

**Aspects of the feeding biology of *Lamproglena clariae*  
Fryer, 1956**

by

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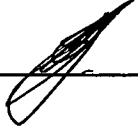
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# ***Don't Quit Poem***

*by anonymous*

**When things go wrong, as they sometimes will,  
When the road you're trudging seems all up hill,  
When the funds are low and the debts are high,  
And you want to smile, but you have to sigh,  
When care is pressing you down a bit,  
Rest! if you must; but don't you quit.**

**Life is queer with its twists and turns,  
As everyone of us sometimes learns,  
And many a failure turns about  
When he might have won had he stuck it out;  
Don't give up, though the pace seems slow;  
You might succeed with another blow.**

**Often the goal is nearer than  
It seems to a faint and faltering man,  
Often the struggler has given up  
When he might have captured the victor's cup.  
And he learned too late, when the night slipped down,  
How close he was to the golden crown.**

**Success is failure turned inside out;  
The silver tint of the clouds of doubt;  
And you never can tell how close you are,  
It may be near when it seems afar;  
So stick to the fight when you're hardest hit;  
It's when things seem worst that you mustn't quit.**

Hierdie werk word opgedra aan my ouma

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## ABSTRACT

There are 39 known species of *Lamproglena* to date. A review of all species including the species name, the author, as well as an accompanying sketch and information regarding the distribution, pathology and host preference is given.

*Lamproglena clariae* is a copepod gill parasite found on *Clarias gariepinus*. It has been observed that they cause extensive gill tissue proliferation, which may interfere with respiration. It is uncertain on which tissue type *Lamproglena* feeds, as red blood is never apparent in the gut of *Lamproglena monodi*, whereas in the cases of both *L. clariae* and *L. barbicola* they undoubtedly feed on blood, proven by the frequently blood-filled gut. Even though the mouthparts are not fully understood as yet, it is deduced that feeding involves only the maxillae and maxillipedes.

Many poecilostomes lack mandibles. Also, in the lernaeids the mandible is appendage is the smallest and from the 39 known *Lamproglena* species, the mandibles are described in only eight species.

This study examines the digestive tract and the structure of the mouthparts using both light and scanning electron microscopy and tracts the nerves to establish if *L. clariae* does possess mandibles.

Specimens were collected from *Clarias gariepinus* in the Vaal Dam after the fish were euthanised and the gills removed. The samples were fixed in an aceto formaldehyde alcohol solution and preserved in 70% ethanol prior to dehydration and embedding in resin. Serial sections were made at 5 µm and stained with a trichrome stain. A schematic as well as graphic reconstruction of the digestive system is presented.

The digestive system consists of three predominant parts, the fore, mid and hindguts. The foregut has a cuticularised epithelium. The oesophagus has a muscle layer

which stretched and contracts in order to aid feeding and it extends into the midgut via a funnel-like structure. There are four designated zones within the midgut. The hindgut is a simple, cuticle lined tube. Cell structures are discussed.

The bilobed protocerebrum in *L. clariae* is present. The deutocerebrum innervates the antennules. The tritocerebrum consist of two lobed parts and innervates the antennules. The ventral nerve cord is situated posterior to the cephalon. It protrudes dorsally, from where the posterior commissures innervates. The anterior commissures innervates closer to the tritocerebrum. The nerves leading to the mandibles are innervated from the anterior commissure. The more posteriorly located commissure innervates the nerve to the seta located between the antennae and the maxillae. Both the nerves to the maxillae and the endopodite to the maxillae are innervated from this commissure.

Mandibles were left out of previous species descriptions of *L. clariae*. Other *Lamproglena* species descriptions, showing the mandibles, revealed slender looking mandibles located in close proximity to the mouth opening. This is contrary to the stout mandibles of *L. clariae*.

Future research topics are highlighted and discussed.

## OPSOMMING

Daar is tot op hede 39 verskillende spesies aan die wetenskap bekend. 'n Oorsig wat al die genus- en spesie name, beskrywer asook 'n skets van elkeen insluit sowel as hul verspreiding, patologie en gasheervoorkeur word verskaf.

