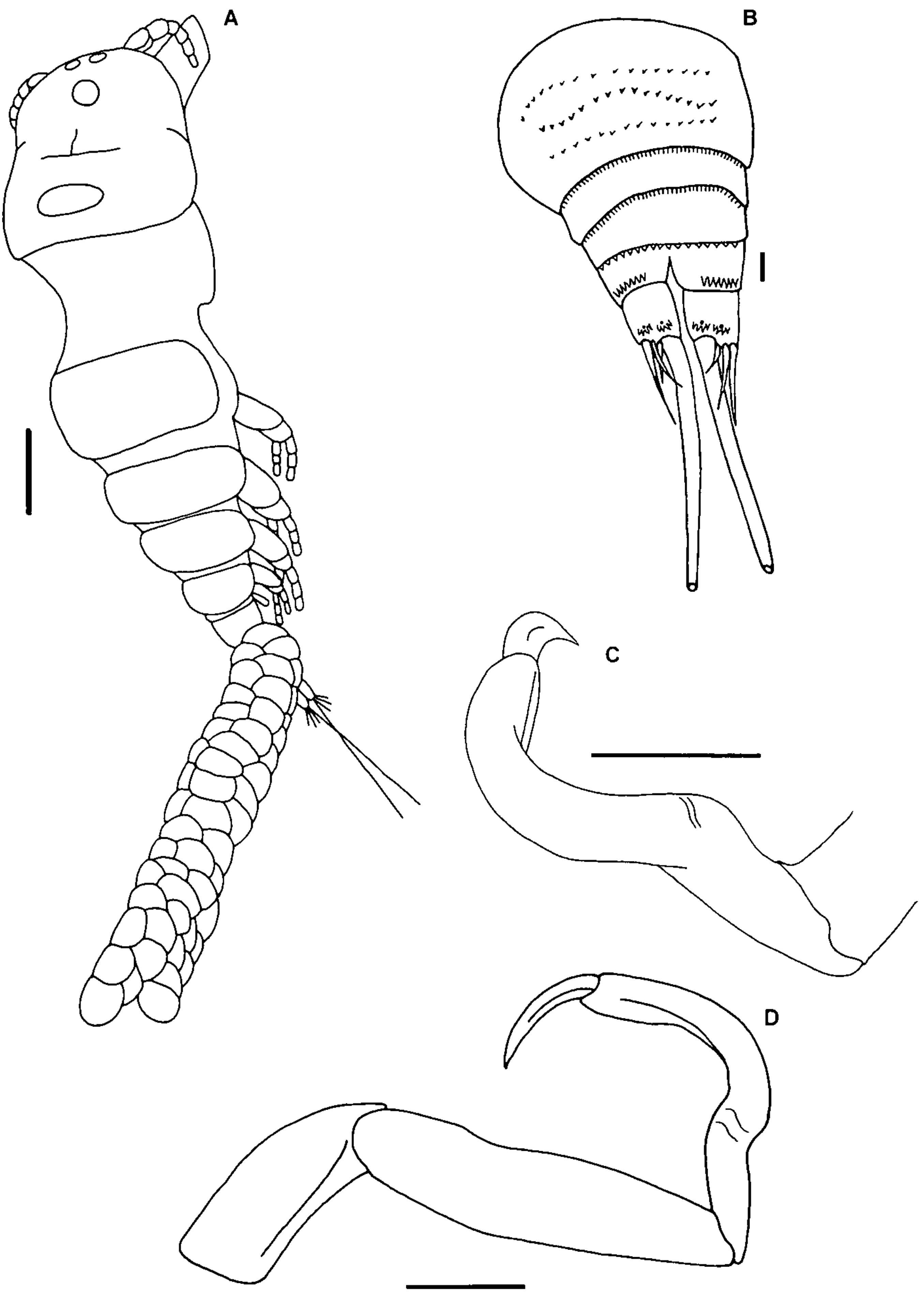
A
B
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Figure 6.2

Line drawings of *Ergasilus* von Nordmann, 1832 sp. A collected from *Synodontis nigromaculatus* Boulenger, 1905 from the Okavango River and Delta

A. Sensory pits and setae on the dorsal surface of the cephalic segment (100µm)

B. Sensory pits and setae on the dorsal surface of the thorax (100µm)

C. Leg 5 (10µm)

D. Intercoxal bar and plate (10µm)

E. Maxilla (10µm)

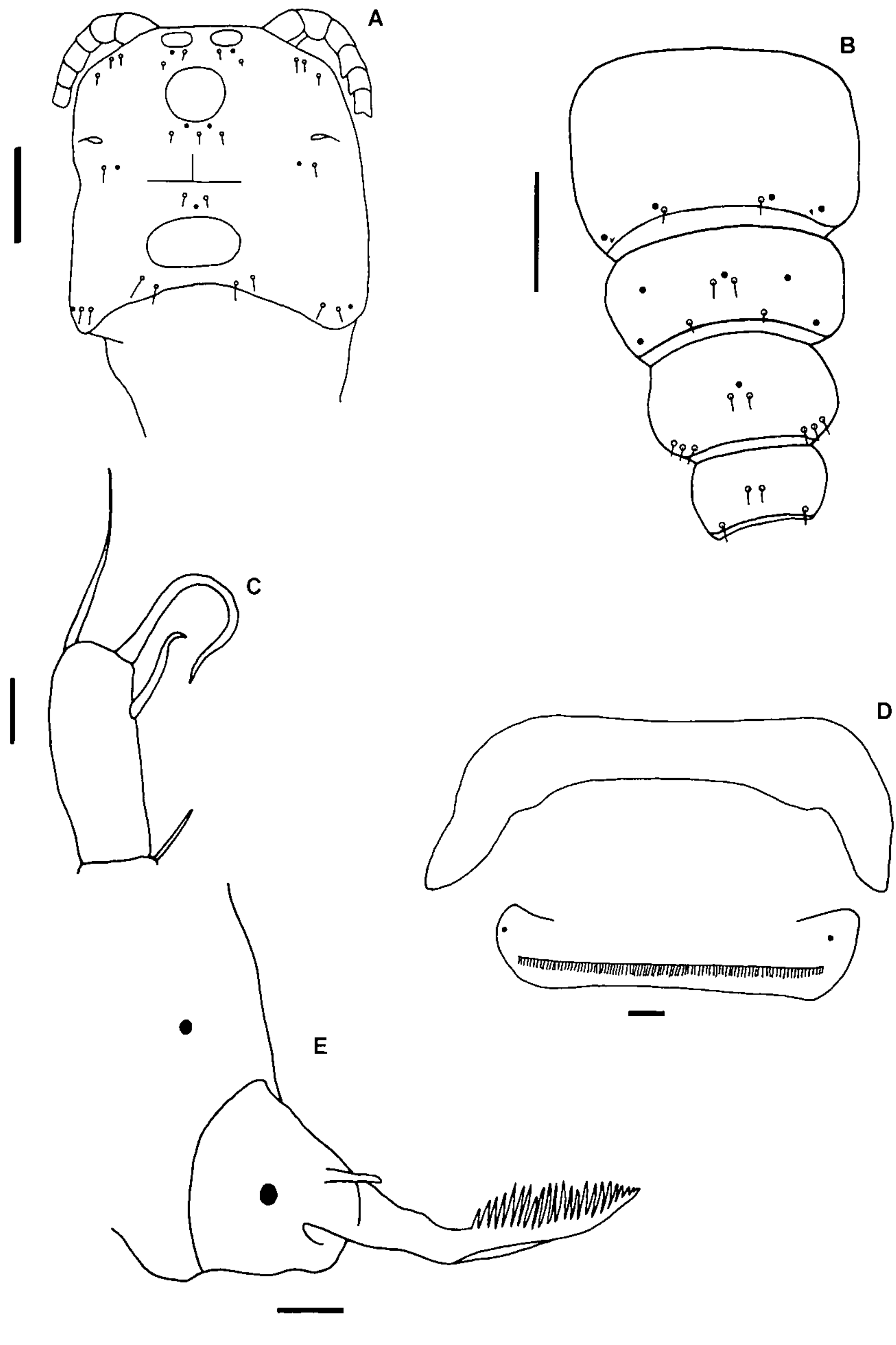
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Figure 6.3

Line drawings of *Ergasilus* von Nordmann, 1832 sp. A collected from *Synodontis nigromaculatus* Boulenger, 1905 from the Okavango River and Delta

A. Leg 1 (10µm)

B. Leg 2 (10µm)

C. Leg 3 (10µm)

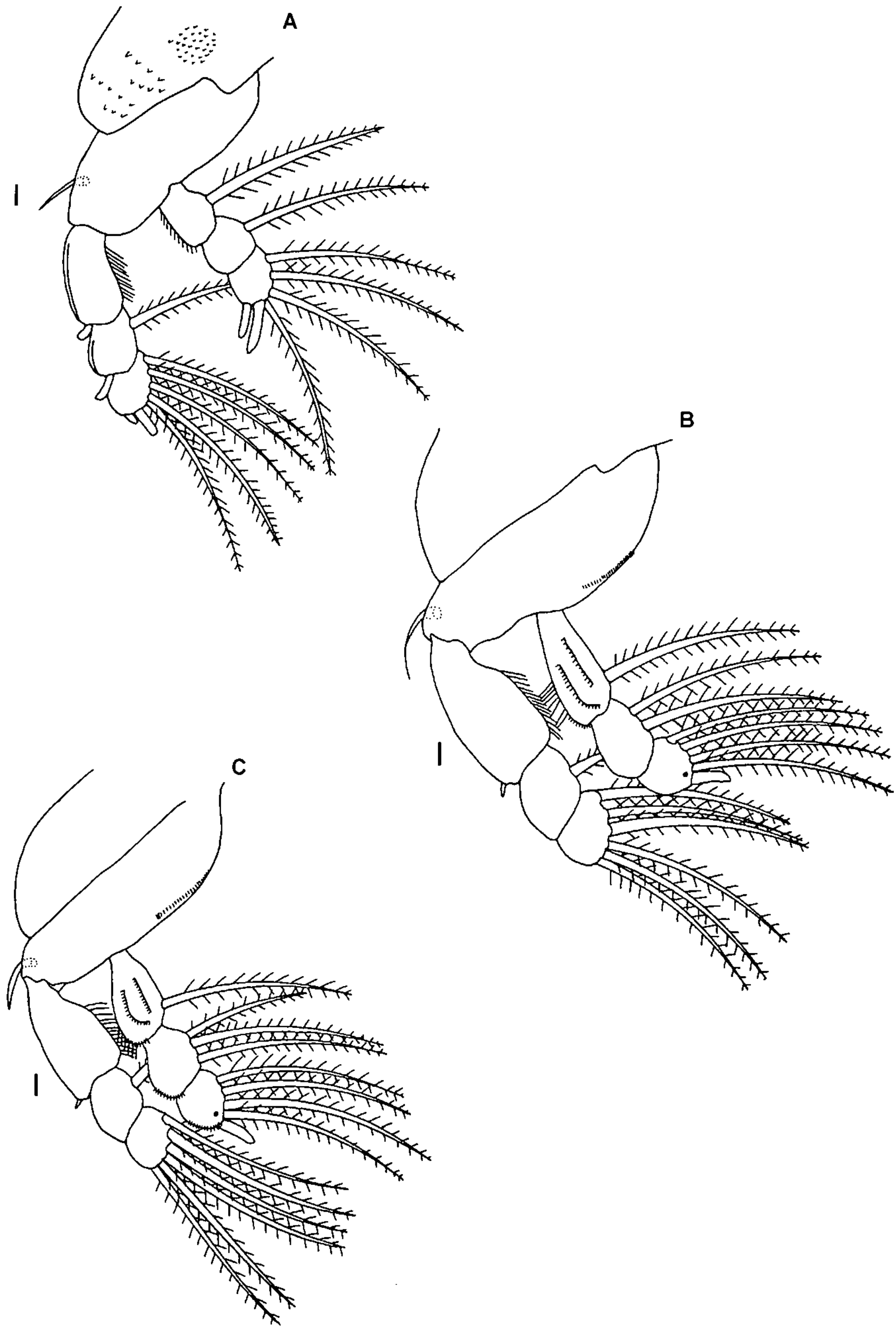
A
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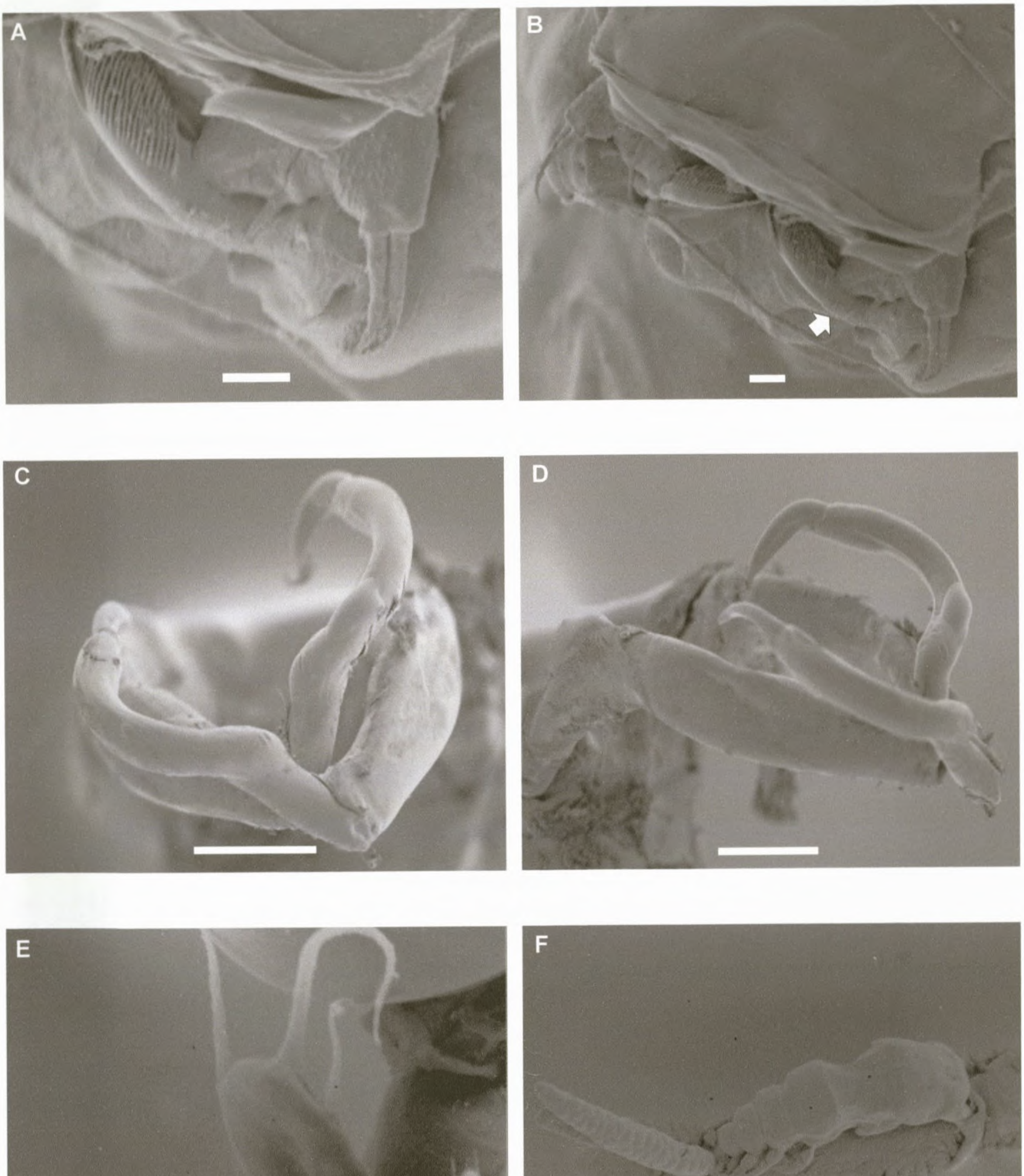
Figure 6.4

Scanning electron micrographs of *Ergasilus* von Nordmann, 1832 sp. A collected from *Synodontis nigromaculatus* Boulenger, 1905 from the Okavango River and Delta

- **A.** Mouthparts (10µm)
- **B.** Mouth, arrow indicates the mouthparts (10µm)
- **C.** Third segment of the antenna (100µm)
- **D.** Lateral view of the antenna (100µm)
- **E.** Dorsal view of leg 5 (10µm)
- **F.** Dorsal view of the whole specimen attached to a gill filament (100µm)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Ergasilus sp. B

Type Host

Rhabdalestes maunensis (Fowler, 1935)

Type Locality

Okavango Delta, upper panhandle region (S18°26'05.0" ; E021°54'23.0")

Other Hosts

Characidae:

Brycinus lateralis (Boulenger, 1900)

Species Description (based on 20 specimens).

Total Length: Average total length 653µm (excluding the furcal setae) (Figs. 6.5A & 6.7F).

Cephalothorax: Oblong cephalic segment, average cephalothoracic width 220µm, length 369µm. Cephalic segment distinctly separated from first thoracic segment. Very few sensory setae present on dorsal surface of cephalic segment, distinct pattern of sensory pits present (Fig. 6.5D).

Ornamentation: Inverted T posterior to circular cephalic structure, anterior to oval cephalic structure. Two deep grooves occur on either side of oval cephalic structure extending to posterior margin.

Pigmentation: Eyespot blue pigmented, situated anterior to circular cephalic marking. Blue pigmentation present in cephalothoracic region.

Mouthparts: Unable to examine details of mouthparts (Fig. 6.7E).

Thorax: Thoracic segments decreasing in size, segments overlap posteriorly. Distinct pattern of sensory setae and pits visible (Fig. 6.5C). Intercoxal plate bordered by row of tooth-like spines, with seta present on each end (Fig. 6.6D).

Legs: Legs one to four bi-ramous, each rami three-segmented, exopodite of leg four two-segmented (Figs. 6.6B&C). First exopodal segment of leg one with group of long, fine comb-like setae along inner margin. First exopodal segment of leg two with group of long, fine comb-like setae along inner margin. Third endopodal segment of legs one and two with sensory pit near distal end. Leg five extremely reduced, one-segmented with single terminal seta, 3x length of leg (Figs. 6.6A & 6.7D). Spine-seta formulae provided in Table 6.2.

Table 6.2: Spine-seta formulae for *Ergasilus* von Nordmann, 1832 sp. B collected from *Rhabdalestes maunensis* (Fowler, 1935) from the Okavango River and Delta

	Coxa	Basis		Segment 1	Segment 2	Segment 3
Leg 1	o	1	Exopodite	I – 0	I – 1	II – 5
			Endopodite	0 – 1	0 – 1	II – 4
Leg 2	0	1	Exopodite	I* - 0	0 – 1	0 – 6
			Endopodite	0 - 1	0 – 2	I – 4
Leg 3	0	1	Exopodite	I* - 0	0 – 1	0 – 6
			Endopodite	0 - 1	0 – 2	I – 4
Leg 4	0	1	Exopodite	0 - 0	0 – 5	-
			Endopodite	0 – 1	0 – 2	I - 3

*very small spine

Abdomen: Four-segmented. Genital complex with three rows of tooth-like scales on dorsal side, inner row consisting of larger scales. Posterior margin of genital complex lined by row of comb-like spines. First and second free abdominal segments with row of comb-like spines along posterior margin. Third free abdominal segment medially split with row of approximately eight tooth-like spines on each side of split (Fig. 6.5B).

Furcal Rami: Longer than third free abdominal segment. Two sensory pits present on each ramus. Two rows of tooth-like spines present posterior to pits on each ramus. Four furcal setae present on each ramus (Fig. 6.5B).

Antennulae: Six-segmented (Fig. 6.7B).

Antennae: Antenna length 303 (260-395)µm, second segment very wide. Third segment with raised area on outer surface near distal end, segment four unadorned (Fig. 6.6E & 6.7A&C).