*Lamproglena clariae* parasiteer op die kieue van *Clarias gariepinus*. Waarneming het bewys dat hul die oorsaak is van uitgebreide keieuweefselproliferasie wat kan lei tot swak respirasie. Dit is onduidelik waarop *Lamproglena* voed as gevolg van die afwesigheid van bloed in the spysverteringskanaal van *L. monodi* teenoor die bloedge vulde spysverteringskanaal van *L. clariae* en *L. barbicola*. Die mondaanhangsels word nog nie ten volle verstaan nie en daarom word die afleiding gemaak dat die maksilla en maksilipede gebruik word vir voeding.

Baie verteenwoordigers van die Peocilostomatoida beskik nie oor mandibels nie. By verteenwoordigers van die Lernaeydae is die mandibel die kleinste struktuur en van die 39 bekende *Lamproglena* spesies, is die mandibels van slegs agt spesies beskryf.

Hierdie studie ondersoek die spysverteringskanaal en mondaanhangsels met behulp van lig- en skandeer elektronmikroskopie en volg die senuwees om te vas te stel of *L. clariae* oor mandibels beskik al dan nie.

*Lamproglena clariae* eksemplare was versamel vanaf *Clarias gariepinus* in die Vaaldam nadat die visse gedood en die keiue verkry is. Die eksemplare is gefikseer in 'n asetoformaldiehydalkohol oplossing en gepreserveer in 70% etanol voordat dit gedehidreer is en in hars ingebed is. Seriesneë is gesny teen 5 µm en gekleur met 'n trichroomkleuring. 'n Skematiese- sowel as grafiese rekonstruksie van die spysverteringskanaal het gevolg.

Die spysverteringskanaal bestaan uit drie dominante gedeeltes naamlik die voor-, middel- asook die agterderm. Die voorderm beskik oor gekutikuleerde epiteelselle. Die esofagus het 'n spierlaag wat saamtrek en ontspan om sodoende voeding aan te help. Die esofagus strek tot binne-in die middelderm deur middel van 'n trechter-vormige struktuur. Die middelderm het vier sones. Die agterderm is 'n eenvoudige, gekutikuleerde buis. Selstrukture word bespreek.

Die protoserebrum in *L. clariae* is tweelobbig. Die deutoserebrum innerveer die antennules. Die tritoserebrum bestaan uit twee lobbe en innerveer die antennulae. Die ventrale koord is posterior tot die sefalon geleë. Dit strek dorsaal vanwaar die posterior kommisure ge-innerveer word. Die anterior kommisures word nader aan die tritoserebrum ge-innerveer. Die senuwees wat na die mandibels lei, word deur die anterior kommisure ge-innerveer. Die seta wat tussen die antennae en antennulae geleë is word deur die meer posterior kommisure ge-innerveer. Beide senuwees wat die maksilla sowel as die endopodite innerveer word deur die bogenoemde kommisure ge-innerveer.

Mandibels is uit spesie beskrywings gelaat. Die spesies wat wel 'n beskrywing van die mandibels het met gepaardgaande sketse, wys delikate mandibels wat naby aan die mond opening geleë is. Hierdie is in teenstelling met die afgestompte mandibels van *L. clariae*.

Toekomstige navorsings moontlikhede word bespreek.



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# INTRODUCTION



**1** *Life*



## **1.1 Copepoda**

The copepods are the most diverse and also largest group of Crustacea (cf. Pesce, 1995). The astounding success of this group of microcrustaceans is a result of their symbiotic interactions with other organisms (Pesce, 1995). They are parasites or intermediate host of all the animal groups. Copepods parasitising the skin and gills of fish are serious pests and thus are of commercial importance in both freshwater and marine fish farms (Pesce, 1995).

## **1.2 Lernaeidae**

According to Ho and Kim (1997), the Lernaeidae is a major family of cyclopoid parasitic copepods. They are parasitic on freshwater fishes and some of them are of the most harmful parasites of aquaculture fishes (Ho and Kim, 1997). The Lernaeidae is comprised of ten genera and subgenera which includes the genus *Lamproglena* (cf. Ho, 1984). *Lernaea* and *Lamproglena* are the two largest genera containing 77% of the known species of this family (Ho, 1994). The genus *Lamproglena* (Nordmann, 1832) is an ecto-parasite with a cosmopolitan distribution comprised of 39 nominated species (Dippenaar, Luus-Powell and Roux, 2001).