Egg Sacs: Egg sacs reaching nearly half the body length, approximately nine eggs in each sac (Figs. 6.5A & 6.7F).

Attachment to Host: Attach to distal third of gill filament, egg sacs do not protrude past end of gill filament.

Remarks: *Ergasilus* sp. B differs from *E. flaccidus, E. lamellifer* and *Ergasilus* sp. A by having a single-segmented fifth leg, while all three species have two-segments. *Ergasilus cunningtoni, E. latus* and *E. sarsi* have single-segmented fifth legs with three setae, *E. macrodactylus* and *E. mirabilis* have single-segmented fifth legs with two setae whilst *Ergasilus* sp. B has a single-segmented fifth leg with one terminal seta. The following three species differ from *Ergasilus* sp. B in the form of the antennae: *Ergasilus nodosus* has a swollen joint between segments two and three, *E. megacheir* has a recurved denticle on the terminal segment, *E. kandti* has a tooth on the distal inner side of the third segment. *Ergasilus* sp. B has unadorned antennal segments, with a very broad second segment and a raised area on the third segment.

Based on the above description and the differences between *Ergasilus* sp. B and the known species there is little doubt that *Ergasilus* sp. B is a new species. The combination of the following characteristics distinguish this species from the others:

- Cephalic segment of a characteristic shape.
- Antenna with a very broad second segment, and a raised area on the third segment.
- Four segmented abdomen with a distint distribution of spines on the ventral surface.
- Fifth leg, single-segmented with one terminal seta.

Figure 6.5

Line drawings of *Ergasilus* von Nordmann, 1832 sp. B collected from *Rhabdalestes maunensis* (Fowler, 1935) collected from the Okavango River and Delta

A. Dorsal view of whole specimen (100μm)

B. Ventral view of the abdomen (10μm)

C. Sensory setae and pits on the dorsal surface of the thorax (100μm)

D. Sensory pits on the dorsal surface of the cephalic segment (10μm)

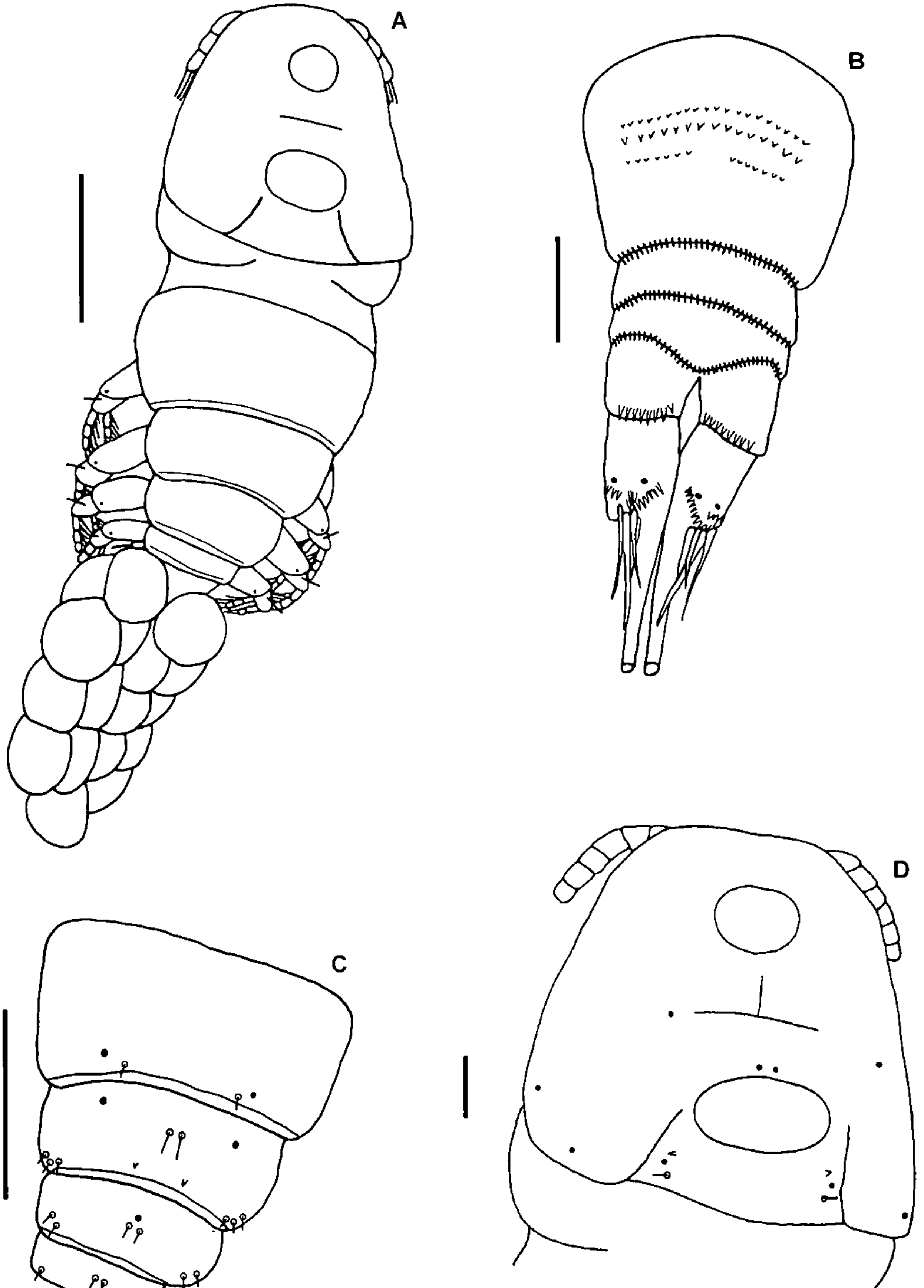

A
B
C
D

Figure 6.6

Line drawings of *Ergasilus* von Nordmann, 1832 sp. B collected from *Rhabdalestes maunensis* (Fowler, 1935) from the Okavango River and Delta

A. Leg 5 (10µm)

B. Leg 1 (10µm)

C. Leg 2 (10µm)

D. Intercoxal bar and plate (10µm)

E. Lateral view of the antenna (10µm)

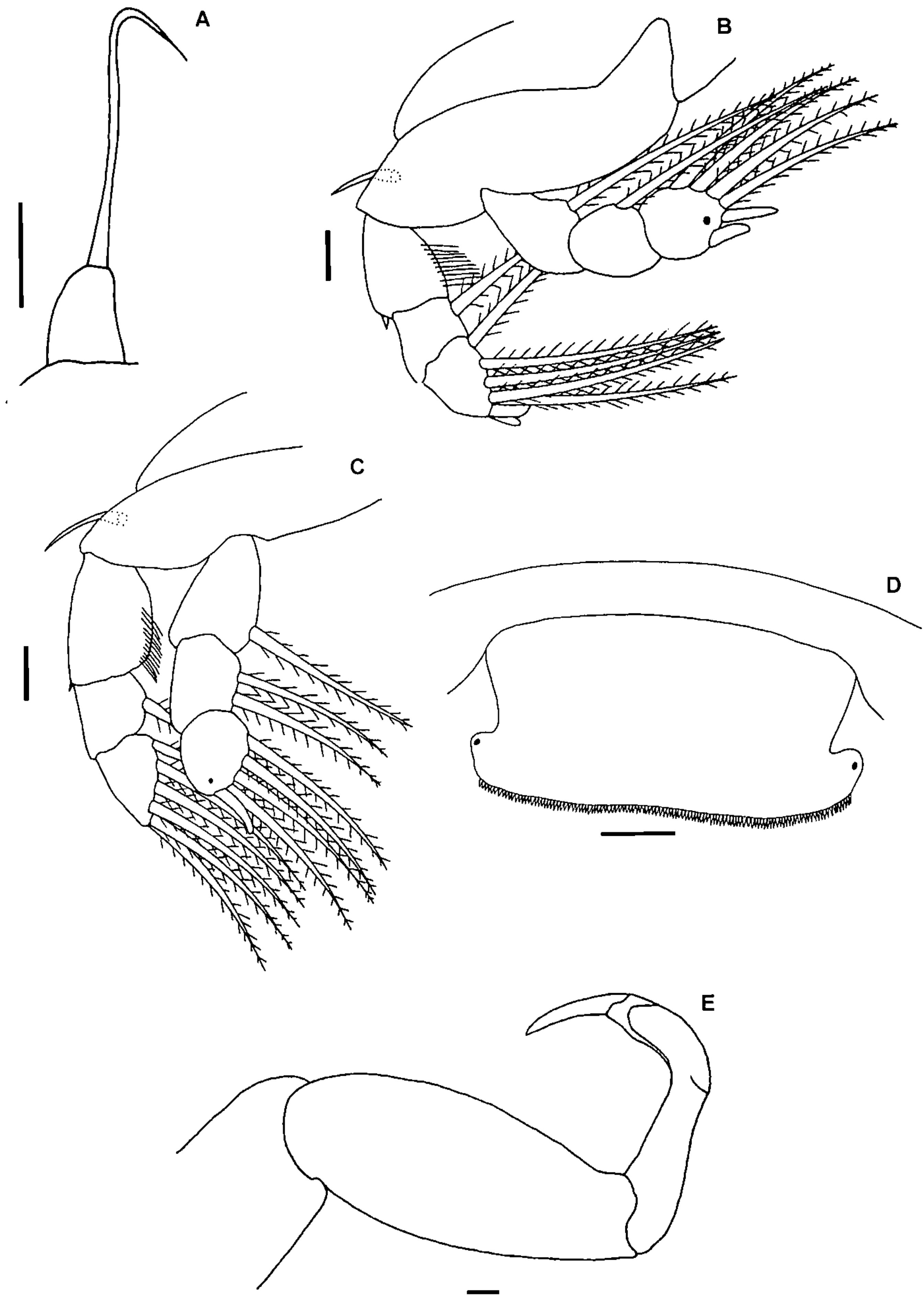

A
B
C
D
E

Figure 6.7

Scanning electron micrographs of *Ergasilus* von Nordmann, 1832 sp. B collected from *Rhabdalestes maunensis* (Fowler, 1935) from the Okavango River and Delta

A. Second and third segments of the antenna (10µm)

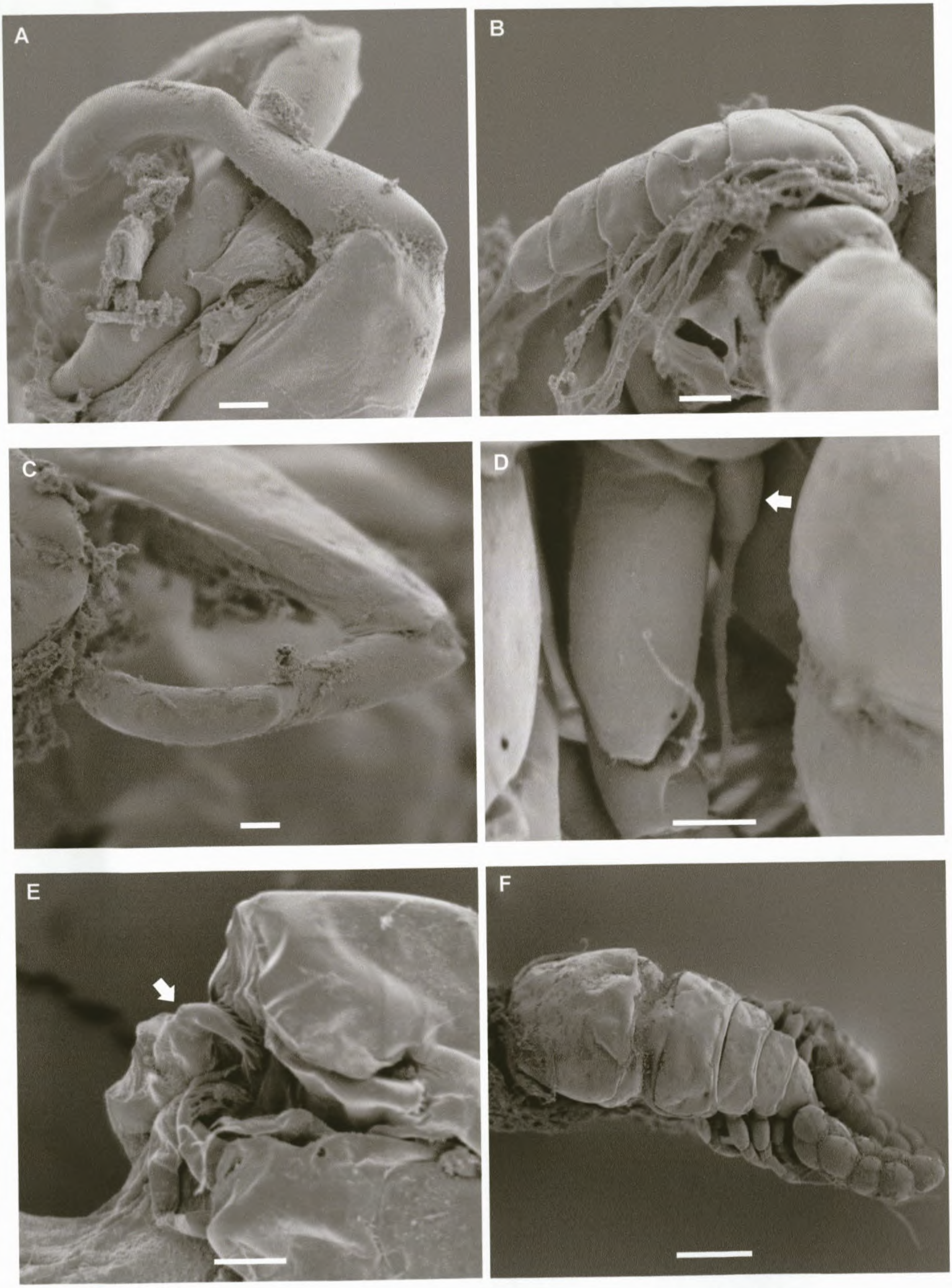
B. Antennule (10µm)

C. Second segment of the antenna (10µm)

D. Dorsal view of leg 5, arrow indicates leg 5 (10µm)

E. Mouth, arrow indicates leg 5 (10µm)

F. Dorsal view of the whole specimen attached to a gill filament (100µm)


A
B
C
D
E
F

Seasonality of the Ergasilids Collected from the Okavango River and Delta

Over the course of the eight years that this study has been underway, crustacean parasites have been collected from 27 fish species from seven of the total 15 familes (Table 6.3). When considering the *Ergasilus* specimens alone, they have been collected from 16 fish species and seven families (Table 6.4). Collections have been conducted during both the winter and summer months, giving very distinct results.

When considering the four surveys that took place during the winter months many fish were collected, but very few were parasitised, such as the following for example:

- *Synodontis nigromaculatus* – 39 collected, 4 parasitised; only 10% were parasitised.
- *Brycinus lateralis* – 39 collected, 3 parasitised; only 8% were parasitised.

But when you consider the same two species, collected during the four summer surveys, the figures are very different:

- *Synodontis nigromaculatus* – 112 collected, 58 parasitised; 52% were parasitised.
- *Brycinus lateralis* – 44 collected, 23 parasitised; 52% were parasitised.

Figure 6.8 illustrates the parasitised fish species that were collected in both summer and winter months, with the total number of fish and the total number parasitised provided. The seasonal differences in the collections are illustrated in Figure 6.9 - winter statistics, and Figure 6.10 - summer statistics. There is also a marked difference in the number of *Ergasilus* specimens collected from the different hosts with 410 specimens collected from *S. nigromaculatus* and 206 specimens collected from *R. maunensis*. These figures can be seen in Table 6.4.

From these statistics it can be deduced that the ergasilids are more prevalent in the summer months than in the winter months. The Okavango Fish Parasite Project is still underway so information will continue to be collected.

Table 6.3: List of all the fish species and families found in the Okavango River and Delta [Compiled using Skelton (2001)], with all the parasitic crustaceans collected between 1997 and 2004. **S.** skin, **G.** gills, **M.** mouth, **1.** *Lamproglena* von Nordmann, 1832 **2.** *Afrolernaea* Fryer, 1956 **3.** *Opistolernaea* Yin, 1960 **4.** *Ergasilus* von Nordmann, 1832 **5.** *Dolops* Audouin, 1837 **6.** *Chonopeltis* Thiele, 1900 **7.** *Argulus* Müller, 1785 **8.** *Lernaea* Linnaeus, 1746

FISH SPECIES AND FAMILIES	1	2	3	4	5	6	7	8
Mormyridae								
Hippopotamyrus ansorgii (Boulenger, 1905)								
Cyphomyrus discorhynchus (Peters, 1852)								
Marcusenius macrolepidotus (Peters, 1852)		G		**G**				
Mormyrus lacerda Castelnau, 1861				**G**		G		
Petrocephalus catostoma (Günther, 1866)				**G**				
Petrocephalus wesselsi (Kramer & van den Bank, 2000)								
Pollimyrus castelnaui (Boulenger, 1911)								
Kneriidae								
Kneria polli Trewavas, 1936								
Parakneria fortuita Penrith, 1973								
Cyprinidae								
Barbus afrovernayi Nichols & Boulton, 1927								
Barbus barotseensis Pellegrin, 1920								
Barbus barnardi Jubb, 1965								
Barbus bifrenatus Fowler, 1935								
Barbus brevidorsalis Boulenger, 1915								
Barbus breviceps Trewavas, 1936								
Barbus codringtoni Boulenger, 1908								
Barbus eutaenia Boulenger, 1904								
Barbus fasciolatus Günther, 1868								
Barbus haasianus David, 1936								
Barbus kerstenii Peters, 1868								
Barbus lineomaculatus Boulenger, 1903								
Barbus miolepis Boulenger, 1902								
Barbus multilineatus Worthington, 1933								
Barbus paludinosus Peters, 1852								
Barbus poechii Steindachner, 1911								
? *Barbus puellus* Nichols& Boulton, 1927								
Barbus radiatus Peters, 1853								
? *Barbus tangandensis* Jubb, 1954								
Barbus thamalakanensis Fowler, 1935								
Barbus unitaeniatus Günther, 1866								
Barbus spp.								
Coptostomabarbus wittei David & Poll, 1937								
Labeo cylindricus Peters, 1852								
Labeo lunatus Jubb, 1963								
Mesobola brevianalis (Boulenger, 1908)								
Opsaridium zambezense (Peters, 1852)								
Distichodontidae								
Hemigrammocharax machadoi Poll, 1967								
Hemigrammocharax multifasciatus Boulenger, 1923								
Nannocharax macropterus Pellegrin, 1925								
Characidae								
Brycinus lateralis (Boulenger, 1900)				**G**				
Hydrocynus vittatus Castelnau, 1861								
Micralestes acutidens (Peters, 1852)								
Rhabdalestes maunensis (Fowler, 1935)				**G**				
Hepsetidae								
Hepsetus odoe (Bloch, 1794)	G			**G**	S			
Claroteidae								
Parauchenoglanis ngamensis (Boulenger, 1911)								

Table 6.3 (cont.): List of all the fish species and families found in the Okavango River and Delta [Compiled using Skelton (2001)], with all the parasitic crustaceans collected between 1997 and 2004. **S.** skin, **G.** gills, **M.** mouth, **1.** *Lamproglena* von Nordmann, 1832 **2.** *Afrolernaea* Fryer, 1956 **3.** *Opistolernaea* Yin, 1960 **4.** *Ergasilus* von Nordmann, 1832 **5.** *Dolops* Audouin, 1837 **6.** *Chonopeltis* Thiele, 1900 **7.** *Argulus* Müller, 1785 **8.** *Lernaea* Linnaeus, 1746

FISH SPECIES AND FAMILIES	1	2	3	**4**	5	6	7	8
Amphiliidae								
Leptoglanis rotundiceps (Hilgendorf, 1905)								
Leptoglanis sp Boulenger, 1902								
Amphilius uranoscopus (Pfeffer, 1889)								
Schilbeidae								
Schilbe intermedius Rüppell, 1832				**G**	M			
Clariidae								
? *Clarias dumerilii* Steindachner, 1866								
Clarias gariepinus (Burchell, 1822)	G	G	G	**G**	G S		S	
Clarias liocephalus Boulenger, 1898								
Clarias ngamensis Castelnau, 1861								
Clarias stappersii Boulenger, 1915					G			
Clarias theodorae Weber, 1897								
Clariallabes platyprosopos Jubb, 1964								
Mochokidae								
Chiloglanis fasciatus Pellegrin, 1936								
Synodontis leopardinus Pellegrin, 1914								
Synodontis macrostigma Boulenger, 1911						S		
Synodontis macrostoma Skelton & White, 1990								
Synodontis nigromaculatus Boulenger, 1905	G			**G**	G	S		
Synodontis thamalakanensis Fowler, 1935				**G**		S		
Synodontis vanderwaali Skelton & White, 1990				**G**		S		S
Synodontis woosnami Boulenger, 1911				**G**				
Cyprinodontidae								
Aplocheilichthys hutereaui (Boulenger, 1913)								
Aplocheilichthys johnstonii Günther, 1893								
Aplocheilichthys katangae (Boulenger, 1912)								
Aplocheilichthys sp. Bleeker, 1863								
Cichlidae								
Hemichromis elongatus (Guichenot, 1859)								
Oreochromis andersonii (Castelnau, 1861)	G		G		G S			
Oreochromis macrochir (Boulenger, 1912)	G		G		G			
Pharyngochromis acuticeps (Steindachner, 1866)	G							
Pseudocrenilabrus philander (Weber, 1897)								
Sargochromis carlottae (Boulenger, 1905)	G							S
Sargochromis codringtoni (Boulenger, 1908)	G							
Sargochromis giardi (Pellegrin, 1903)	G							
Sargochromis greenwoodi (Bell-Cross, 1975)	G							
Serranochromis altus Winemiller & Kelso-Winemiller, 1990								
Serranochromis angusticeps (Boulenger, 1907)	G			**G**				S
Serranochromis longimanus (Boulenger, 1911)								
Serranochromis robustus (Günther, 1864)	G				S			
Serranochromis macrocephalus (Boulenger, 1899)	G			**G**	S			
Serranochromis thumbergi (Castelnau, 1861)	G							
Tilapia rendalli rendalli (Boulenger, 1896)	G				S			S
Tilapia ruweti (Poll & Thys van den Audenaerde, 1965)								
Tilapia sparrmanii A. Smith, 1840	G							S

Table 6.3 (cont.): List of all the fish species and families found in the Okavango River and Delta [Compiled using Skelton (2001)], with all the parasitic crustaceans collected between 1997 and 2004. **S.** skin, **G.** gills, **M.** mouth, **1.** *Lamproglena* von Nordmann, 1832 **2.** *Afrolernaea* Fryer, 1956 **3.** *Opistolernaea* Yin, 1960 **4.** *Ergasilus* von Nordmann, 1832 **5.** *Dolops* Audouin, 1837 **6.** *Chonopeltis* Thiele, 1900 **7.** *Argulus* Müller, 1785 **8.** *Lernaea* Linnaeus, 1746

FISH SPECIES AND FAMILIES	1	2	3	4	5	6	7	8
Anabantidae								
Microctenopoma intermedium (Pellegrin, 1920)								
Ctenopoma multispine Peters, 1844								
Mastacembelidae								
Aethiomastacembelus frenatus (Boulenger, 1901)								
Aethiomastacembelus vanderwaali (Skelton, 1976)								

Table 6.4: List of all the fish species collected from the Okavango Delta in both winter and summer, with the total fish collected (T), the total fish parasitised (P) and the total number of ergasilids collected (TE), shaded areas indicate the fish species on which *Ergasilus* von Nordmann, 1832 specimens were collected.

Fish species and Families	**WINTER**			**SUMMER**			**TOTAL**			**TE**
Family Mormyridae	**T**	**P**	**%**	**T**	**P**	**%**	**T**	**P**	**%**	
Mormyrus lacerda Castelnau, 1861	28	5	**18**	2	1	**50**	30	5	**17**	14
Marcusenius macrolepidotus (Peters, 1852)	104	1	**1**	14	4	**29**	118	5	**4**	6
Petrocephalus catastoma (Günther, 1866)	16	0	**0**	14	2	**14**	30	2	**7**	7
Pollimyrus castelnaui (Boulenger, 1911)	1	0	**0**	1	0	**0**	2	0	**0**	0
Family Cyprinidae										
Barbus bifrenatus Fowler, 1935	19	0	**0**	0	0	**0**	19	0	**0**	0
B. thamalakanensis Fowler, 1935	38	0	**0**	3	0	**0**	41	0	**0**	0
B. barnardi Jubb, 1965	37	0	**0**	0	0	**0**	37	0	**0**	0
B. fasciolatus Günther, 1868	3	0	**0**	1	0	**0**	4	0	**0**	0
B. radiatus Peters, 1853	7	0	**0**	0	0	**0**	7	0	**0**	0
B. haasianus David, 1936	39	0	**0**	0	0	**0**	39	0	**0**	0
B. poechii Steindachner, 1911	52	0	**0**	36	0	**0**	88	0	**0**	0
B. eutaenia Boulenger, 1904	3	0	**0**	0	0	**0**	3	0	**0**	0
B. multilineatus Worthington, 1933	42	0	**0**	0	0	**0**	42	0	**0**	0
B. afrovernayi Nichols & Boulton, 1927	60	0	**0**	0	0	**0**	60	0	**0**	0
B. unitaeniatus Günther, 1866	1	0	**0**	0	0	**0**	1	0	**0**	0
B. kerstenii Peters, 1868	0	0	**0**	1	0	**0**	1	0	**0**	0
B. paludinosus Peters, 1852	67	0	**0**	0	0	**0**	67	0	**0**	0
Labeo lunatus Jubb, 1963	4	0	**0**	0	0	**0**	4	0	**0**	0
Coptostomabarbus wittei David & Poll, 1937	20	0	**0**	0	0	**0**	20	0	**0**	0
Mesobolo brevianalis (Boulenger, 1908)	1	0	**0**	0	0	**0**	1	0	**0**	0
Family Distichodontidae										
Hemigrammocharax multifasciatus Boulenger, 1923	18	0	**0**	0	0	**0**	18	0	**0**	0
H. machadoi	7	0	**0**	0	0	**0**	7	0	**0**	0
Family Characidae										
Micralestes acutidens (Peters, 1852)	55	0	**0**	20	0	**0**	75	0	**0**	0
Brycinus lateralis (Boulenger, 1900)	39	3	**8**	44	23	**52**	83	24	**29**	33
Rhabdalestes maunensis (Fowler, 1935)	51	0	**0**	131	76	**58**	182	76	**42**	206
Hydrocynus vittatus Castelnau, 1861	49	0	**0**	15	0	**0**	64	0	**0**	0
Family Hepsetidae										
Hepsetus odoe (Bloch, 1794)	128	1	**1**	51	7	**21**	179	8	**9**	2
Family Schilbeidae										
Schilbe intermedius Rüppel, 1832	60	0	**0**	48	10	**21**	108	10	**9**	135
Family Claroteidae										
Parauchenoglanis ngamensis (Boulenger, 1911)	0	0	**0**	1	0	**0**	1	0	**0**	0
Family Clariidae										
Clarias gariepinus (Burchell, 1822)	63	2	**3**	37	3	**8**	100	5	**5**	10
C. stappersii Boulenger, 1915	2	0	**0**	2	0	**0**	4	0	**0**	0
C. theodorae Weber, 1897	28	0	**0**	1	0	**0**	29	0	**0**	0
C. ngamensis Castelnau, 1861	1	0	**0**	0	0	**0**	1	0	**0**	0

Table 6.4 (cont.): List of all the fish species collected from the Okavango Delta in both winter and summer, with the total fish collected (T), the total fish parasitised (P) and the total number of ergasilids collected (TE), shaded areas indicate the fish species on which *Ergasilus* von Nordmann, 1832 specimens were collected.

Fish species and Families	**WINTER**			**SUMMER**			**TOTAL**			**TE**
Family Mochokidae	**T**	**P**	**%**	**T**	**P**	**%**	**T**	**P**	**%**	
Synodontis nigromaculatus Boulenger, 1905	39	4	**10**	112	58	**52**	151	62	**41**	410
S. woosnami Boulenger, 1911	14	0	**0**	8	4	**50**	22	4	**18**	12*
S. thamalakanensis Fowler, 1935	5	1	**20**	10	4	**40**	15	5	**33**	21
S. macrostigma Boulenger, 1911	4	0	**0**	6	0	**0**	10	0	**0**	0
S. vanderwaali Skelton & White, 1990	2	0	**0**	42	27	**64**	44	27	**64**	157
S. leopardinus Pellegrin, 1914	0	0	**0**	2	0	**0**	2	0	**0**	0
Family Poeciliidae										
Aplocheilichthys johnstoni Günther, 1893	44	0	**0**	1	0	**0**	45	0	**0**	0
A. hutereaui (Boulenger, 1913)	205	0	**0**	0	0	**0**	205	0	**0**	0
A. katangae (Boulenger, 1912)	55	0	**0**	0	0	**0**	55	0	**0**	0
Family Cichlidae									**0**	
Pseudocrenilabrus philander (Weber, 1897)	270	0	**0**	7	0	**0**	277	0	**0**	0
Pharyngochromis acuticeps (Steindachner, 1866)	30	0	**0**	3	0	**0**	33	0	**0**	0
Sargochromis carlottae (Boulenger, 1905)	28	0	**0**	5	0	**0**	33	0	**0**	0
S. codringtonii (Boulenger, 1908)	6	0	**0**	1	0	**0**	7	0	**0**	0
S. giardi (Pellegrin, 1903)	9	0	**0**	1	0	**0**	10	0	**0**	0
S. greenwoodi (Bell-Cross, 1975)	27	0	**0**	2	0	**0**	29	0	**0**	0
S. mortimeri (Bell-Cross, 1975)	1	0	**0**	0	0	**0**	1	0	**0**	0
Serranochromis altus Winemiller & Kelso-Winemiller, 1990	3	0	**0**	0	0	**0**	3	0	**0**	0
S. angusticeps (Boulenger, 1907)	39	2	**5**	21	7	**33**	60	9	**15**	103
S. longimanus (Boulenger, 1911)	2	0	**0**	0	0	**0**	2	0	**0**	0
S. macrocephalus (Boulenger, 1899)	29	0	**0**	20	10	**50**	49	10	**20**	164
S. robustus (Günther, 1864)	11	0	**0**	3	0	**0**	14	0	**0**	0
S. thumbergi (Castelnau, 1861)	3	0	**0**	7	0	**0**	10	0	**0**	0
Tilapia sparrmanii A. Smith, 1840	178	0	**0**	20	0	**0**	198	0	**0**	0
T. ruweti (Poll & Thys van den Audenaerde, 1965)	23	0	**0**	0	0	**0**	23	0	**0**	0
T. rendalli (Boulenger, 1896)	99	1	**1**	26	0	**0**	125	1	**1**	2
Oreochromis andersonii (Castelnau, 1861)	114	2	**2**	28	0	**0**	142	2	**1**	5
O. macrochir (Boulenger, 1912)	19	0	**0**	67	0	**0**	86	0	**0**	0
Family Anabantidae										
Ctenopoma multispine (Peters, 1844)	25	0	**0**	0	0	**0**	25	0	**0**	0
Microctenopoma intermedium (Pellegrin, 1920)	58	0	**0**	0	0	**0**	58	0	**0**	0

* no adult *Ergasilus* specimens found, only copepodites

Figure 6.8: Graph representing all sixteen fish species collected from the Okavango River and Delta on which ergasilids were found, with the column in the background being the total number of fish collected and the column in the foreground being the number of fish parasitised.

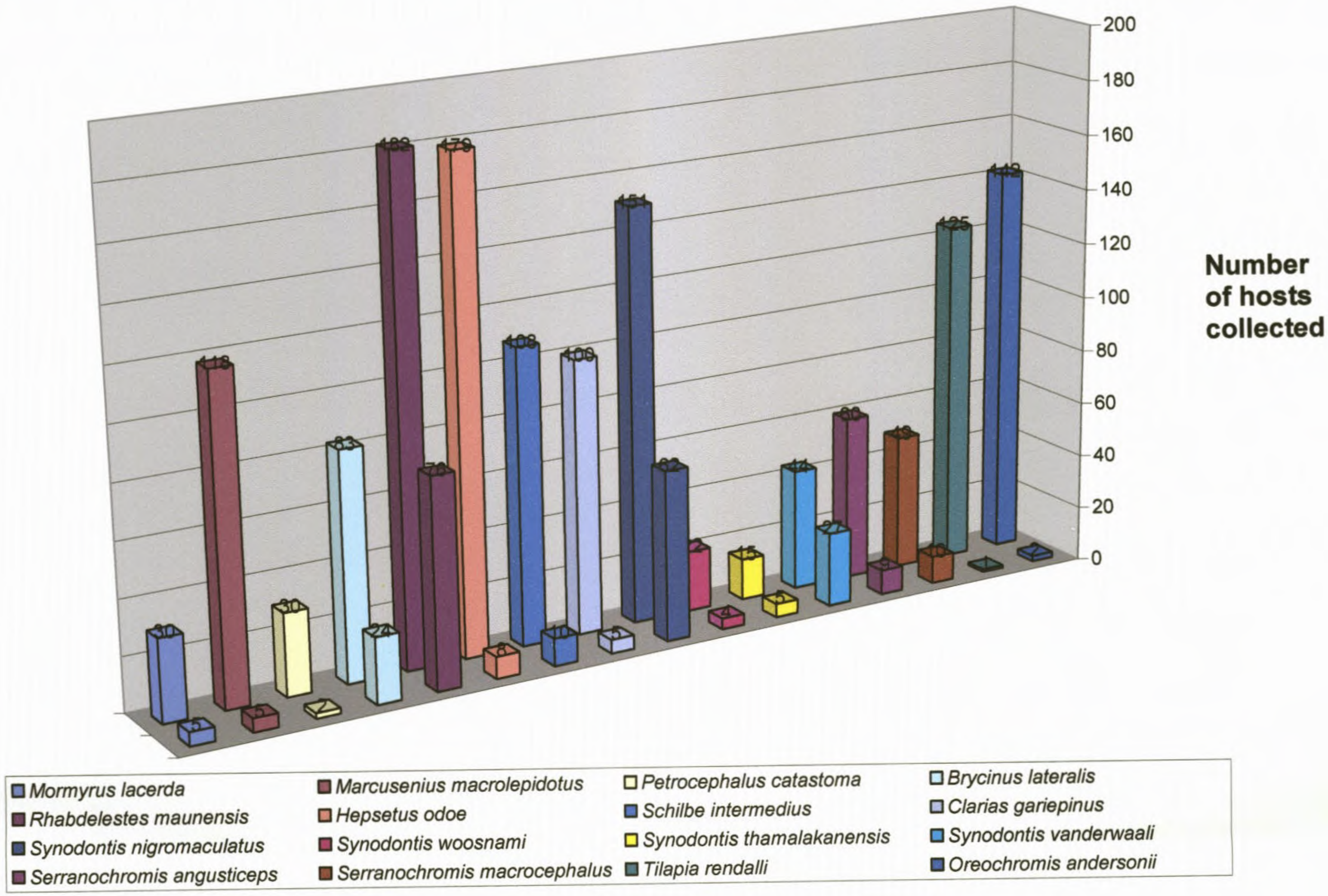


Figure 6.9: Graph representing all sixteen fish species collected from the Okavango River and Delta on which ergasilids were found in the winter months of June to August, with the column in the background being the total number of fish collected and the column in the foreground being the number of fish parasitised.

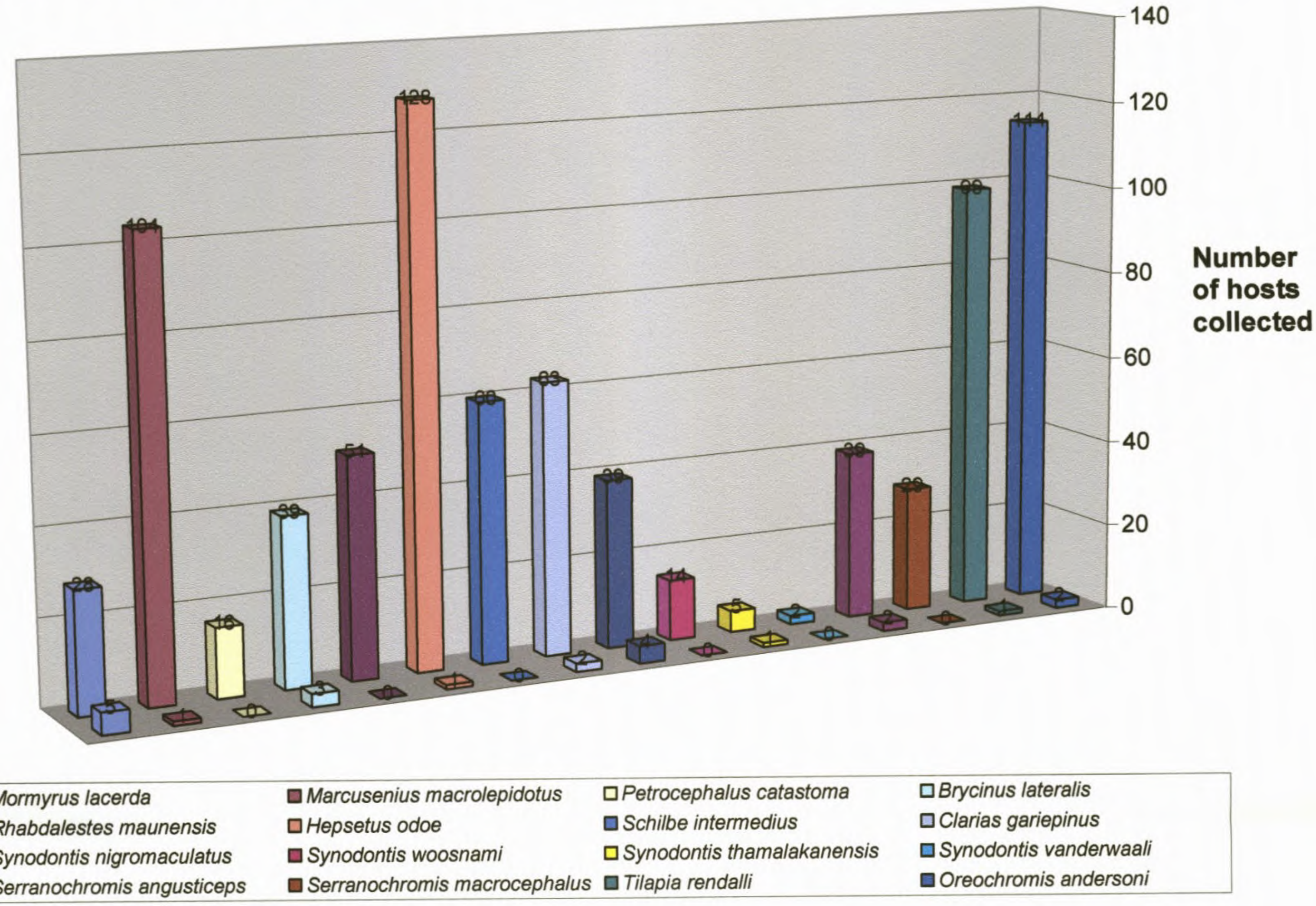
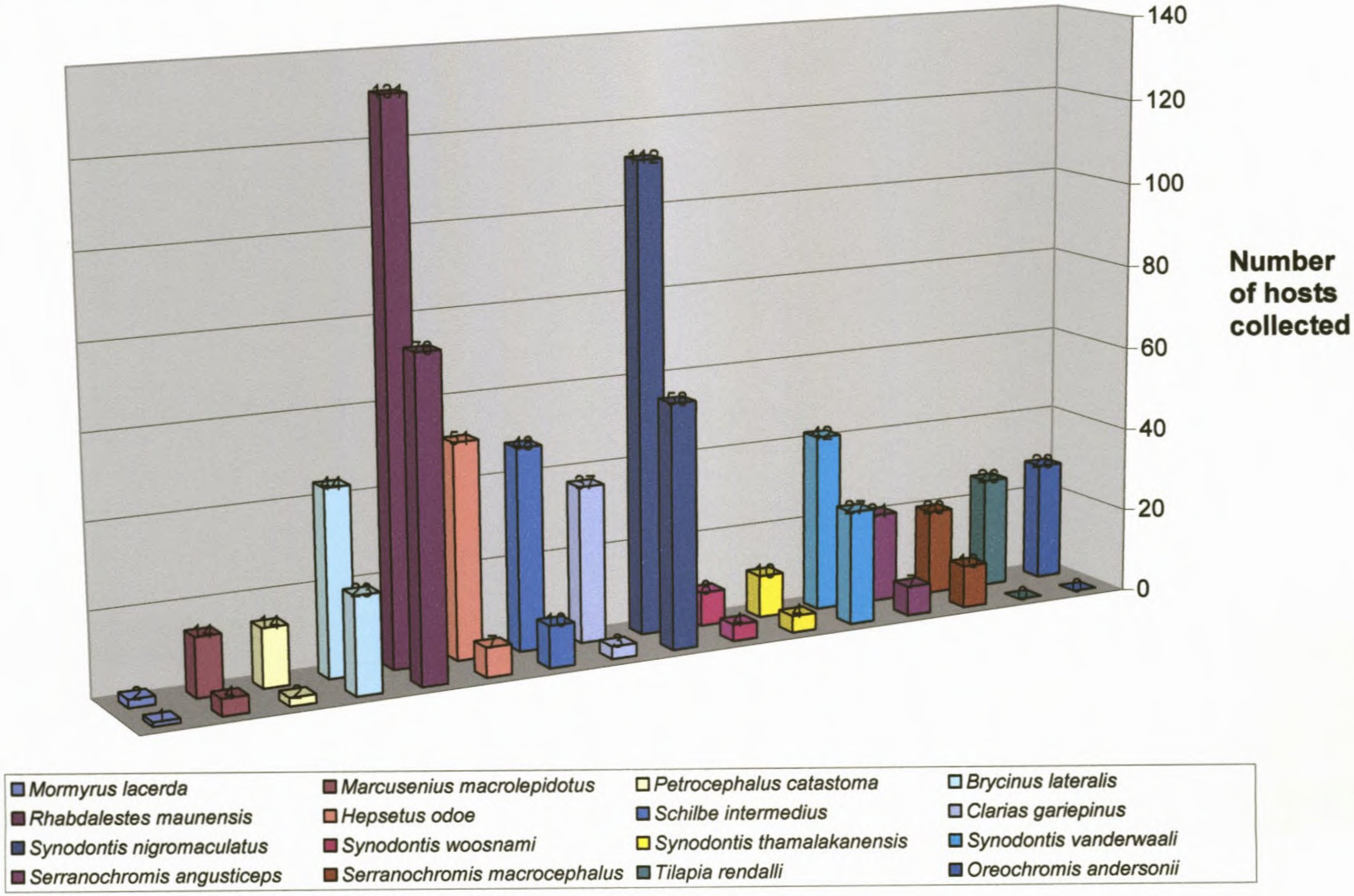