## **1.3 *Lamproglena***

*Lamproglena pulchella* Nordmann, 1832, is the type species of the genus. In the species redescription Kumarie, Khera and Gupta (1989) define the species as having an elongated, cylindrical body. The body has a fiddle shape and is comprised of a cephalosome and postcephalic trunk (Huys and Boxshall, 1991). The cephalosome consists of six fused somites and the postcephalic trunk of nine somites and in addition there is the anal somite, which represents the telson (Boxshall, 1992). The first thoracic somite (maxilliped-bearing) is fully

incorporated into the cephalosome which consists of five cephalic somites (Boxshall, 1992).

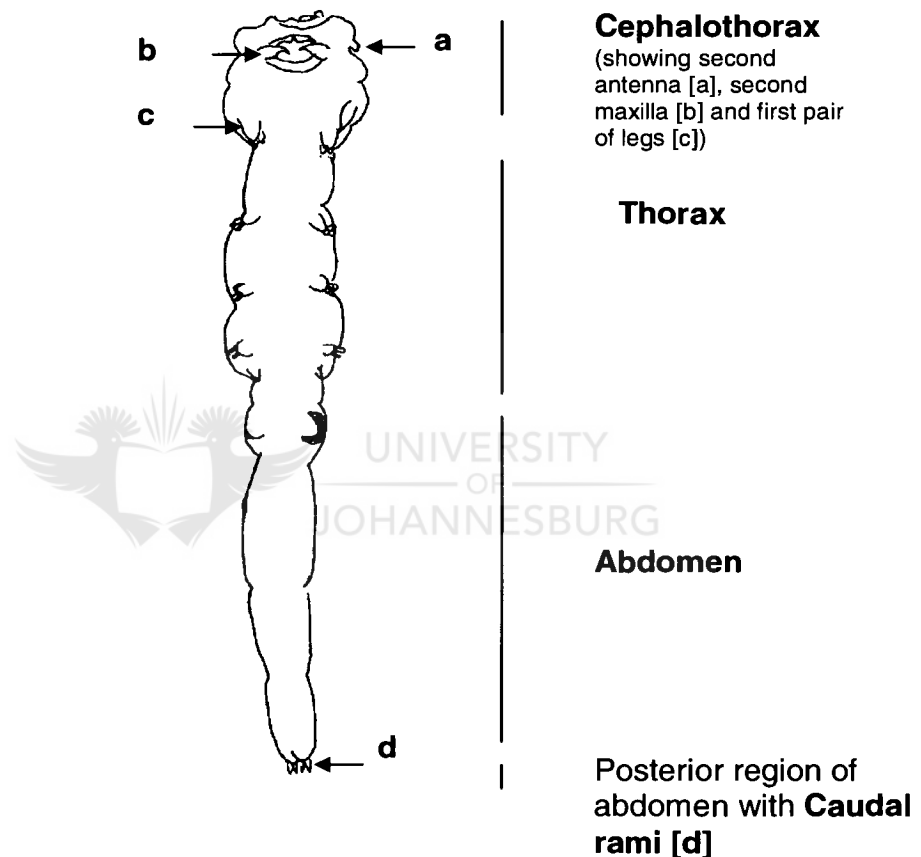
According to Kumarie *et al.*, (1989), the cephalothorax of *L. pulchella* has two constrictions on the lateral margins. They found that the 'neck' is formed by the second thoracic segment which is short and narrow. The thorax consists of the third, fourth and fifth thoracic segments with both the third and fourth segments broad and fused and the fifth segment short and narrow and it is in the shape of a 'neck' between the thoracic segments and the genital segment (Kumarie *et al.*, 1989).

The genital segment is barrel-shaped with two dorsolateral oviduct orifices (Kumarie *et al.*, 1989). Usually two egg strings are present. The abdomen is long with three indistinct segments (Kumarie *et al.*, 1989) and the first abdominal segment is longer than the second and third segments, with the third segment comparatively smaller than the second. The caudal rami are long and well developed, forceps-like and each caudal ramus is tipped with two small tubercles and two spines (Kumarie *et al.*, 1989).