Figure 6.10: Graph representing all sixteen fish species collected from the Okavango River and Delta on which ergasilids were found in the summer months of October to January, with the column in the background being the total number of fish collected and the column in the foreground being the number of fish parasitised.



6.2 Results from Lake Malawi

Descriptions of the Species Collected

***Ergasilus* sp. C**

Type Host

Petrotilapia genalutea Marsh, 1983

Type Locality

Lake Malawi, southeastern arm (Fig. 3.7)

Other Hosts

Aristichromis christyi Trewavas, 1935
Melanochromis auratis (Boulenger, 1897)
Petrotilapia nigra Marsh, 1983
P. tridentiger Trewavas, 1935
Pseudotropheus tropheops Regan, 1922
Rhamphochromis sp. Regan, 1922
Stigmatochromis woodi Regan, 1922
Taenilethrinops praeorbitalis (Regan, 1922)
Tyrannochromis macrostoma Regan, 1922
T. nigriventer Eccles, 1989

Species Description (based on 25 specimens)

Total Length: Mean length 0.76mm (0.7-0.8mm range) excluding the furcal setae (Figs. 6.11A & 6.13A).

Cephalothorax: Cephalic segment quadrangular, distinctly separated from first cephalic segment (Figs. 6.11A&D).

Ornamentation: Oval and circular cephalic structures present, with raised U-shaped marking (no inverted T structure) situated between these two structures. Two small oval structures present, anterior to circular cephalic structure. Distinct distribution of sensory setae and pits on cephalic segment.

Pigmentation: Preserved material was examined, no pigmentation visible.

Mouthparts: Unable to examine details of mouthparts (Fig. 6.13B).

Thorax: Thoracic segments decreasing gradually posteriorly. Sensory setae and pits present on dorsal side of thoracic segments one to four (Fig. 6.11E), absent on segment five. Plate on intercoxal bar of legs 1-3 with fine comb-like spines along posterior margin, single sensory pit on both posterior corners (Fig. 6.11C).

Legs: Spine-seta formula similar to other *Ergasilus* species (Figs. 6.12A-C & 6.13E). Ventral surface of coxa of leg one with three groups of small tooth-like scales, basis with two larger groups of small tooth-like scales. Ventral surface of basis of legs two and three with line of small comb-like spines. Ventral surface of basis of leg four with line of larger tooth-like spines. Dorsal surface of exopod of legs one to three possessing ridges of comb-like spines, two ridges on segments one and two, one ridge on segment three. Leg five two-segmented, basal segment with single seta, distal segment with two teminal setae (Figs. 6.12E & 6.13F). Spine-seta formula provided in Table 6.5.

Table 6.5: Spine-seta formula for *Ergasilus* von Nordmann, 1832 sp. C collected from *Petrotilapia genalutea* Marsh, 1983 from the southeastern arm of Lake Malawi

	Coxa	Basis		Segment 1	Segment 2	Segment 3
Leg 1	o	1	Exopodite	I – 0	I – 1	II – 5
			Endopodite	0 – 1	0 – 1	II – 4
Leg 2	0	1	Exopodite	I – 0	0 – 1	0 – 6
			Endopodite	0 – 1	0 – 2	I – 4
Leg 3	0	1	Exopodite	I – 0	0 – 1	0 – 6
			Endopodite	0 – 1	0 – 2	I – 4
Leg 4	0	1	Exopodite	I – 0	0 – 5	-
			Endopodite	0 – 1	0 – 2	I – 3

Abdomen: Four-segmented. Genital segment with small comb-like spines along posterior ventral margin. Segment two and three with small comb-like spines along posterior ventral margin. Segment four with line of approximately eight larger tooth-like spines (Fig. 6.11B).

Furcal Rami: Longer than wide with two sensory pits near posterior end, posterior to sensory pits are two groups of tooth-like spines (Fig. 6.11B), first group with approximately twelve spines, second group with approximately ten spines. Four furcal setae present.

Antennulae: Six-segmented.

Antennae: Four-segmented, second segment unadorned, when viewed ventrally possesses large bulge on inner side. Segment three very straight with small central notch, inner margin possesses blade-like lamella beginning medially towards distal end of segment three. Segment four unadorned (Figs. 6.12D & 6.13C&D).

Egg Sacs: Average length 0.47mm with approximately eleven eggs in each sac (Figs. 6.11A & 6.13A).

Attachment on Host: Attach to distal end of gill filament, with egg sacs protruding.

Remarks: *Ergasilus* sp. C differs from *Ergasilus* sp. B., *E. cunningtoni, E. kandti, E. latus, E. macrodactylus, E. megacheir, E. mirabilis* and *E. sarsi* by having a two-segmented fifth leg, while these eight species all have single-segmented fifth legs. *Ergasilus* sp. A, *E. nodosus, E. flaccidus* and *E. lamellifer* differ from *Ergasilus* sp. C in the form of their antennae. *Ergasilus* sp. A has an unadorned antenna with a twisted third segment, and *E. nodosus* has a swollen joint between segment two and three. *Ergasilus flaccidus* has a chitinous finger at the distal end of the second antennal segment, *E. lamellifer* has a blade-like chitinous lamella on the inner margin of the second antennal segment. *Ergasilus* sp. C has a very straight third antennal segment with a small central notch, the inner margin of this segment possesses a blade-like lamella beginning medially towards the distal end.

Based on the above description and the differences between *Ergasilus* sp. C and the known species there is little doubt that *Ergasilus* sp. C is a new species. The combination of the following characteristics distinguish this species from the others:

- Cephalic segment has a raised U-shaped structure situated between the oval and circular cephalic structure.
- Legs one to three with distinct ridges of comb-like spines on the outer margin.
- Antenna with a notch on the outer margin of segment three and a blade-like lamella beginning medially towards the distal end on the inner margin.

Figure 6.11

Line drawings of *Ergasilus* von Nordmann, 1832 sp. C collected from *Petrotilapia genalutea* Marsh, 1983 from the south-eastern arm of Lake Malawi

A. Dorsal view of whole specimen (100µm)

B. Ventral view of abdomen (50µm)

C. Intercoxal bar and plate (100µm)

D. Sensory setae and pits on the dorsal surface of the cephalic segment (100µm)

E. Sensory setae and pits on the dorsal surface of the thorax (100µm)

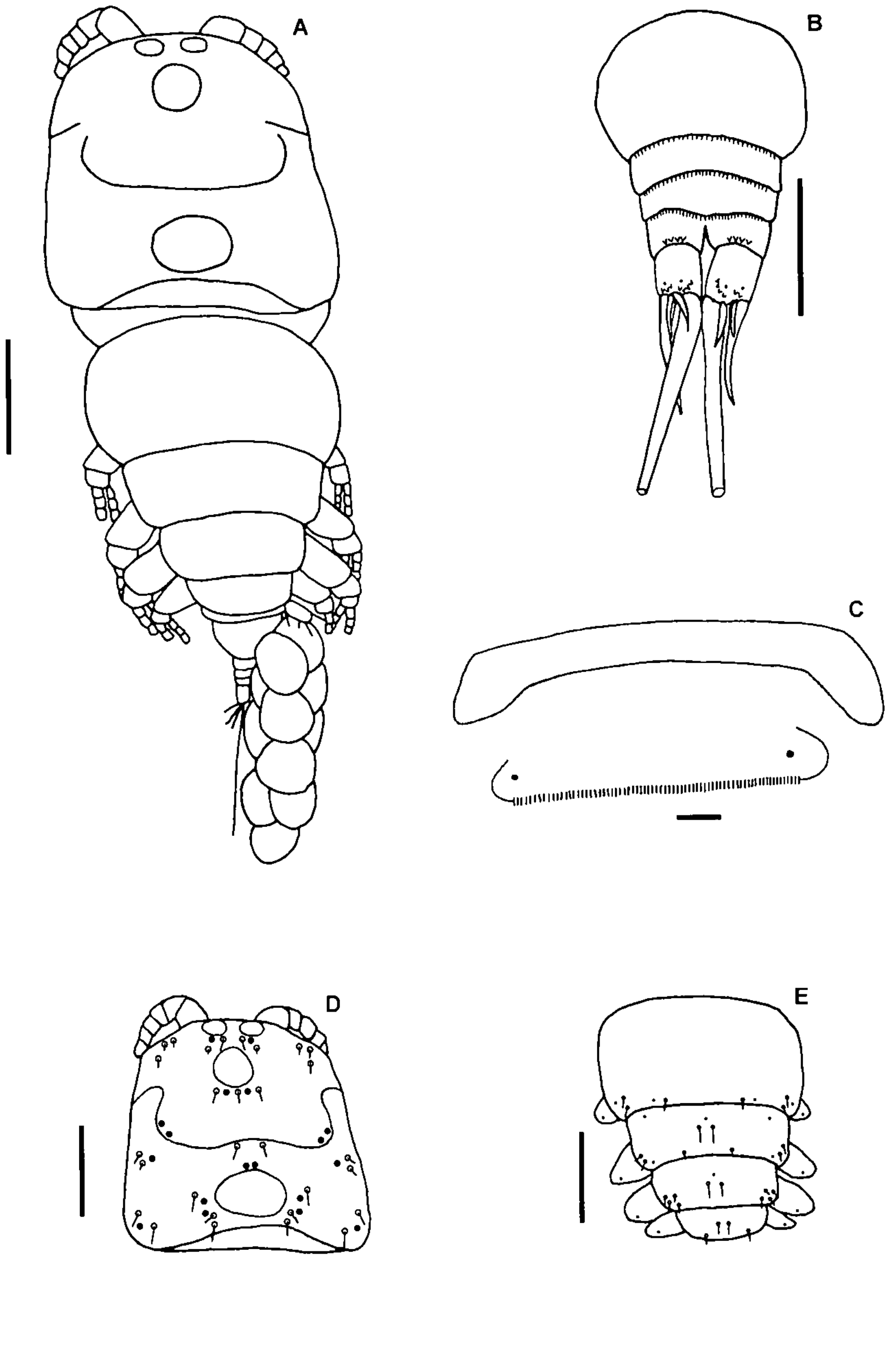

A
B
C
D
E

Figure 6.12

Line drawings of *Ergasilus* von Nordmann, 1832 sp. C collected from *Petrotilapia genalutea* Marsh, 1983 from the south-eastern arm of Lake Malawi

A. Leg 1 (50µm)

B. Leg 2 (50µm)

C. Leg 4 (50µm)

D. Lateral view of the antenna (100µm)

E. Leg 5 (10µm)

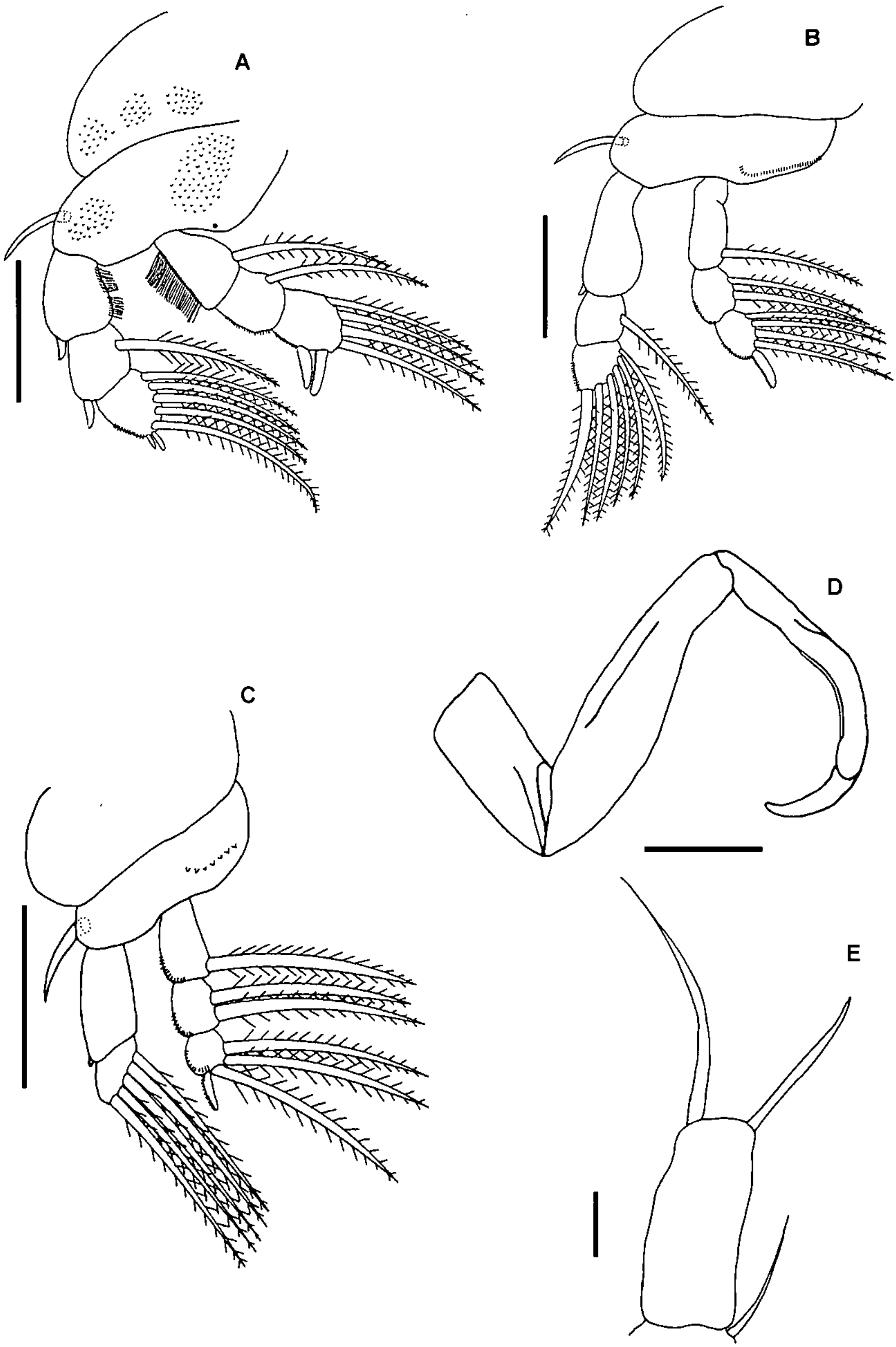

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Figure 6.13

Scanning electron micrographs of *Ergasilus* von Nordmann, 1832 sp. C collected from *Petrotilapia genalutea* Marsh, 1983 from the south-eastern arm of Lake Malawi

A. Dorsal view of the whole specimen attached to a gill filament (100µm)

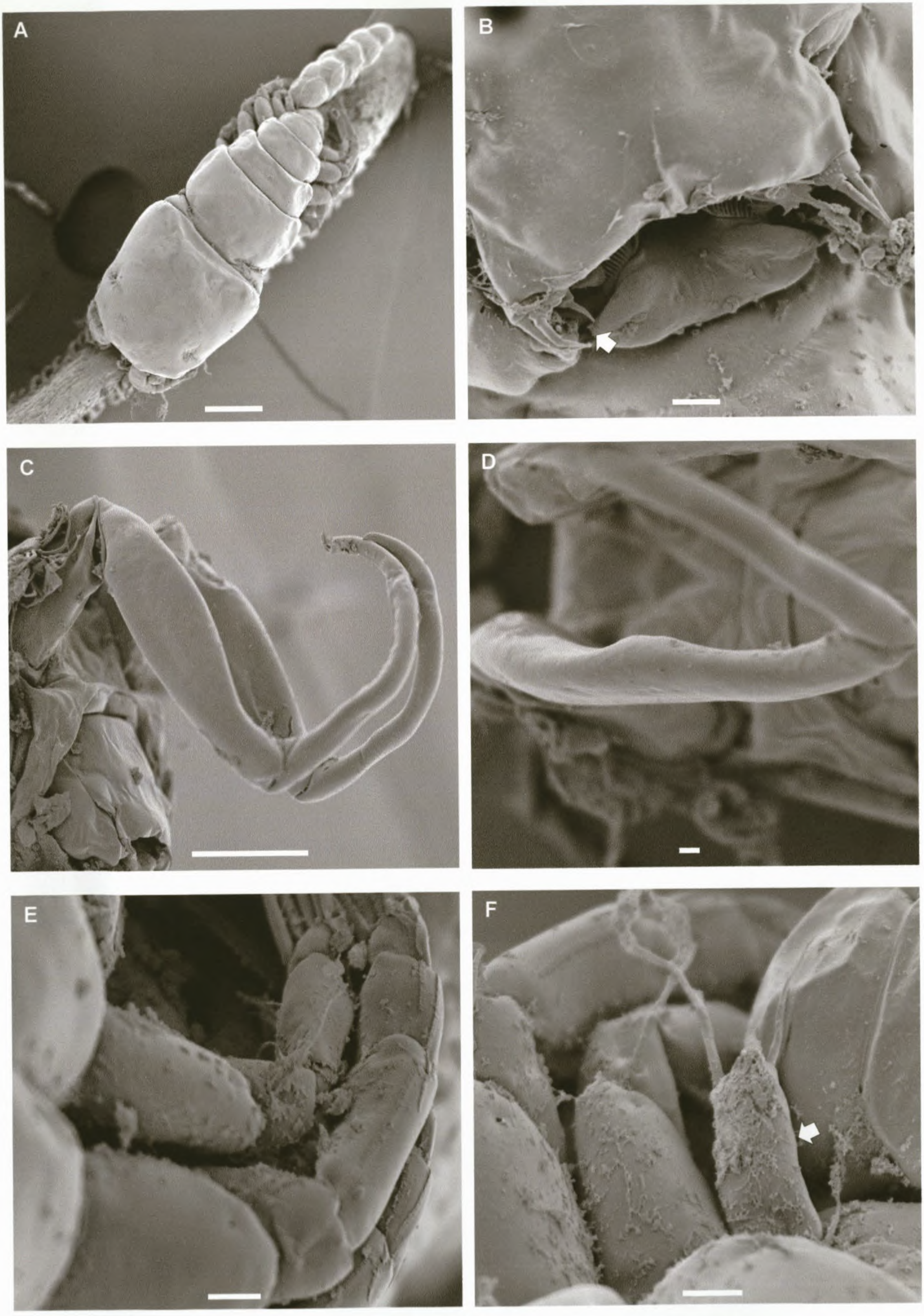
B. Mouth, arrow indicates the mouthparts (10µm)

C. Lateral view of the antenna (100µm)

D. Third segment of the antenna (10µm)

E. Dorsal view of the legs (10µm)

F. Dorsal view of leg 5, arrow indicates leg 5 (10µm)


A
B
C
D
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F

Paraergasilus sp. A

Type Host

Pseudotropheus tropheops Regan, 1922

Type Localities

Lake Malawi, southeastern arm (Fig. 3.7)

Other Hosts

Aristichromis christyi Trewavas, 1935
Genyochromis mento Trewavas, 1935
Lichnochromis vellicans Trewavas, 1935
Petrotilapia genalutea Marsh, 1983
Pseudotropheus elongatus Fryer, 1956
Tyrannochromis macrostoma Regan, 1922
T. nigriventer Eccles, 1989

Species Description (based on 5 specimens)

Total Length: 410µm (excluding furcal setae) (Fig. 6.14A&B & 6.17A).

Cephalothorax: First thoracic segment fused to cephalic segment forming pentagonal cephalothorax. Bulges outwards when viewed laterally. Anterior border slightly pointed.

Ornamentation: No ornamentation visible when examined using light and scanning electron microscopy.

Pigmentation: Preserved material, no colour visible.

Mouthparts: Maxilla two-segmented, second segment with seta medially situated on anterior margin, second segment ending in spinulose area (Figs. 6.16 & 6.17E).

Thorax: Thoracic segments decreasing in size, segments overlap posteriorly in certain specimens. Fifth segment reduced, dorsally visible.

Legs: Legs one to four, biramous. Rami of legs one to three three-segmented, exopod of leg four two-segmented (Figs. 6.15C&D & 6.17F). Coxa of leg one with very small spine, basis with single row of seven tooth-like spines near base of endopod. All setae on endopod of leg one non-plumose, outer margin of segment two and three with group of small tooth-like spines. Inner margin of segment one of exopod with two small hair-like setae, outer margin of segment two with large protrusion tipped by six tooth-like spines. Segment three with sensory pit near the outer edge, small blade-like spine directly posterior to sensory pit, small unadorned spine situated alongside it on outer margin and small protrusion with three small tooth-like spines on inner margin. First segment of exopod of leg two with a group of nine hair-like setae on the inner margin. Endopod of leg two with inner margins of segments one to three bordered by single rows of small comb-like spines. Sensory pit near distal end of segment three of exopod. Leg five greatly reduced, three setae present, two terminal, one lateral. Longest terminal seta longer than entire segment, second seta half of segment length. Lateral seta situated halfway along segment, shorter than shortest terminal seta (Fig. 6.15A). Spine-seta formula provided in Table 6.6.

Table 6.6: Spine-seta formula for *Paraergasilus* Markewitsch, 1937 sp. A collected from *Pseudotropheus tropheops* Regan, 1922 from the southeastern arm of Lake Malawi

	Coxa	**Basis**		**Segment 1**	**Segment 2**	**Segment 3**
Leg 1	0 - I	1 – 0	Exopodite	I – 0	0 – 1*	II – 5*
			Endopodite	0 – 1	0 – 1	0 – 3
Leg 2	0 – 0	1 - 0	Exopodite	0 – 0	0 – 1	0 – 5
			Endopodite	0 – 0	0 – 2	I – 4
Leg 3	-	-	Exopodite	-	-	-
			Endopodite	-	-	-
Leg 4	-	-	Exopodite	-	-	-
			Endopodite	-	-	-

*non-plumose setae

Abdomen: Four-segmented. Large genital segment present, when viewed ventrally both sides bordered by short setae, posterior margin bordered by small tooth-like spines. Posterior margin of first and second free abdominal segments bordered by small comb-like setae. Third segment medially split, with group of seven small tooth-like setae on either side of medial split (Fig. 6.14D).

Furcal Rami: Twice as long as wide, posterior margin bordered by comb-like spines, with single sensory pit near inner posterior margin. Each furcal ramus possessing three furcal setae, one long, two short. Longest setae not extending past egg sacs (Fig. 6.14D).

Antennulae: Five-segmented (Fig. 6.17C).

Antennae: Three-segmented, first and second segment with sensory pit situated near distal end. Third segment with three unadorned spines, approximately equaling length of segment two (Figs. 6.15B & 6.17D).

Egg Sacs: Egg sacs 260μm long, approximately 16 eggs present in each sac (Figs. 6.14C & 6.17B).

Attachment to Host: Unknown, were found loose between *Ergasilus,* which were collected from the cichlids.

Remarks: *Paraergasilus* sp. A differs from *P. lagoonaris* and *P. minutus* by the spine-seta formula of legs one to four. In addition *P. lagoonaris* has egg sacs which equals half the length of the furcal setae, while *Paraergasilus* sp. A has egg sacs longer than the furcal setae.

Based on the above description and the differences between *Paraergasilus* sp. A and the known species there is little doubt that *Paraergasilus* sp. A is a new species. The combination of the following characteristics distinguish this species from the others:

- Shape of the cephalothorax.
- Spine-seta formula of legs one and two is vastly different.
- Egg sacs are twice the length of the furcal setae.

Figure 6.14

Line drawings of *Paraergasilus* Markewitsch, 1937 sp. A collected from *Pseudotropheus tropheops* Regan, 1922 from the south-eastern arm of Lake Malawi

A. Dorsal view of whole specimen (100µm)

B. Lateral view of whole specimen (100µm)

C. Egg sac (50µm)

D. Ventral view of abdomen (50µm)

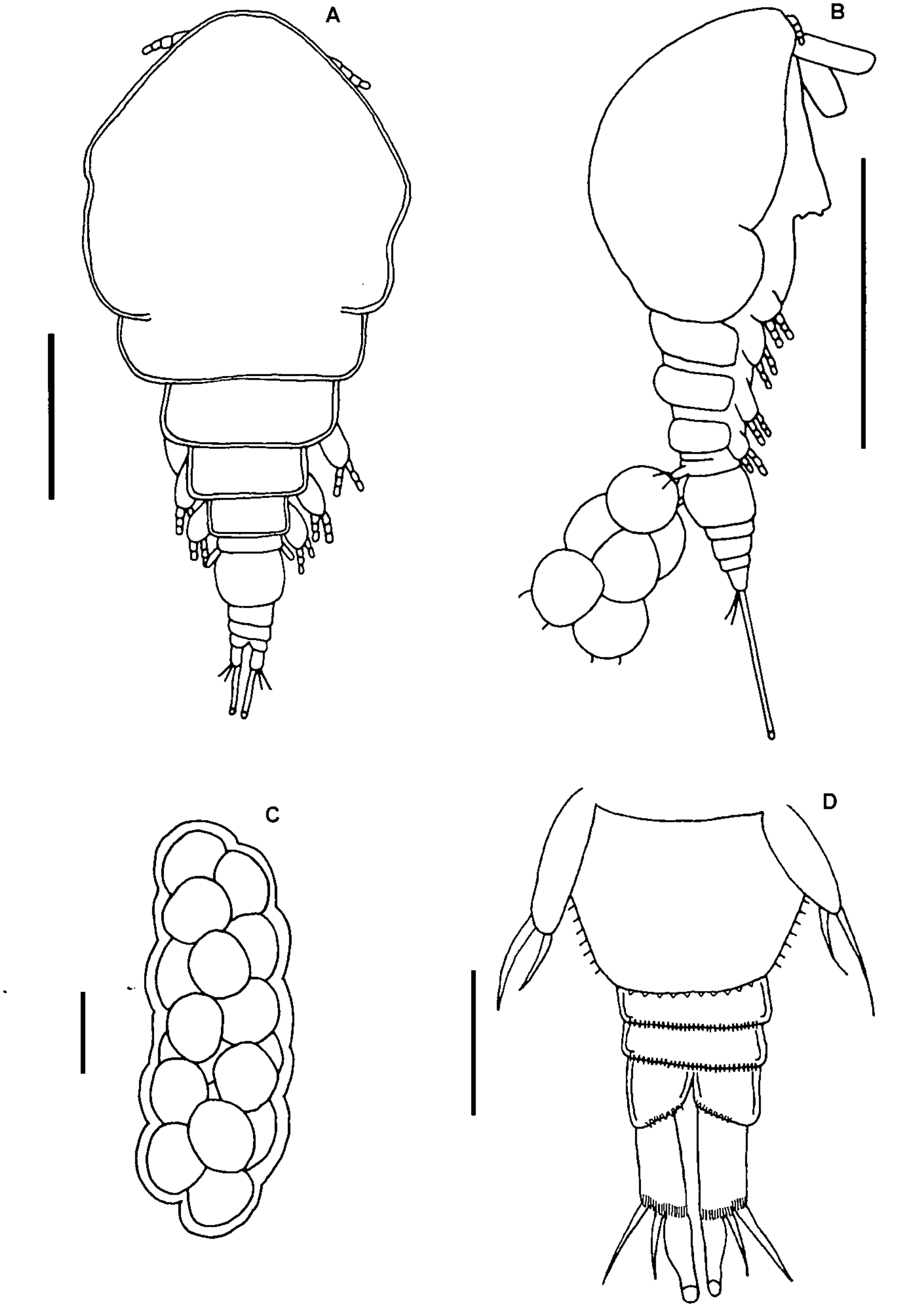
A
B
C
D

Figure 6.15

Line drawings of *Paraergasilus* Markewitsch, 1937 sp. A collected from *Pseudotropheus tropheops* Regan, 1922 from the south-eastern arm of Lake Malawi

- **A.** Leg 5 (10μm)
- **B.** Lateral view of antenna (10μm)
- **C.** Leg 2 (10μm)
- **D.** Leg 1 (10μm)

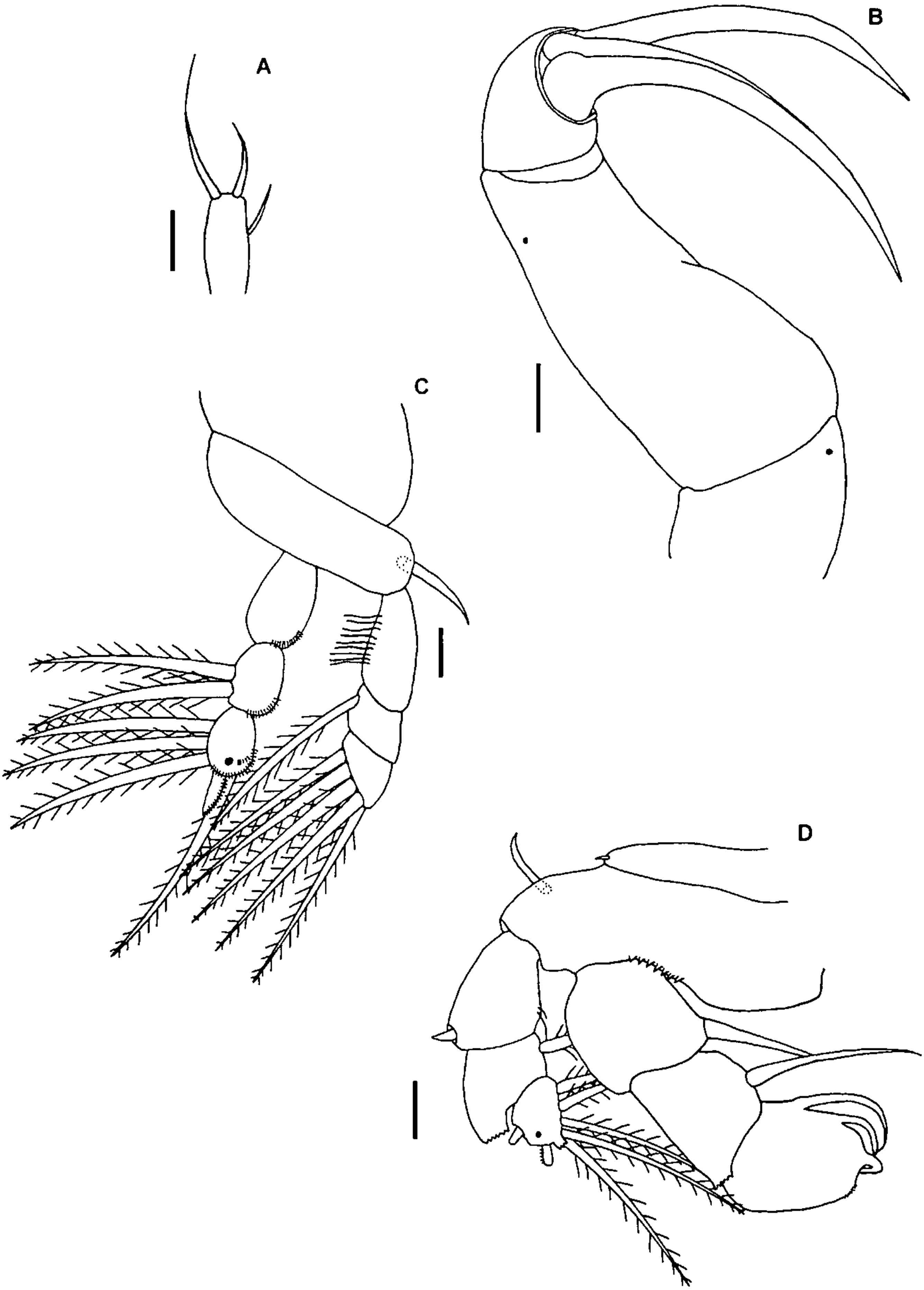
A
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Figure 6.16

Line drawing of the maxilla (10μm) of *Paraergasilus* Markewitsch, 1937 sp. A collected from *Pseudotropheus tropheops* Regan, 1922 from the south-eastern arm of Lake Malawi

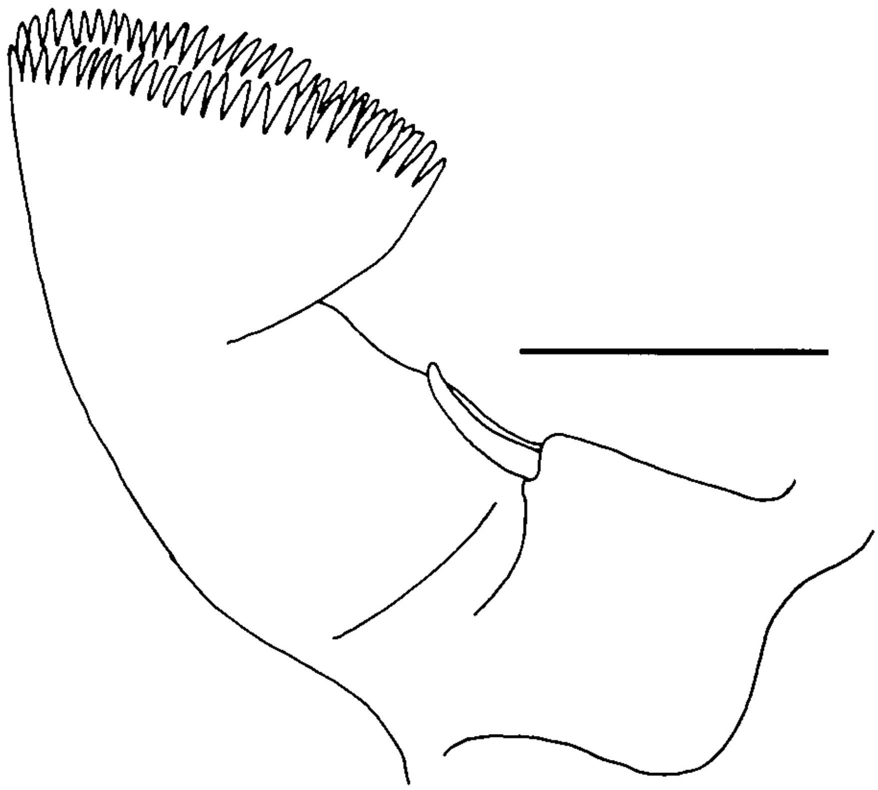
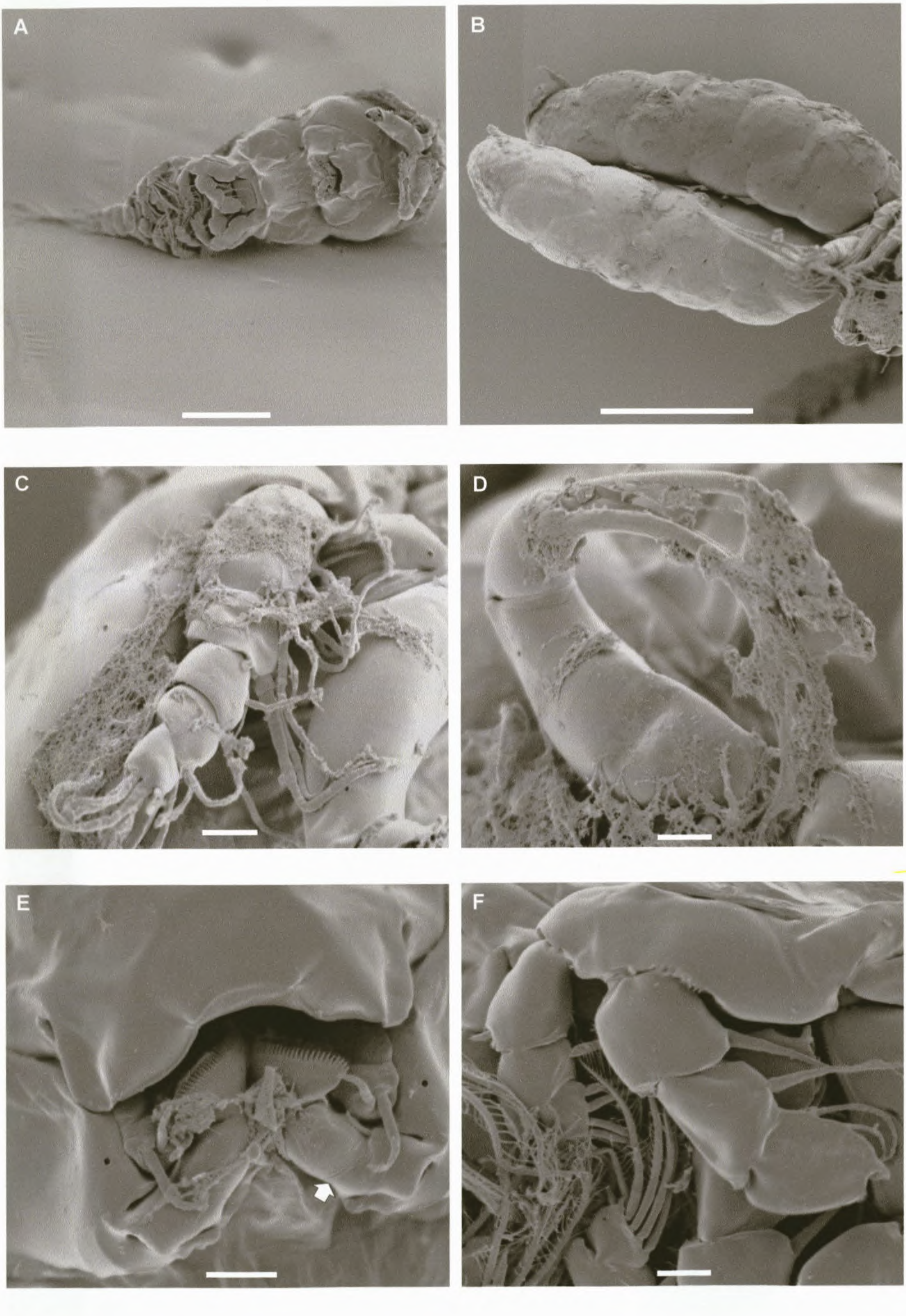


Figure 6.17

Scanning electron micrographs of *Paraergasilus* Markewitsch, 1937 sp. A collected from *Pseudotropheus tropheops* Regan, 1922 from the south-eastern arm of Lake Malawi

- **A.** Ventral view of the whole specimen (100µm)
- **B.** Egg sacs (100µm)
- **C.** Antennule (10µm)
- **D.** Antenna (10µm)
- **E.** Mouth, arrow indicates the mouthparts (10µm)
- **F.** Leg 1 (10µm)


A
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F

The Fish Species and Parasitic Crustaceans Collected from Lake Malawi

During this study of the cichlids of Lake Malawi, 37 fish species were collected, 29 were found to be parasitised by crustacean parasites, 28 were parasitised by ergasilids (Table 6.7).