The antennule (or first antenna) of *L. pulchella* is indistinctly segmented, with two segments and is armed with numerous setae dorsolaterally (Kumarie *et al.*, 1989). Five setae are present on the second segment (Kumarie *et al.*, 1989). The second antenna is described by Kumarie *et al.*, (1989) as small and characterised by four distinct segments. The first is long and broad where-as the second segment is less broad with a lateral seta. The third segment on the second antenna has two apical setae. The fourth segment on the second antenna is tipped with four apical setae (Kumarie *et al.*, 1989).

According to Kumarie *et al.*, (1989) the first maxilla resembles a spine. The second maxilla consists of two segments of which the first is large and broad and the second terminates in a claw (Kumarie *et al.*, 1989) (Figure 1). There is no mention of mandibles in the redescription, but Huys and Boxshall (1991) stated that copepod mandibles are typically biramous and characterised by a two

segmented protopod, no mention about the mandibles of *Lamproglena* is made. In species where the mandible is present the segment closest to the organism is the coax and has a large gnathobase attached as the first segment (Huys and Boxshall, 1991). The maxillipeds are well developed, each having three strong robust recurved claws (Kumarie *et al.*, 1989). Five pairs of biramous thoracic legs are present (Kumarie *et al.*, 1989).



**Figure 1:** *Lamproglena pulchella*, adult female, ventral view, redrawn from Kumarie *et al.*, (1989).

*Lamproglena pulchella* Nordmann was described in 1832. Nordmann described two other species (*Lamproglena lichiae* and *Lamproglena hemiprichii*) within the same paper but all descriptions are without figures and descriptions.

Zimmermann added *Lamproglena weneri* in 1922 and Wilson wrote the species description of *Lamproglena angusta* in 1924.

Filhol described the biology of *Lamproglena pulchella* in 1936. Yü did a synopsis of the genus *Lamproglena* Nordmann with description of a new species from North China (*Lamproglena chinensis*) in 1937.

Capart (1943) gave descriptions for *Lamproglena inermis*, *Lamproglena minuta* as well as *Lamproglena robusta*. He stated that they all belong to the family Dichelestiidae and gave full descriptions of all the abovementioned species as well as *Lamproglena chinensis* Yü 1937 and an unnamed *Lamproglena* species. Capart gave a species description of *Lamproglena monodi* in 1944.

*Lamproglena curta* was described in 1950 by Gussev. Also in 1950, Sproston, Yin and Hu described *Lamproglena carassi*. Kirtisinghe described *Lamproglena chinensis sprostoni* in 1950. Capart gave species descriptions of both *Lamproglena wilsoni* and *Lamproglena elongata* in 1956. In the same year, Fryer described *Lamproglena nyasae* and *Lamproglena clariae*. *Lamproglena cleopatra* was described in 1957 by Humes.

Dollfus described *Lamproglena aubentoni* in 1960. In 1961 Fryer described *Lamproglena barbicola*. In 1964 Fryer and Paperna described *Lamproglena intercedens* and *Lamproglena jordani* respectively. Fryer described *Lamproglena cornuta* 1965. A year later Suchenko and Allanmuratov described *Lamproglena markewitschi*.

Kuang described *Lamproglena brevis*, *Lamproglena cylindrata*, *Lamproglena forficata*, *Lamproglena mongtinensis* and *Lamproglena yunnanensis* all in 1977.

Thomas and Hameed described *Lamproglena krishnai* in 1984. In the following year Kuang and Qian described *Lamproglena cirrhinae*, *Lamproglena heterognatha* and *Lamproglena meridiona*.

In 1989 Kumarie *et al.* described *Lamproglena cavasi*, *Lamproglena indica* as well as *Lamproglena seenghalae*.




*Lamproglena semilabecola* was described in 1991 by Liu and Wang. Kuang described *Lamproglena dibara* in the same year. In the following year Manohar, Seenappa and Ventkateshappa (1992) did a species description of *Lamproglena hospetensis*. Battish and Brar, in 1993, described *Lamproglena gurayai*.





The description of *Lamproglena hoi* was done by Dippenaar *et al.*, (2001). Recently, Van As and Van As described *Lamproglena hepseti* in 2007.