The total number of fish species on which *Ergasilus* specimens were found can be seen in Table 6.8, here the total number of fish is given, with the number that were parasitised and the percentage of parasitised hosts. The graphical representation of this is provided in Figure 6.18. The number of parasites collected from these hosts is also provided in Table 6.8.

The total number of fish on which *Paraergasilus* specimens were found can be seen in Table 6.9. The total number of fish collected, total number of fish parasitised and the percentage of parasitised hosts is also provided in this table. A graphical representation is provided in Figure 6.19.

The study presently being conducted in Lake Malawi is primarily on the cichlids of the lake, this means that there is no information about the seasonality of the ergasilids of the lake.

Table 6.7: List of most of the fish genera and families found in Lake Malawi, with all the fish species [Compiled using Ribbink *et al.* (1983) and Konings (1990)] and parasitic crustaceans collected between 1995 and 1996.

FISH GENERA AND SPECIES	*Ergasilus*	*Lamproglena*
Cichlidae		
Alticorpus spp. Stauffer & McKaye, 1988		
Aristochromis spp. Trewavas, 1935		
A. christyi Trewavas, 1935	x	x
Astatotilapia spp. Pellegrin, 1904		
Aulonocara spp. Regan, 1922		
Buccochromis spp. Eccles & Trewavas, 1989		
Champsochromis spp. Boulenger, 1915		
Chilotilapia spp. Boulenger, 1908		
Copadichromis spp. Eccles & Trewavas, 1989		
C. eucinostomus (Regan, 1922)	x	x
Corematodus spp. Boulenger, 1897		
Cyathochromis spp. Trewavas, 1935		
Cynotilapia spp. Regan, 1922		
Cyrtocara spp. Boulenger, 1902		
Dimidiochromis spp. Eccles & Trewavas, 1989		
D. kiwinge (Ahl, 1927)		
Diplotaxodon spp. Trewavas, 1935		
Docimodus spp. Boulenger, 1897		
Exochochromis spp. Eccles & Trewavas, 1989		
Fossorochromis spp. Eccles & Trewavas, 1989		
Genyochromis spp. Trewavas, 1935		
G. mento Trewavas, 1935	x	x
Gephyrochromis spp. Boulenger, 1901		
Hemitilapia spp. Boulenger, 1902		
Iodotropheus spp. Oliver & Loiselle, 1972		
Labidochromis spp. Trewavas, 1935		
L. velicans Trewavas, 1935	x	x
Labeotropheus spp. Ahl, 1926		
L. fuelleborni Ahl, 1927	x	x
Lethrinops spp. Regan 1922		
Lichnochromis spp. Trewavas, 1935		
L. acuticeps Trewavas, 1935	x	
Maravichromis spp. Eccles & Trewavas, 1989		
Melanochromis spp. Trewavas, 1935		
M. auratus (Boulenger, 1897)	x	x
M. melanopterus Trewavas, 1935	x	
M. vermivorus Trewavas, 1935	x	
Nimbochromis spp. Eccles & Trewavas, 1989		
Nyassachromis spp. Eccles & Trewavas, 1989		
Otopharynx spp. Regan, 1920		
O. pictus (Trewavas, 1935)		
Oreochromis spp. Günther, 1889		
Oreochromis spp. Günther, 1889		
Petrotilapia spp. Trewavas, 1935		
Petrotilapia spp. Trewavas, 1935	x	
P. genalutea Marsh, 1983	x	x
P. nigra Marsh, 1983	x	x
P. tridentiger Trewavas, 1935	x	

Table 6.7 (cont.): List of most of the fish genera and families found in Lake Malawi, with all the fish species [Compiled using Ribbink *et al.* (1983) and Konings (1990)] and parasitic crustaceans collected between 1995 and 1996.

FISH GENERA AND SPECIES	*Ergasilus*	*Lamproglena*
Placidochromis spp. Eccles & Trewavas, 1989		
P. johnstoni 'gold' (Günther, 1893)	x	
Protomelas spp. Eccles & Trewavas, 1989		
P. annectans (Regan, 1922)	x	x
P. taeniolatus (Trewavas, 1935)		x
Pseudotropheus spp. Regan, 1922		
P. barlowi McKaye & Stauffer, 1986	x	
P. elongatus 'aggressive' Fryer, 1956	x	x
P. livingstoni (Boulenger, 1899)		
Pseudotropheus 'muzinzi' Regan, 1922		
P. tropheops Regan, 1922	x	
P. tropheops 'broadmouth' Regan, 1922	x	
P. tropheops 'orange chest' Regan, 1922	x	
P. zebra 'redtop' (Boulenger, 1899)	x	
Rhamphochromis spp. Regan, 1922		
Rhamphochromis spp. Regan, 1922	x	
Serranochromis spp. Regan, 1920		
Sciaenochromis spp. Eccles & Trewavas, 1989		
Stigmatochromis spp. Eccles & Trewavas, 1989		
S. woodi (Regan, 1922)	x	x
Taeniochromis spp. Eccles & Trewavas, 1989		
Taeniolethrinops spp. Eccles & Trewavas, 1989		
T. praeorbatilis (Regan, 1922)	x	x
Tilapia spp. Smith, 1840		
Tramitichromis spp. Eccles & Trewavas, 1989		
Trematocranus spp. Trewavas, 1935		
T. placodon (Regan, 1922)	x	
Tyrannochromis spp. Eccles & Trewavas, 1989		
T. macrostoma (Regan, 1922)	x	x
T. nigriventer Eccles, 1989	x	x
Anguillidae		
Anguilla spp. Schrank, 1798		
Aplocheilidae		
Nothobranchius spp. Peters, 1868		
Bagridae		
Bagrus spp. Bosc, 1816		
B. meridionalis Günther, 1893	x	
Characidae		
Brycinus spp. Valenciennes, 1849		
Clariidae		
Bathyclarias spp. Jackson, 1959		
B. nyasensis (Worthington, 1933)		
Clarias spp. Scopoli, 1777		
Cyprinidae		
Barbus spp. Cuvier & Cloquet, 1861		
Cheilobarbus spp. Smith, 1841		
Labeo spp. Cuvier, 1817		
L. cylindricus Peters, 1852		
Opsaridium spp. Peters, 1854		
Pseudobarbus spp. Smith, 1841		

Table 6.7 (cont.): List of most of the fish genera and families found in Lake Malawi, with all the fish species [Compiled using Ribbink *et al.* (1983) and Konings (1990)] and parasitic crustaceans collected between 1995 and 1996.

FISH GENERA AND SPECIES	*Ergasilus*	*Lamproglena*
Mochokidae		
Chiloglanis spp. Peters, 1868		
Synodontis spp. Cuvier, 1816		
S. njassae Keilhack, 1908		
Mormyridae		
Marcusenius spp. Gill, 1862		
Mormyrops spp. Müller, 1843		
Mormyrus spp. Linnaeus, 1758		
Petrocephalus spp. Marcusen, 1854		
Poeciliidae		
Aplocheilichthys spp. Bleeker, 1863		

Table 6.8: List of the total number fish species collected in Lake Malawi, with the total fish collected (T), the total fish parasitised (P) and the total number of *Ergasilus* von Nordmann, 1832 found on each fish species.

FISH GENERA AND SPECIES	T	P	%	Total *Ergasilus*
Cichlidae				
Aristochromis christyi Trewavas, 1935	2	2	**100**	120
Copadichromis eucinostomus (Regan, 1922)	2	2	**100**	3
Genyochromis mento Trewavas, 1935	3	3	**100**	9
Labidochromis velicans Trewavas, 1935	3	3	**100**	3
Labeotropheus fuelleborni Ahl, 1927	3	3	**100**	2
Lichnochromis acuticeps Trewavas, 1935	1	1	**100**	1
Melanochromis auratus (Boulenger, 1897)	6	6	**100**	13
M. melanopterus Trewavas, 1935	1	1	**100**	6
M. vermivorus Trewavas, 1935	5	2	**20**	5
Petrotilapia spp. Trewavas, 1935	2	1	**50**	6
P. genalutea Marsh, 1983	25	9	**36**	12
P. nigra Marsh, 1983	10	8	**80**	8
P. tridentiger Trewavas, 1935	20	9	**45**	7
Placidochromis johnstoni 'gold' (Günther, 1893)	2	2	**100**	2
Protomelas annectans (Regan, 1922)	4	4	**100**	11
Pseudotropheus barlowi McKaye & Stauffer, 1986	5	3	**60**	4
P. elongatus 'aggressive' Fryer, 1956	1	1	**100**	3
P. tropheops Regan, 1922	7	7	**100**	2
P. zebra 'redtop' (Boulenger, 1899)	8	2	**25**	2
Rhamphochromis spp. Regan, 1922	6	6	**100**	121
Stigmatochromis woodi (Regan, 1922)	3	3	**100**	51
Taenilethrinops praeorbatilis (Regan, 1922)	2	2	**100**	32
Trematocranus placodon (Regan, 1922)	2	1	**50**	5
Tyrannochromis macrostoma (Regan, 1922)	4	4	**100**	50
T. nigriventer Eccles, 1989	1	1	**100**	37
Bagridae				
Bagrus meridionalis Günther, 1893	2	1	**50**	2

Table 6.9: List of all the fish species collected from Lake Malawi that were parasitised by *Paraergasilus* Markewitsch, 1937, with the total number of fish collected (T), the total number of fish parasitised (P) and the total number of *Paraergasilus* collected.

FISH GENERA AND SPECIES	**T**	**P**	**%**	**Total *Paraergasilus***
Cichlidae				
Aristochromis christyi Trewavas, 1935	2	1	**50**	1
Genyochromis mento Trewavas, 1935	3	2	**66**	2
Lichnochromis acuticeps Trewavas, 1935	1	1	**100**	3
Petrotilapia genalutea Marsh, 1983	25	9	**36**	6
Pseudotropheus elongatus 'aggressive' Fryer, 1956	1	1	**100**	1
P. tropheops Regan, 1922	7	1	**14**	2
Tyrannochromis macrostoma (Regan, 1922)	4	3	**75**	4
T. nigriventer Eccles, 1989	1	1	**100**	1

Figure 6.18: Graph representing all twenty six fish species collected from Lake Malawi on which ergasilids were found, with the column in the background being the total number of fish collected and the column in the foreground being the number of fish parasitised.

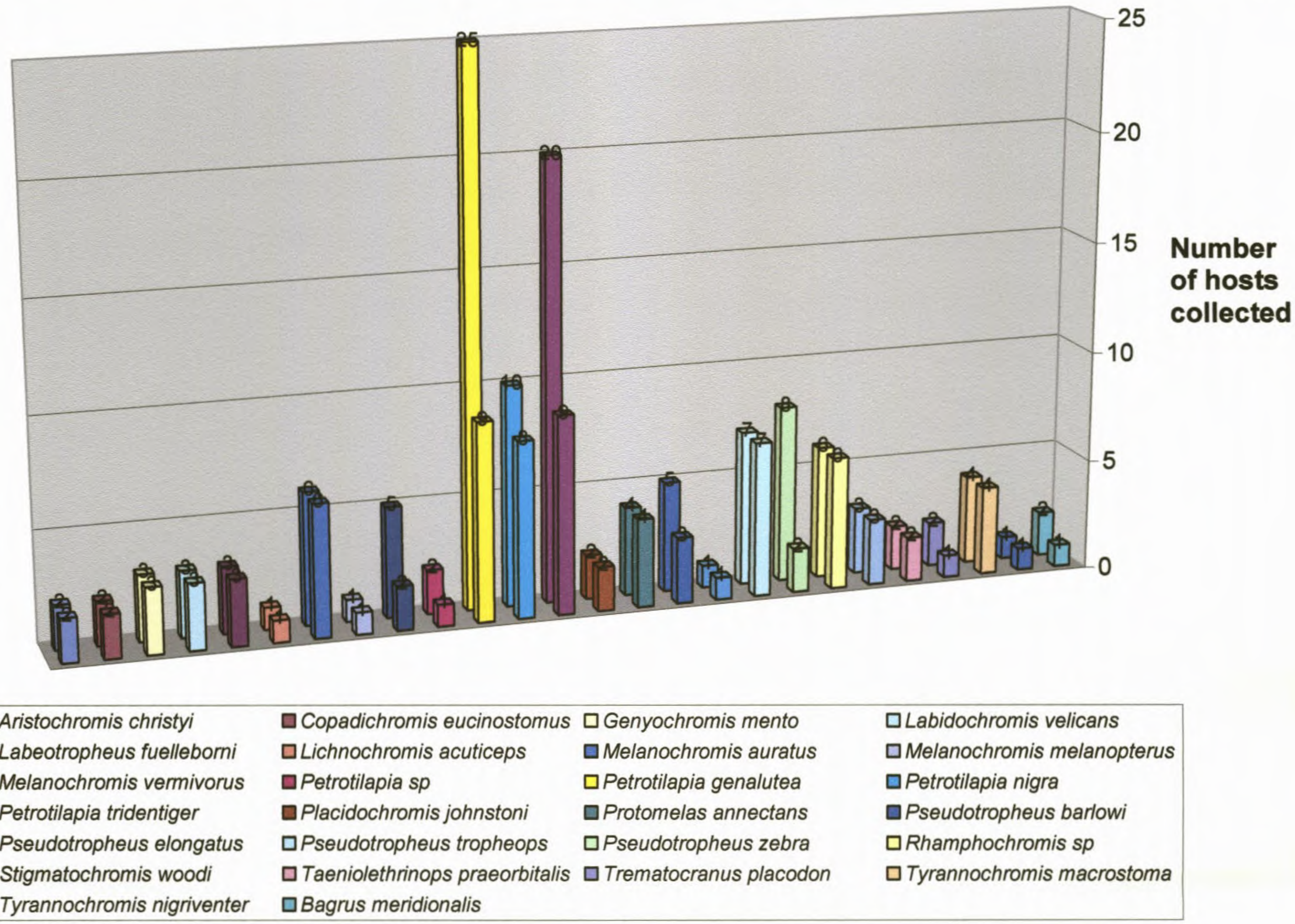
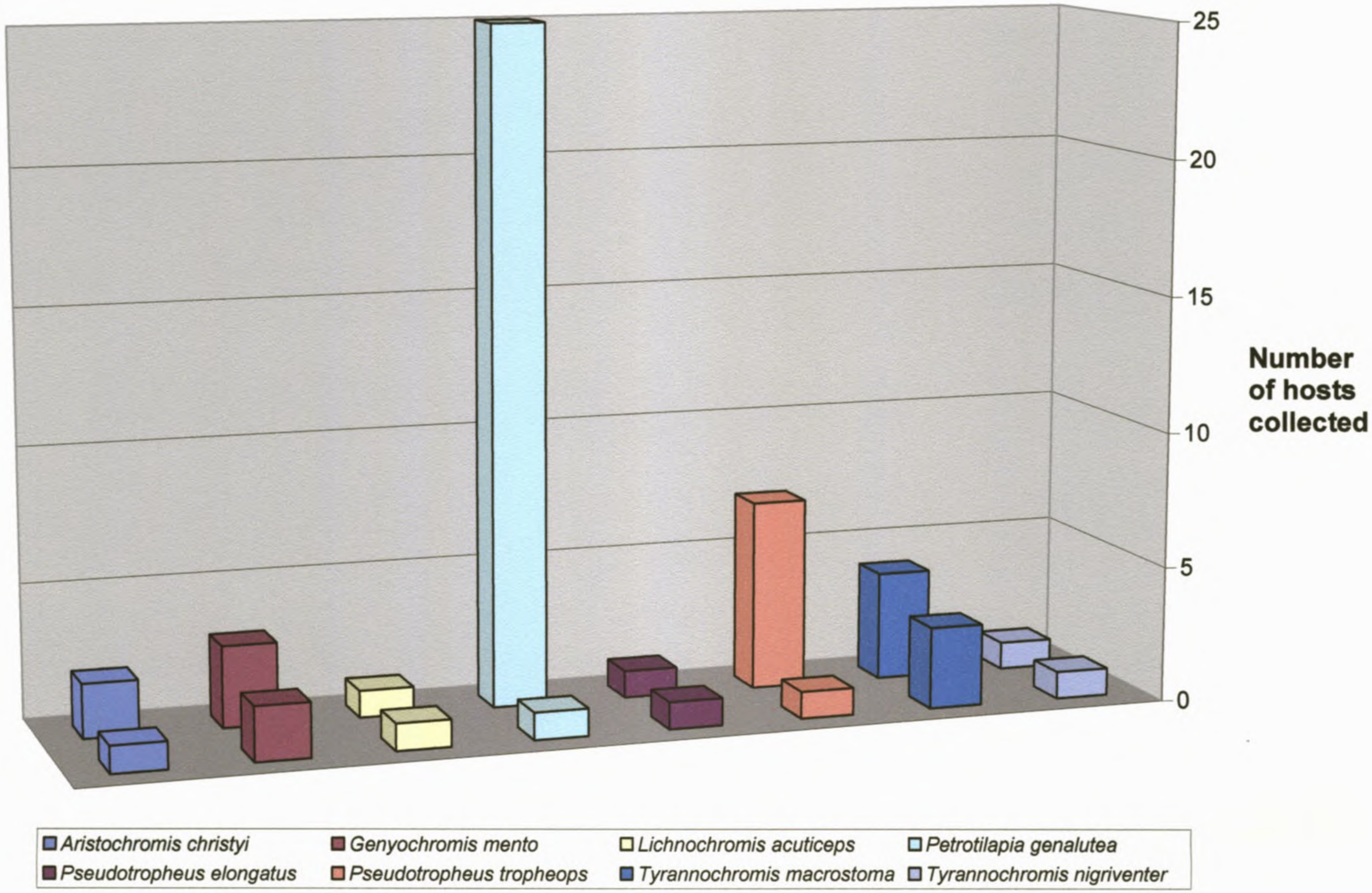


Figure 6.19: Graph representing all eight fish species collected from Lake Malawi on which *Paraergasilus* Markewitsch, 1937 specimens were found, with the column in the background being the total number of fish collected and the column in the foreground being the number of fish parasitised.