Dippenaar, *et al.* summarised the genus in 2001. Since then an additional four species have been described, which brings the total of described species to 39.







**Table 1: *Lamproglena* species with their descriptors and the year in which the description was published, notes on and a sketch of the total specimen.**

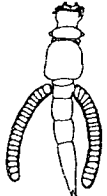



Number	Species	Author	Notes	Sketch
1	<i>Lamproglena pulchella</i>	Von Nordmann, 1832		 <p>Redrawn from Piasecki (1993)</p>
2	<i>Lamproglena hemiprichii</i>	Von Nordmann, 1832	<p>Junior Synonym.</p> <p><i>L. aubentoni</i></p> <p>Dollfus, 1960 (cf. Fryer, 1964)</p>	 <p>Redrawn from Dollfus (1960)</p>
3	<i>Lamproglena lichiae</i>	Von Nordmann, 1832		 <p>Redrawn from Piasecki (1993)</p>

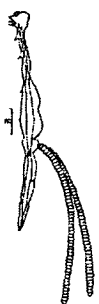

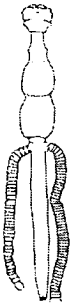
4	<i>Lamproglena weneri</i>	Zimmermann, 1922		Redrawn from Sproston <i>et al.</i> , (1950)
5	<i>Lamproglena angusta</i>	Wilson, 1924		Redrawn from Wilson (1924)
6	<i>Lamproglena compacta</i>	Markewitsch, 1936		Redrawn from Markewitsch (1936)
7	<i>Lamproglena orientalis</i>	Markewitsch, 1936		Redrawn from Markewitsch (1936)


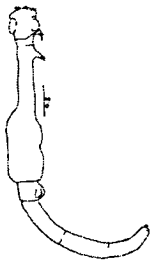


8	<i>Lamproglena chinensis</i>	Yü, 1937		 <p>Redrawn from Yü (1937)</p>
	<i>Lamproglena ophiocephali</i>	Yamaguti, 1939	<p>Junior Synonym of</p> <p><i>L. chinensis</i> Yu, 1937</p> <p>(cf. Sproston, <i>et al.</i>, 1950)</p>	 <p>Redrawn from Yamaguti (1939)</p>
9	<i>Lamproglena robusta</i>	Capart, 1943		 <p>Redrawn from Capart (1943)</p>
10	<i>Lamproglena minuta</i>	Capart, 1943		 <p>Redrawn from Capart (1943)</p>






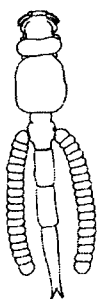



11	<i>Lamproglena inermis</i>	Capart, 1943		Redrawn from Capart (1943)
12	<i>Lamproglena monodi</i>	Capart, 1944		Redrawn from Capart (1944)
13	<i>Lamproglena curta</i>	Gushev, 1950		Redrawn from Gushev (1950)
14	<i>Lamproglena carassii</i>	Sproston, Yin and Hu, 1950		Redrawn from Sproston <i>et al.</i> , (1950)



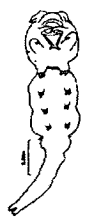

15	<i>Lamproglena chinensis sprostoni</i>	Kirtisinghe, 1950		 <p>Redrawn from Kirtisinghe (1950)</p>
16	<i>Lamproglena wilsoni</i>	Capart, 1956		 <p>Redrawn from Capart (1956)</p>
17	<i>Lamproglena elongata</i>	Capart, 1956		 <p>Redrawn from Capart (1956)</p>
	<i>Lamproglena nyasae</i>	Fryer, 1956	Junior Synonym of <i>L. monodi</i> (cf. Fryer 1959)	 <p>Redrawn from Fryer (1956)</p>


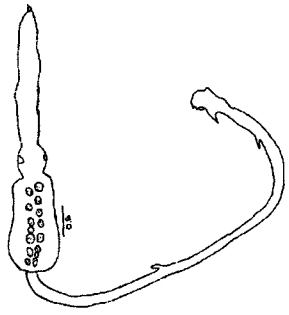


18	<i>Lamproglena clariae</i>	Fryer, 1956		 <p>Redrawn from Fryer (1956)</p>
19	<i>Lamproglena cleopatra</i>	Humes, 1957		 <p>Redrawn from Kabata (1979)</p>
	<i>Lamproglena aubentoni</i>	Dollfus, 1960	<p>Junior Synonym of</p> <p><i>L. hemiprichii</i></p> <p>(cf. Fryer, 1964)</p>	 <p>Redrawn from Dollfus (1960)</p>