Chapter 7

The Phylogeny and Taxonomy of the African Ergasilids

7.1 The Phylogeny of the African Freshwater *Ergasilus* species

The only phylogenetic analysis done on any ergasilid genus was by El-Rashidy & Boxshall (2001a) on all the *Paraergasilus* species. No analysis has been done on either the *Ergasilus* or *Dermoergasilus* species. Therefore it was decided to do a phylogenetic analysis on the African freshwater species, using morphological characters. A character matrix (Table 7.2) was constructed using 13 species, 10 previously described and three described in this dissertation, as well as an outgroup. Thirty-six morphological characters were taken from the literature on all the included species, all these characters and states are listed in Table 7.1. The information that is missing was identified using '?' as the symbol. Initially it was decided to make two phylogenetic trees using two different outgroups from the same family as the *Ergasilus* species, the following were selected because they are endemic to Africa and they are the most thoroughly described; *Paraergasilus lagoonaris* and *Dermoergasilus mugilis* Oldewage & van As, 1988. The information for *D. mugilis* was taken from Oldewage & van As (1988). The analysis using *P. lagoonaris* as the outgroup was inconclusive, this could be because they were too similar to compare using the characters decided on. The options chosen using PAUP version 4.4 were first parsimony, branch and bound, as well as using the distance method which gave two equally parsimonious trees, the most suitable tree is provided in Figure 7.1.

Table 7.1: Character set and character states of the African freshwater *Ergasilus* sp. von Nordmann, 1832

No.	Character	States	Score
1	Relationship between cephalic and 1st thoracic segment	Separate/fused	0/1
2	Number of furcal setae	5set/4set/3set	0/1/2
3	Ornamentation on furcal setae	Unadorned/adorned	0/1
4	Spines on ventral surface of abdomen	Absent/present	0/1
5	Number of segments on antennulae	6seg/5seg	0/1
6	Cuticular sheath covering entire antenna	Absent/present	0/1
7	Armament on antennal segment 2	Unadorned/adorned	0/1
8	Armament on antennal segment 2	Unadorned/enlarged joint	0/1
9	Armament on antennal segment 2	Unadorned/broad	0/1
10	Armament on antennal segment 2	Unadorned/spine	0/1
11	Armament on antennal segment 2	Unadorned/lamella	0/1
12	Armament on antennal segment 3	Unadorned/adorned	0/1
13	Armament on antennal segment 3	Unadorned/enlarged joint	0/1
14	Armament on antennal segment 3	Unadorned/indented	0/1
15	Armament on antennal segment 3	Unadorned/medially twisted	0/1
16	Armament on antennal segment 3	Unadorned/lamella	0/1
17	Armament on antennal segment 3	Unadorned/spines	0/1
18	Armament on antennal segment 4	Present/absent	0/1
19	Armament on antennal segment 4	Unadorned/adorned	0/1
20	Armament on antennal segment 4	Unadorned/spine	0/1
21	Outer spine on 1st seg. of exopod, leg 1	Present/absent	0/1
22	Outer spine on 1st seg. of exopod, leg 2	Present/absent	0/1
23	Inner setae on 2nd seg. of exopod, leg 2	Present/absent	0/1
24	Inner setae on 2nd seg. of exopod, leg 2	2setae/1seta	0/1
25	Outer spine on 1st seg. of exopod of leg 3	Present/absent	0/1
26	Inner setae on 2nd seg. of exopod, leg 3	Present/absent	0/1
27	Outer spine on 1st seg. of exopod, leg 4	Present/absent	0/1
28	Inner setae on 2nd seg. of exopod, leg 4	5setae/4setae	0/1
29	Inner setae on 1st seg. of endopod, leg 4	Present/absent	0/1
30	Inner setae on 2nd seg. of endopod, leg 4	Present/absent	0/1
31	Inner setae on 2nd seg. of endopod, leg 4	2setae/1seta	0/1
32	Inner setae on 3rd seg. of endopod, leg 4	6or5set/3set/2set	0/1/2
33	Presence of leg 5	Present/absent	0/1
34	Presence of basal segment on leg 5	Present/absent	0/1
35	Number of lateral setae on leg 5	1 lateral/no lateral	0/1
36	Number of terminal setae on leg 5	2terminal/1terminal	0/1

Motivation for the Choice of the Morphological Characters

- **Character 1:** The relationship between the cephalic and thoracic segments is very important as the presence of a definite separation of these two characteristics is a less advanced feature. This is because in the immature stages the cephalic segment is visibly separate from the first thoracic segment, making it a plesiomorphic feature.

  0 - separate

  1 - fused

- **Character 2:** The total number of furcal setae is of taxonomic importance. Here the presence of five setae is seen as plesiomorphic, because those with four and three setae would have lost a segment during development, making those with three setae apomorphic. The scores given to these states are as follows:

  0 - five setae

  1 - four setae

  2 - three setae

- **Character 3:** The presence of ornamentation (setules) on the furcal setae is seen as an apomorphic feature as only one species has this. That is why in this analysis the absence of ornamentation is seen as a plesiomorphic feature.

  0 – unadorned furcal setae

  1 – adorned furcal setae

- **Character 4:** The presence of spines on the ventral surface of the abdomen is of taxonomic importance. In the past the ergasilids were free-living, they then evolved into fish parasites, the presence of spines on the ventral surface could be an adaptation to assist the organism to grip the hosts gill filaments. This means that the absence of these spines would be a plesiomorphic state, compared to those with ventral spines.

  0 – spines on the ventral surface of the abdomen are absent

  1 – spines on the ventral surface of the abdomen are present

- **Character 5:** The total number of antennulae segments is also of taxonomic importance. Here the presence of six segments is seen as a plesiomorphic characteristic, because those with five segments would have lost a one during development.

    0 - six segments on the antennulae

    1 – five segments on the antennulae

- **Character 6:** The presence or absence of a cuticular sheath covering the antennae is of taxonomic importance. Here the presence of the cuticular sheath is seen as an apomorphic feature, because it would have appeared during the organism's development.

    0 – absence of a cuticular sheath on the antennae

    1 – presence of a cuticular sheath on the antennae

- **Characters 7-11:** The presence or absence of armature on the antennae is of major taxonomic importance. Here the presence of armature on the second antennal segment is seen as an apomorphic feature, because it would have appeared during the organism's development and tends to help it grip the gill filaments of the host. There are various features which are found on the second antennal segment such as an enlarged joint (char. 8), very broad segment (char. 9), a spine (char. 10) or a lamella (char. 11).

    0 – unadorned second antennal segment

    1 – adorned antennal second segment

- **Character 12-17:** The presence or absence of armature on the antennae is also a very important taxonomic feature. Here the presence of an adorned third antennal segment is seen as an apomorphic feature, because any extra feature would have appeared during the organism's development and tends to help it grip the gill filaments of the host. The following features can occur on the third antennal segment – enlarged joint (char. 13), indented segment (char. 14), medially twisted segment (char. 15), lamella (char. 16) or spines (char. 17).

    0 – unadorned third antennal segment

    1 – adorned third antennal segment

- **Character 18-20:** The presence or absence of armature on the antennae is of major taxonomic importance. Here the absence of the fourth antennal segment is seen as an apomorphic feature, because the trend is that when an organism loses a segment during development it tends to be more advanced. Here the presence of a fourth segment (char. 18), presence of spines (char. 20) or other adornment (char. 19) is supplied.

  0 – fourth antennal segment present

  1 – fourth antennal segment absent

- **Character 21-22:** The presence or absence of setae or spines on the legs is of taxonomic importance. Here the absence of an outer spine on the first segment of the exopod of leg one and two is seen as an apomorphic feature, because with the change from a free-living to a parasitic life means that in the adult stage the legs are not necessary. So during the development the more advanced organisms would lose setae on the legs.

  0 – presence of the spine

  1 – absence of the spine

- **Character 23:** The presence or absence of setae or spines on the legs is of taxonomic importance. Here the absence of an inner seta on the second segment of the exopod of leg two is seen as an apomorphic feature, because with the change from a free-living to a parasitic life means that in the adult stage the legs are not necessary. So during the development the more advanced organisms would lose setae on the legs.

  0 – presence of the inner setae

  1 – absence of the inner setae

- **Character 24:** The presence or absence of setae or spines on the legs is of taxonomic importance. Here the presence of different numbers of inner setae on the second segment of the exopod of leg two is seen is an important feature. The presence of two setae is viewed as plesiomorphic than those with one seta, because with the change from a free-living to a parasitic life means that in the adult stage the legs are not necessary. So during the development the more advanced organisms would lose setae on the legs.

  0 – two setae

  1 – one seta

- **Character 25:** The presence or absence of setae or spines on the legs is of importance. Here the absence of the outer spine on the first segment of the exopod of leg three is seen as an apomorphic feature, because with the change from a free-living to a parasitic life means that in the adult stage the legs are not necessary. So during the development the more advanced organisms would lose setae on the legs.

  0 – presence of the outer spine

  1 – absence of the outer spine

- **Character 26:** The presence or absence of setae or spines on the legs is of taxonomic importance. Here the absence of the inner setae on the second segment of the exopod of leg three is seen as an apomorphic feature, because with the change from a free-living to a parasitic life means that in the adult stage the legs are not necessary. So during the development the more advanced organisms would lose setae on the legs.

  0 – presence of the inner setae

  1 – absence of the inner setae

- **Character 27:** The presence or absence of setae or spines on the legs is of taxonomic importance. Here the absence of the outer spine on the first segment of the exopod of leg four is seen as an apomorphic feature, because with the change from a free-living to a parasitic life means that in the adult stage the legs are not necessary. So during the development the more advanced organisms would lose setae on the legs.

  0 – presence of the outer spine

  1 – absence of the outer spine

- **Character 28:** The presence or absence of setae or spines on the legs is of importance. Here the number of inner setae on the second segment of the exopod of leg four is very important. The species with five setae is viewed as less advanced than those with four setae. This is because with the change from a free-living to a parasitic life means that in the adult stage the legs are not necessary. So during the development the more advanced organisms would lose setae on the legs.

  0 – five setae

  1 – four setae

- **Character 29-30:** The presence or absence of setae or spines on the legs is of taxonomic importance. Here the absence of the inner setae on the first and second segment of the endopod of leg four is seen as an apomorphic feature. This is because with the change from a free-living to a parasitic life means that in the adult stage the legs are not necessary. So during the development the more advanced organisms would lose setae on the legs.

  0 – presence of the inner setae

  1 – absence of the inner setae

- **Character 31:** The presence or absence of setae or spines on the legs is of taxonomic importance. Here the number of inner setae on the second segment of the endopod of leg four is very important. The presence of two setae is viewed as plesiomorphic compared to those with one seta that are apomorphic. This is because with the change from a free-living to a parasitic life means that in the adult stage the legs are not necessary. So during the development the more advanced organisms would lose setae on the legs.

  0 – two setae

  1 – one setae

- **Character 32:** The presence or absence of setae or spines on the legs is of taxonomic importance. Here the number of inner setae on the third segment of the endopod of leg four is very important. The presence of six or five setae is viewed as a plesiomorphic feature than those with two seta. This is because with the change from a free-living to a parasitic life means that in the adult stage the legs are not necessary. So during the development the more advanced organisms would lose setae on the legs.

  0 – six or five setae

  1 – three setae

  2 – two setae

- **Character 33:** The fifth leg is of taxonomic importance when comparing the different species. The presence of a fifth leg is viewed as a plesiomorphic character, while the absence of the leg is an apomorphic character. This is because all but one species possess a fifth pair of legs.

  0 – presence of a fifth leg

  1 – absence of the fifth leg

- **Character 34:** The fifth leg is of taxonomic importance. The presence of a two-segmented fifth leg is viewed as a plesiomorphic character, while the presence of a single-segmented fifth leg is an apomorphic character. This is because all indications show that as the organisms evolve the fifth leg decreases.

  0 – presence of a basal segment on the fifth leg

  1 – absence of a basal segment on the fifth leg

- **Character 35:** The fifth leg is of taxonomic importance when comparing the different species. The presence of a lateral seta on the fifth leg is viewed as a plesiomorphic character, while the absence of a lateral seta fifth leg is an apomorphic character. This is because all indications show that as the organisms evolve the fifth leg decreases in size.

  0 – one lateral seta on the fifth leg

  1 – absence of a lateral seta on the fifth leg

- **Character 36:** The fifth leg is of taxonomic importance when comparing the different species. The number terminal setae is very important when comparing the species, two terminal setae on the fifth leg is viewed as a plesiomorphic character, while one terminal seta on the fifth leg is an apomorphic character. This is because all indications show that as the organisms evolve the fifth leg decreases in size.

  0 – two terminal setae on the fifth leg

  1 – one terminal seta on the fifth leg

Table 7.2: Character matrix for the phylogenetic analysis of the African freshwater *Ergasilus* sp. von Nordmann, 1832 species with *Dermoergasilus mugilis* Oldewage & van As, 1988 as the outgroup

	E. cunningtoni Capart, 1944	*E. flaccidus* Fryer, 1965	*E. kandti* van Douwe, 1912	*E. lamellifer* Fryer, 1961	*E. latus* Fryer, 1960	*E. macrodactylus* (Sars, 1909)	*E. megacheir* (Sars, 1909)	*E. mirabilis* Oldewage & van As, 1987	*E. nodosus* Wilson, 1928	*E. sarsi* Capart, 1944	*Ergasilus* sp. A	*Ergasilus* sp. B	*Ergasilus* sp. C	*D. mugilis* Oldewage & van As, 1988
1	0	?	1	?	1	1	?	0	0	0	0	0	0	1
2	2	1	2	1	0	1	1	1	2	2	1	1	1	2
3	0	0	0	0	0	0	0	0	1	0	0	0	0	0
4	0	1	1	0	0	0	0	1	0	?	1	1	1	0
5	0	1	1	0	0	0	0	0	1	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	1
7	0	1	0	1	0	0	1	0	0	0	0	1	0	0
8	0	0	0	1	0	0	1	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	1	0	0
10	0	1	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	1	0	0	0	0	0	0	0	0	0	0
12	1	0	1	0	0	0	0	0	1	1	1	1	1	0
13	0	0	0	0	0	0	0	0	1	0	0	0	0	0
14	1	0	0	0	0	0	0	0	0	1	0	1	0	0
15	0	0	1	0	0	0	0	0	0	0	1	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0	1	0
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	1	0	0	0	0	0	0	0
20	0	0	0	0	0	0	1	0	0	0	0	0	0	0
21	0	0	0	0	1	0	0	0	?	?	0	0	0	0
22	0	0	0	1	1	0	1	0	?	?	0	0	0	1
23	0	0	0	0	0	0	0	0	?	?	0	0	0	1
24	0	1	0	0	0	0	1	1	?	?	0	0	0	?
25	0	0	1	1	1	0	1	0	0	?	0	0	0	1
26	0	1	0	0	0	0	1	0	0	?	0	0	0	1
27	1	0	1	0	0	1	1	0	0	?	0	1	0	1
28	0	0	0	0	0	0	0	0	1	?	0	0	0	0
29	0	0	0	0	0	0	0	0	1	?	0	0	0	1
30	0	0	0	0	0	0	0	1	1	?	0	0	0	1
31	0	1	0	0	0	1	1	?	?	?	0	0	0	?
32	1	1	1	1	1	1	0	1	2	?	1	1	1	0
33	0	0	0	0	0	0	0	0	1	0	0	0	0	0
34	1	0	1	0	1	1	1	1	1	1	0	1	0	1
35	0	1	?	1	0	0	0	0	?	0	0	0	1	0
36	0	0	?	0	0	1	1	0	?	0	0	1	0	0

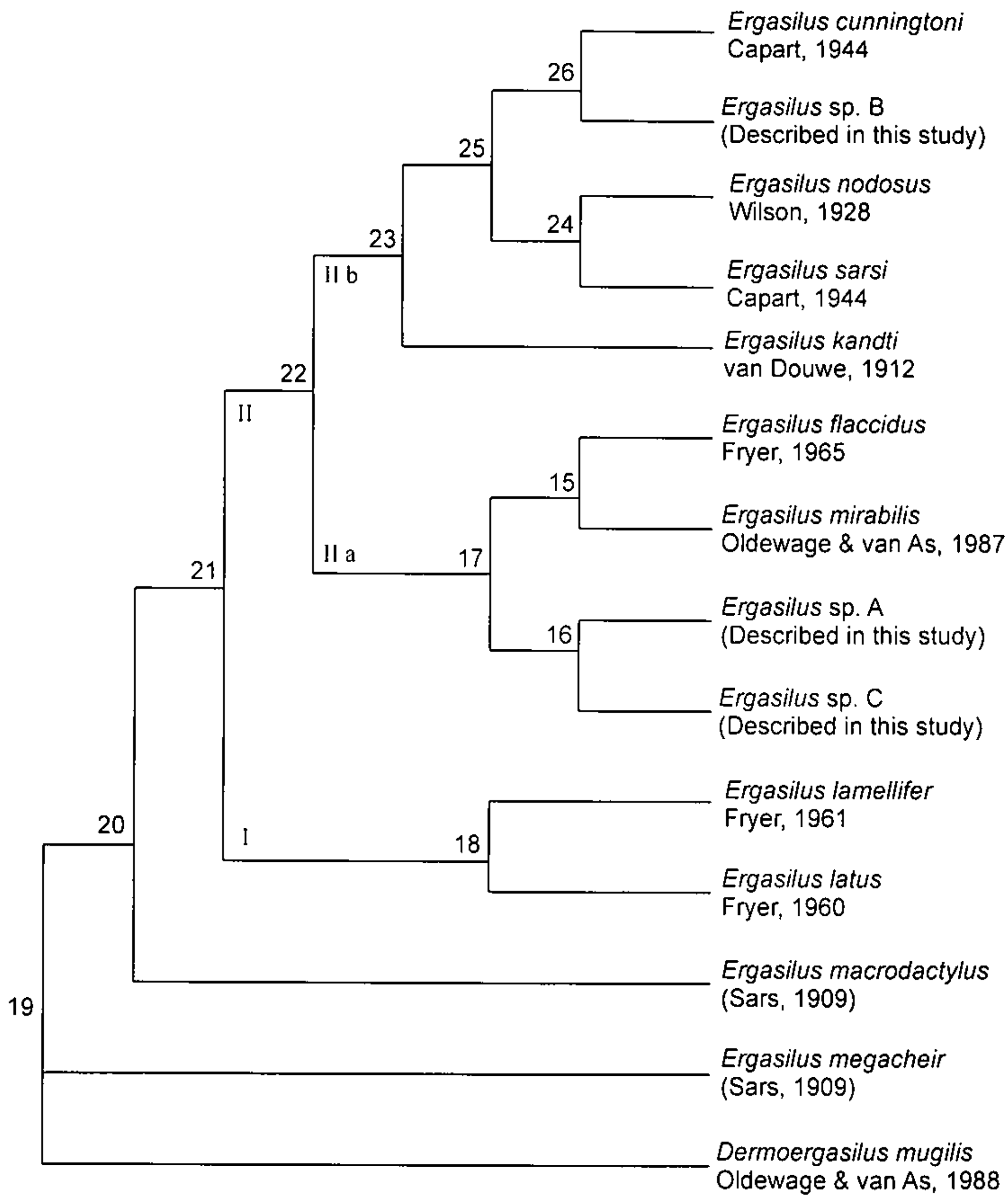


Figure 7.1: Phylogenetic tree generated using PAUP version 4.4, illustrating the relationships between all thirteen freshwater African *Ergasilus* sp Nordman, 1832 with *Dermoergasilus mugilis* Oldewage & van As, 1988 as the outgroup, using the characters from Table 7.1

Discussion of the Phylogenetic Analysis

The phylogenetic tree (Fig. 7.1) was created using the parsimony and distance methods. The outgroup used in this analysis was *Dermoergasilus mugilis,* which belongs to the same family as the *Ergasilus* species. The species branch off into various clusters, these are identified using roman numerals. In this tree the species most closely related to the outgroup with 19 shared characteristics was *E. megacheir,* the next species was *E. macrodactylus* with 20 shared characters.