20	<i>Lamproglena barbicola</i>	Fryer, 1961		 <p>Redrawn from Fryer (1961)</p>
	<i>Lamproglena intercedens</i>	Fryer, 1964	Transferred to <i>Catlaphilla</i> (cf. Ho, 1998)	 <p>Redrawn from Fryer (1964)</p>
21	<i>Lamproglena jordani</i>	Paperna, 1964		 <p>Redrawn from Paperna (1964)</p>
22	<i>Lamproglena cornuta</i>	Fryer, 1964		 <p>Redrawn from Fryer (1964)</p>

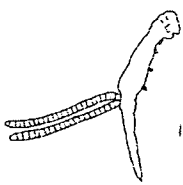



23	<i>Lamproglena markewitschi</i>	Suchenko and Allanmuratov, 1966		Redrawn from Suchenko and Allanmuratov (1966)
24	<i>Lamproglena brevis</i>	Kuang, 1977		Redrawn from Kuang (1977)
25	<i>Lamproglena cylindrata</i>	Kuang, 1977		Redrawn from Kuang (1977)

26	<i>Lamproglena forficata</i>	Kuang, 1977		Redrawn from Kuang (1977)
27	<i>Lamproglena mongtinensis</i>	Kuang, 1977		Redrawn from Kuang (1977)
28	<i>Lamproglena yunnanensis</i>	Kuang, 1977		Redrawn from Kuang (1977)
29	<i>Lamproglena krishnai</i>	Thomas and Hameed, 1984		Redrawn from Thomas and Hameed (1984)

30	<i>Lamproglena cirrhinae</i>	Kuang and Qian, 1985		Redrawn from Kuang and Qian (1985)
31	<i>Lamproglena heterognatha</i>	Kuang and Qian, 1985		Redrawn from Kuang and Qian (1985)
32	<i>Lamproglena meridiona</i>	Kuang and Qian, 1985		Redrawn from Kuang and Qian (1985)
33	<i>Lamproglena cavasii</i>	Kumarie, Khera and Gupta, 1989		Redrawn from Kumarie <i>et al.</i> , (1989)

34	<i>Lamproglena indica</i>	Kumarie, Khera and Gupta, 1989		 <p>Redrawn from Kumarie <i>et al.</i>, (1989)</p>
	<i>Lamproglena seenghalae</i>	Kumarie, Khera and Gupta, 1989	Transferred to <i>Indolernaea</i> (cf. Ho, 1998)	 <p>Redrawn from Kumarie <i>et al.</i>, (1989)</p>
35	<i>Lamproglena semilabecola</i>	Liu and Wang, 1991		 <p>Redrawn from Liu and Wang (1991)</p>
36	<i>Lamproglena dibara</i>	Kuang, 1991		 <p>Redrawn from Kuang (1991)</p>



37	<i>Lamproglena hospetensis</i>	Manohar <i>et al.</i> , 1992		 <p>Redrawn from Manohar (1992)</p>
	<i>Lamproglena gurayai</i>	Battish and Brar, 1993	Transferred to <i>Indolernaea seenghalae</i> (cf. Ho, 1998)	 <p>Redrawn from Battish and Brar (1993)</p>
38	<i>Lamproglena hoi</i>	Dippenaar, Luus-Powell and Roux, 2001		 <p>Redrawn from Dippenaar <i>et al.</i>, (2001)</p>
39	<i>Lamproglena hepseti</i>	Van As and Van As, 2007		 <p>Redrawn from Van As and Van As (2007)</p>

In 1968, Fryer stated that *Lamproglena* is most abundant in the African, Palaertic and Oriental regions. Since then, 11 species were described on freshwater fishes of Africa and the remaining number was from Asia (Kuang and Qian, 1985). The number of African species has increased to 15. Kumarie *et al.*, (1989) organised the known species within two groups. Group I, includes species with an elongated, cylindrical body, whereas Group II have short and compact bodies (Kumarie *et al.*, 1989).