The tree then branches off into two clusters: I and II, the first contains *E. latus* and *E. lamellifer* with 18 shared characters between them. The following are some of the characteristics that are shared between these two species - the spine-seta formula are alike except for the first segment of leg one, three-segmented abdomen, six-segmented antennule, four furcal setae and both species have a cephalothorax that is fused to a segment of leg one.

Cluster II branches off to form two more clusters: II a and II b, cluster II a splits into two. The first is a monophyletic group containing *Ergasilus* sp. A and *Ergasilus* sp. C sharing 16characters, with the following characteristics shared between the two - the spine-seta formula is the same in each species; four-segmented abdomen; six-segmented antennule and four furcal setae.

The second cluster is also a monophyletic group including *E. flaccidus* and *E. mirabilis* sharing 15 characters. These two species with the following being a few of the shared characteristics – the spine-seta formula for legs one to four are similar, with differences on the third segments of legs one to three; four furcal rami and a four-segmented abdomen.

Cluster II b splits into two, the first has *E. kandti* standing alone, while the second has two clusters, the first cluster shares 24 characters and include *E. nodosus* and *E. sarsi,* with the following an example of some of the shared characteristics – cephalothorax of similar shape; four-segmented abdomen and three furcal setae.

The second cluster shares 26 characters and include *E. cunningtoni* and *Ergasilus* sp. B, both these species share the following characteristics – cephalothorax is of a similar shape; six-segmented antennulae; four-segmented abdomen and a similar spine-seta formula.

When comparing the relationship with the outgroup, *E. megacheir* is the closest with the least differences, and *E. cunningtoni* and *Ergasilus* sp. B being the furthest away with the most differences. There is no indication that the groups are separated by geographical distribution, with most of the species in the clusters originating from different regions and parasitising different hosts.

7.2 A Taxonomic Key for the African freshwater *Ergasilus* species

The only taxonomic key created for species of *Ergasilus,* is by Lin and Ho (1998) on the *Ergasilus* species parasitising the coastal fish of the world. No key has as yet been created for the African freshwater *Ergasilus* species.

1	**a.** Antennulae six-segmented	...3
	b. Antennulae five-segmented	...2
2	**a.** Leg five, two-segmented, basal segment with a single seta, distal segment with two terminal setae	...*E. flaccidus* Fryer, 1965 (page 65)
	b. Leg five, one-segmented	...*E. kandti* van Douwe, 1912 (page 70)
	c. Leg five, absent	...*E. nodosus* Wilson, 1928 (page 107)
3	**a.** Leg five, two-segmented, basal segment with one seta, distal segment with a lateral seta and two terminal setae	...*Ergasilus* sp. A (page 128)
	b. Leg five, two-segmented, basal segment with one seta, distal segment with two terminal setae	...4
	c. Leg five, one-segmented	...5
4	**a.** Abdomen three-segmented	...*E. lamellifer* Fryer, 1961 (page 75)
	b. Abdomen four-segmented	...*Ergasilus* sp. C (page 158)

5 **a.** Leg five, one-segmented with three setae ...6

b. Leg five, one-segmented with two setae ...7

c. Leg five, one-segmented with one seta ...*Ergasilus* sp. B (page 140)

6 **a.** Furcal rami with three furcal setae ...*E. sarsi* Capart, 1944 (page 113)

b. Furcal rami with five furcal setae ...*E. latus* Fryer, 1960 (page 80)

7 **a.** Antennae unadorned ...8

b. Antennae with a recurved denticle on the terminal segment ...*E. megacheir* (Sars, 1909) (page 92)

c. Antennae with an indentation on the third segment ...*E. cunningtoni* Capart, 1944 (page 59)

8 **a.** Abdomen, four-segmented ...*E. mirabilis* Oldewage & Van As, 1987 (page 99)

b. Abdomen, three-segmented ...*E. macrodactylus* (Sars, 1909) (page 85)

Chapter 8

General Discussion

Due to the fact that discussions have been provided in each of the previous chapters, this chapter will deal with other issues affecting the Okavango River and Delta and Lake Malawi, with a general discussion of the interactions between the crustacean parasites and their fish hosts. There are many major problems facing the freshwater habitats of the African continent and the Okavango River and Delta and Lake Malawi are no exceptions. There are two major influences that have a negative effect on the Okavango Delta; they are the climate and human influences.

During the various other studies of fish parasites of the Okavango many tests on the water quality and oxygen levels were conducted. It was found that in the areas of fast flowing water, such as the main stream, the oxygen saturation levels are extremely low, generally between the 50 and 70%. In areas where you would expect low oxygen saturation levels, such as in the isolated lagoons the oxygen levels can be as low as 3mg/l, this can be lethal to many fish species. Because of the adverse conditions in which the fish have to live (consider the fact that the Okavango Delta is situated in a desert!) many strategies have been developed to ensure survival (Skelton 2001). Certain fish species, such as the representatives of the Clariidae, have accessory air-breathing structures, allowing these fish to crawl over dry ground to reach water.

Many species have had to develop new breeding strategies to ensure that their eggs will survive these conditions which would normally kill the eggs and young larvae. One of these strategies is mouthbrooding which is found in certain cichlid genera, where usually the adult male provides shelter and ventilated area where the eggs and fry are able to develop (Skelton 2001). Another strategy is to construct a floating nest made out of foam and one of the parents guarding it from predation, this practice is found in the African pike *Hepsetus odoe* (Bloch, 1794) and the blackspot climbing perch *Microtenopoma intermedium* (Pellegrin, 1920) (Merron *et al.* 1990). Cattle ranching is the main type of agriculture in Botswana; this is a major problem because the country is very dry and prone to drought. With the Okavango Delta being the country's only permanent natural body of water, in the past this meant that in times of drought, the ranchers, in order to save their cattle, took them to the delta. This affected the entire delta negatively, because the cattle would graze in areas where the game occurred, forcing them away from the better grazing areas causing increased mortality. Because of this intermingling of wildlife and domesticated animals there was a major problem with diseases, such as sleeping sickness, foot-and-mouth and Rinderpest, being spread between the two (Balfour *et al.* 1999). This resulted in the government erecting many veterinary cordons to the south and west of the wetlands, in order to stop the spreading of diseases (Bailey 1998). Unfortunately this has had serious negative effects on the wildlife, inhibiting the movement of the larger species such as elephant, buffalo and wildebeest. This problem was highlighted in a tragic event in 1984 when approximately 50 000 migrating wildebeest died when they were prevented by the fence from reaching the water (Owens & Owens 1984).

Other problems faced are the over hunting by sporting hunters. There are quotas but these are often ignored. Poaching is as big a problem in Botswana as it is in the rest of Africa. One of the main reasons may be because many people are unemployed and are living far below the breadline, forcing them to either hunt for food or to create an income.

The problems affecting the Delta's water are numerous, these include over fishing, encroachment on the floodplain, insecticide pollution and invasive plants. Over fishing in the Delta is becoming a big factor in the depletion of the fish stocks. Traditionally the people living in the delta have exploited the fish stocks on a subsistence level, which generally had a very small effect on the fish populations. The Botswana government has a commercial fishing programme running in the Delta, which yields approximately 1200 tonnes/year (Merron and Bruton 1986). At the moment there are measures used to prevent the over-exploitation of the fish stock by banning certain sizes of gill nets, which catch immature fish, and by exploiting the fish species that are abundant such as the Silver Catfish *Schilbe intermedius* Rüppell, 1832. The increase of recreational fishing has a great impact on the fish stock, with people catching far too many fish. This problem is being corrected by ensuring that the fishermen must get licenses to fish, that fish are only caught at certain times of year (not during the spawning season), and that each fisherman should have a daily limit on the number of fish caught (Merron 1994). Another major problem is the uncontrolled use of motor boats on the river; this increases the erosion of the banks, the effects of which can be seen in Figure 8.1A.

Many of the local fishermen use a burning technique to catch fish; this is done by setting up nets at the edge of the papyrus, then setting the papyrus alight which drives the fish into the nets. Even though these fires do sometimes occur naturally those caused by humans must be stopped. Unfortunately many of these fires get out of control and end up burning large tracts of papyrus, depleting the oxygen levels in the water, killing the young fish that shelter there and in turn cause a drop in the population growth (Figs. 8.1C&D).

The problem of people and their activities encroaching on the floodplain is increasing. Many activities do no harm to the environment, such as the collection of reeds and thatch which are used as building material (Fig. 8.1B). The Okavango Delta has very distinct wet and dry seasons, during the dry season areas that were underwater are exposed. These areas are then farmed or overgrazed and in certain areas are settled on permanently, all these activities can result in a reduced floodplain area, and a decrease in the annual exchange of nutrients between the land and the water (Bruton and Merron 1985).

Due to the importance of cattle ranching to Botswana's economy many programmes have been launched in order to eradicate the tsetse fly. This is only done in the regions where cattle are present; the fish aren't always affected by the spraying depending on the chemicals that are used. It has been found that when organochlorine endosulfan is used the population densities of many fish species were reduced, for example the nesting density of *Tilapia rendalli* (Boulenger, 1896) is reduced by 75% after this insecticide was used (Merron 1994). There are many other types of insecticides that can be used and don't have a negative effect on the fish and other aquatic organisms.

The introduction of invasive plants into the Delta is also a major problem. The Moremi Wildlife Reserve has experienced a few outbreaks of *Salvinia molesta*, which is an exotic aquatic plant that has a very rapid growth rate. Without natural predators these plants can cover an entire lagoon, cutting of the sunlight, reducing the oxygen content and forcing aquatic organisms out of the area. These plants can be biologically controlled using the weevil *Cyrtobagous salviniae* that feeds on the plant. Once the plant dies off the weevils have nothing to feed on and they too die off. This method has worked in the past in Zimbabwe and South Africa (Merron 1994). Hopefully this plant will not continue to spread through the Delta.

The problems facing Lake Malawi are very similar to those affecting the Okavango Delta, any large water body experiences similar ecological problems. A vast majority of the human population living on the lakeshore live below the breadline and rely on subsistence agriculture and fishing for survival. This has a large impact on the aquatic fauna and flora of the lake, with an increase in runoff from the surrounding farmlands. The introduction of commercial fishing is having the same effect on the lake as it has had in Lake Victoria, the indigenous fish population is being overexploited, and if this carries on without any intervention the fish population will be severely affected.

All these environmental factors have an effect on the fish of the freshwater bodies and their fish parasites. Many crustacean parasites have been collected from the Okavango River and Delta and Lake Malawi, such as *Chonopeltis liversedgei* van As & van As, 1999 from the Okavango Delta (van As & van As 1999) and *Lamproglena monodi* Capart, 1944 from Lake Malawi. Many parasites are species specific, such as *C. liversedgei* which is only found on the western bottlenose *Mormyrus lacerda* Castelnau, 1861 while others are found on a wide variety of fish species, such as *Ergasilus kandti*

Figure 8.1

Photographs from the Okavango Delta

A. Erosion of the river bank

B. Makoros with bundles of thatch that are collected by the locals

C. Papyrus burning can occur naturally or lit by the local fishermen

D. A burnt expanse of papyrus

E. *Synodontis nigromaculatus* Boulenger, 1905 were collected with very high infestations by *Ergasilus* von Nordmann, 1832 species

F. An example of a high infestation of *Ergasilus* on a single gill arch

G. Two *Ergasilus* specimens attached to a single gill filament, with the arrow indicating the swollen epithelial tissue

H. A *Lamproglena* von Nordmann, 1832 specimen attached to a gill filament


A
B
C
D
E
F
G
H

which has been collected from twelve different hosts. The number of hosts that a parasite has, can have a very big impact on the parasite's survival. If the parasite only has one host, it faces a greater risk of dying out if something happens to the host species.

The *Ergasilus* parasites have various free living stages with a parasitic adult stage, many features have changed from resembling the free living forms to a more parasitic form, for example the antenna which has been reduced to a four-segmented appendage that is used to grasp onto the gill filaments of the fish host. Other adaptations have occurred, such as the reduction of the legs, with the fifth legs being reduced to a single tiny segment on species such as *Ergasilus* sp. B, and have disappeared entirely in others such as *E. nodosus*. During this study it has been observed that in certain cases the grasping action has caused severe damage to the filament, with swollen epithelial cells covering the antennae (Fig. 8.1G). The obstruction to the blood flow from the filaments can negatively affect the fish host when there are high numbers of parasites on a single gill arch. Over a hundred *Ergasilus* specimens were found attached to a single arch of *Synodontis nigromaculatus* Boulenger, 1905 from the Okavango Delta (Figs. 8.1E&F).

Studies conducted in America have found that a high number of *Ergasilus cyprinaccus* Rogers, 1969 coupled with an infection by any bacteria can cause mortalities (Rogers 1969). A study by Einszporn (1965) on the feeding activity of the parasites indicated that this activity has a negative effect on the host, with a wide variety of cell types consumed such as epithelial cells, mucous cells, erythrocytes and leucocytes with the main components being the red blood cells. The study also found that the prolonged attachment to the gill filament as well as the continuous feeding leaves permanent damage to the gills. When you take the damage that these parasites can cause to the gills, the added pressure of an anoxic environment can cause the host to experience extreme stress and possibly death. When viewed in this light having more than one host can be very beneficial to the parasite.

Another major problem facing the host is that they are often exposed to multiple infestations of parasitic crustaceans. During this study the *Ergasilus* specimens were found sharing a gill filament with other parasites such as different *Lamproglena* von Nordmann, 1832 and *Trichodina* Ehrenberg, 1830 species and Monogenea van Beneden, 1858. The presence of all these parasites on the fragile gill filaments can be very detrimental towards the host, even more so if adverse environmental factors are present, such as if the papyrus has been burnt or the water levels are very low. Both these occurrences have been known to cause fish deaths in the past. The African *Ergasilus* species do not show any host specificity, whereas the *Lamproglena* (Fig. 8.1H) species usually are species specific. The information provided in Table 6.3 illustrates that many fish species are host to a wide variety of crustacean parasites, with *Clarias gariepinus* (Burchell, 1822) collected from the Okavango Delta being parasitised by *Lamproglena, Afrolernaea* Fryer, 1956, *Opistolernaea* Yin, 1960, *Ergasilus* and *Dolops* Audouin, 1837 on the gills, as well as *Dolops* and *Argulus* Müller, 1785 on the skin. Even though certain fish species are host to many different crustacean parasites, others such as the cyprinids have never been recorded as hosts to any of the crustacean parasites in the Delta. This is something which will be investigated in the future as part of the Okavango Fish Parasite Project.

The survival of the fish and their parasites are entirely dependent on the environmental conditions of the areas in which they occur. If we do not manage these habitats properly, we will cause many species to face extinction, it would be a terrible shame to lose this amazing diversity of life that is found in the freshwater habitats of the African continent.

Chapter 9

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Abstract

Ten *Ergasilus* von Nordmann, 1832 species and two *Paraergasilus* Markewitsch, 1937 species have been described from African freshwater habitats since the beginning of the twentieth century. As part of this study, the information for these known species was put together to form a complete review of the freshwater African ergasilids with the distribution, description and drawings of all 12 species included. A substantial amount of research has been conducted from the major systems of Africa, but very little has been done in southern Africa. In this study specimens were collected from the Okavango River and Delta and Lake Malawi using a wide variety of collection methods. After the specimens were examined it was found that the material included four new species, two from each study area. The two new species from the Okavango Delta include *Ergasilus* sp. A from *Synodontis nigromaculatus* Boulenger, 1905 and *Ergasilus* sp. B from *Brycinus lateralis* (Boulenger, 1900). The seasonality and host specificity of the ergasilids collected from the Okavango Delta was discussed, and it was found that the *Ergasilus* species are not host specific and are more prevalent in the summer months. The species from Lake Malawi include *Ergasilus* sp. C from *Petrotilapia genalutea* Marsh, 1983 and *Paraergasilus* sp. A from *Pseudotropheus tropheops* Regan, 1922. A review of all the fish species and parasitic crustaceans collected from Lake Malawi is provided, no conclusion could be made on the seasonality of the ergasilids from Lake Malawi due to a lack of information. A phylogenetic analysis was conducted for all the freshwater *Ergasilus* species using *Dermoergasilus mugilis* Oldewage & van As, 1988 as the outgroup. Finally a taxonomic key was compiled for *Ergasilus*, including all the known and new species.

Keywords: Southern Africa, freshwater, fish parasites, ergasilids, morphology, taxonomy

Sedert die begin van die twintigste eeu is tien spesies van *Egasilus* Von Nordmann, 1832 en twee *Paraergasilus* Markowitsch, 1937 spesies uit Afrika varswaterhabitats beskryf. As deel van hierdie studie is die kennis oor hierdie twee bekende spesies saamgevoeg in 'n volledige oorsig van die verspreiding, beskrywings en illustrasies van al 12 verteenwordigers van varswater Ergasilidae van Afrika. 'n Groot gedeelte van die navorsing gaan oor die hoof rivierstelsels van Afrika, maar min navorsing is oor suidelike-Afrika gedoen. Vir hierdie studie is verskeie metodes gebruik om eksemplare in die Okavangorivier en –delta en die Malawimeer te versamel. In die material wat versamel is, was daar twee nuwe spesies van elk van die versamelingsgebiede. Die Okavangodelta het twee nuwe spesies opgelewer, nl. *Egasilus* sp. A op *Synodontus nigromaculatus* Boulenger, 1905 en *Ergasilus* sp. B op *Brycinus lateralis* (Boulenger, 1900). Die seisoenaliteit en gasheerspesifisiteit van die Okavangodelta ergasilide word bespreek en dit is bevind dat die *Ergasilus* spesies nie gasheer spesifiek is nie en dat hulle meer dikwels in die somermaande voorkom. Die spesies van die Malawimeer sluit in *Ergasilus* sp. C van *Petrotilapia genalutea* Mars, 1983 en *Paraergasilus* sp. A van *Pseudotropheus tropheops* Regan, 1922 in. 'n Oorsig van al die visspesies en die parasitiese krustasiërs wat uit die Malawimeer versamel is, word gegee. As gevolg van gebrekkige inligting kon geen uitsluitsel oor die seisoenaliteit van die ergasilide van die Malawimeer gemaak word nie. 'n Filogenetiese analise vir al die varswater *Ergasilus* spp. is gedoen, met die gebruik van *Dermoergasilus mugilis* Oldewage & Van As, 1988 as buitegroep. 'n Taksonomiese sleutel wat al die bekende en nuwe spesies van *Ergasilus* insluit, is opgestel.

Acknowledgements

I would like to acknowledge and express my sincere appreciation to the following people and institutions:

- **My supervisors Dr Liesl and Prof. Jo van As:** for being included as a member of the research group, for the amazing field trips, and all the support and guidance during my studies.

- **Prof. Linda Basson:** for helping me and especially for putting up with all my questions.

- **Prof. Sherman Hendrix:** for allowing me to use the ergasilid specimens he collected from Lake Malawi, for providing the photographs of the Lake and for assisting me whenever I needed extra information.

- **My parents and family:** for all their love, support and useful advice throughout my studies.

- **Candice, Linki, Elindi and all the post graduate students:** for all their help with the fieldwork and for the amazing times we had on all the excursions.

- **The Centre for Confocal and Electron Microscopy, UFS:** for allowing me to use the SEM and for providing assistance whenever needed.

- **National Research Foundation (NRF):** for the bursaries received in support of my studies.

- **Debswana Diamond Company:** for their financial support of the Okavango Fish Parasite Project

- **The Department of Zoology and Entomology, UFS:** for allowing me to be part of such an interesting and involved department, and for allowing me to use the departmental facilities.