In Tables 2 and 3, the species are listed according to distribution and are provided with a symbol which corresponds with the symbols on Figures 2-4.

#### **1.4 Geographical distribution of *Lamproglena***

Hosts and localities for each of the described species are summarised in Tables 2 - 4 and Figures 4 -7.



**Table 2: Summary of the distribution of *Lamproglena* spp. with the host, locality and references.**

Symbol		Species	Host	Reference	Locality
A	1	<i>Lamproglena angusta</i>	<i>Malapterus electricus</i>	Fryer (1968)	Nile River , Egypt
				Kumarie <i>et al.</i> , (1989)	Sudan
B	1	<i>Lamproglena barbicola</i>	<i>Barbus attianalis radcliffi</i>	Fryer (1968)	Nile River, Egypt
				Kumarie <i>et al.</i> , (1989)	Lake Victoria, Kenya
C1	1	<i>Lamproglena clariae</i>	Clariidae gen. sp.	Fryer (1956)	Lakes Malawi, Victoria and Albert (in Malawi, Kenya and Uganda respectively)
C2			<i>Clarias mossambicus</i>	Fryer (1961)	Banga River tributary of Luweya
C3			<i>Heterobranchus longifilis</i>	Fryer (1961)	Iragalla, Malagarasi Swamps South Africa Nile, Congo and Zambezi Rivers, Lake Nyasa
C4			<i>Clarias lazera</i>	Kumarie <i>et al.</i> , (1989) Fryer (1968)	White Nile near Khartoum Edward-George , Sudan
				Thurston (1970)	Lake System, Kazinga Channel, Uganda
C5			<i>Clarias anguillaris</i>	Shotter (1977)	Galma River, lakes around Zaria in Nigeria
C6			<i>Clarias gariepinus</i>	Euler and Avenant-Oldewage (1992)	Olifants River South Africa
				Marx and Avenant-Oldewage (1996)	Cuando River Namibia
D	1	<i>Lamproglena cleopatra</i>	<i>Labeo forskalii</i>	Kumarie <i>et al.</i> , (1989)	Nile River, Egypt
E	1	<i>Lamproglena cornuta</i>	<i>Heterobranchus bidorsalis</i>	Kumarie <i>et al.</i> , (1989)	Nile River, Egypt
				Fryer (1964)	Lake No (small lake in upper reaches of Nile)
F	1	<i>Lamproglena elongata</i>	<i>Citharinus citharus</i>	Fryer (1968) Kumarie <i>et al.</i> , (1989)	Nile River, Sudan

G1	<sup>1</sup>	<i>Lamproglena hemiprichii</i>	<i>Hydrocyon</i> spp.	Fryer (1965)	Lake Tanganyika, Albertville, Tanzania
G2			<i>Hydrocyon forskalii</i>	Fryer (1965)	Lake Albert, Uganda
G3			<i>Hydrocyon lineatus</i>	Kumarie <i>et al.</i> , (1989)	South Africa
G4			<i>Myletes dentex</i>	Fryer (1968)	Nile, Niger, Volta, Congo and Zambezi Rivers, Northern Africa
H	<sup>1</sup>	<i>Lamproglena intercedens</i>	<i>Labeo cylindricus</i>	Fryer (1964)	Ghana (Sielo Tuni Stream, Black Volta)
			<i>Citharinus</i> spp	Fryer (1968)	Chad River, Africa
				Kumarie <i>et al.</i> , (1989)	Kenya
I1	<sup>1</sup>	<i>Lamproglena monodi</i>	<i>Haplochromis</i> spp	Fryer (1965)	Lake Edward, Democratic Republic of the Congo
I2			<i>Tilapia macrochir</i>	Fryer (1965)	Luapula River, Kasanga
I3			<i>Serranochromis codringtonii</i>	Douëllou and Erlwanger (1994)	Lake Kariba, Zimbabwe
I4			<i>Hepsetus odoe</i>	Avenant-Oldewage and Oldewage (1993)	Kwando River, Caprivi, Namibia
I5			<i>Hemichromis fasciatis</i>	Fryer (1965)	Lake Albert, Uganda
J	<sup>1</sup>	<i>Lamproglena nyasae</i>	<i>Haplochromis</i> sp	Fryer (1965)	South Africa
K	<sup>1</sup>	<i>Lamproglena weneri</i>	<i>Bagrus bayad</i>	Fryer (1968)	Nile River, Egypt
L	<sup>1</sup>	<i>Lamproglena wilsoni</i>	<i>Clarotes laticeps</i>	Kumarie <i>et al.</i> , (1989)	Sudan
				Fryer (1965)	Niger River, Sudan
M	~ <sup>1</sup>	<i>Lamproglena hoi</i>	<i>Barbus</i> spp	Dippenaar <i>et al.</i> , (2001)	Spekboomriver, South Africa
N	~ <sup>1</sup>	<i>Lamproglena hepsetii</i>	<i>Hepsetus odoe</i>	Van As and Van As (2007)	Okavango Delta, Botswana

Explanation of symbols. Letter in column 1 corresponds with symbols in Figure 4.

<sup>1</sup> indicates species in Group I according to Kumarie, *et al.*, (1989)

~ indicates species which has not yet been placed in a specific Group. Following Kumarie, *et al.*, (1989) the ungrouped species were sorted into the two Groups. [Group I = ~<sup>1</sup>, Group II = ~<sup>2</sup>]

**Table 3: Summary of the distribution of *Lamproglena* spp, their hosts and references from the Palaearctic and Oriental region.**

Symbol		Species	Host	Reference	Locality
G5	<sup>1</sup>	<i>Lamproglena hemiprichii</i>	<i>Hydrocynus dentex</i>	Von Nordmann 1832	Red Sea
O	<sup>1</sup>	<i>Lamproglena lichiae</i>	<i>Scomberoides lysan</i>	Piasecki (1993)	Red Sea close to Saudi Arabia
P1	<sup>2</sup>	<i>Lamproglena ophiocephali</i>	<i>Ophiocephalus argus</i>	Kumarie et al., (1989)	China and Japan
P2			<i>Channa striatus</i>	Battish and Brar (1993)	Sutlej River, Ludhiana, Punjab, India
P3			<i>Scardinius erythrophthalmus</i>	Soylu (1990)	India
P4			<i>Capoeta trutta</i>	Sağlam (1992)	Keban Dam Lake, Turkey
Q	<sup>1</sup>	<i>Lamproglena jordani</i>	Fish (species not identified)	Kumarie et al., (1989)	Israel (also found in the Palaearctic region)
R	<sup>2</sup>	<i>Lamproglena chinensis</i>	<i>Anabus testudineus</i>	Ho and Kim (1997)	Thailand, China
S1	<sup>2</sup>	<i>Lamproglena pulchella</i>	<i>Blicca bjoerkna</i>	Ponyi and Molnar (1969)	Black, Caspian and Aral Seas (also found in the Palaearctic region)
S2			<i>Capoeta trutta</i>	Sağlam (1998)	Keban Dam Lake, Turkey
S3			<i>Chondrostoma regius</i>	Mhaisen et al., (1986)	Shatt-Al-Arab River Asia
S4			<i>Aspius vorax</i>	Kumarie et al., (1989)	Black, Caspian and Aral seas
S5			<i>Leuciscus idus</i>	Kumarie et al., (1989)	Black, Caspian and Aral seas
S6			<i>Aspius aupin</i>	Piasecki (1993)	Punjab, India
S7			<i>Channa punctatus</i>	Kumarie et al., (1989)	Black, Caspian and Aral seas
S8			<i>Leuciscus cephalus albus</i>	Stojanovski et al., (2006)	Macedonia
S9			<i>Leuciscus cephalus</i>	Jirsa et al., (2006)	Pielach-, Melkrivier, Austria Uvac rivier, Serbia Yugoslavia
				Bykovskaya-Pavloskja et al., (1964)	Parts of Western Europe
T	<sup>2</sup>	<i>Lamproglena brevis</i>	<i>Tor brevifilis</i>	Kumarie et al., (1989)	China
U	<sup>2</sup>	<i>Lamproglena carassi</i>	<i>Carassius auratus</i>	Sproston et al., (1950)	China

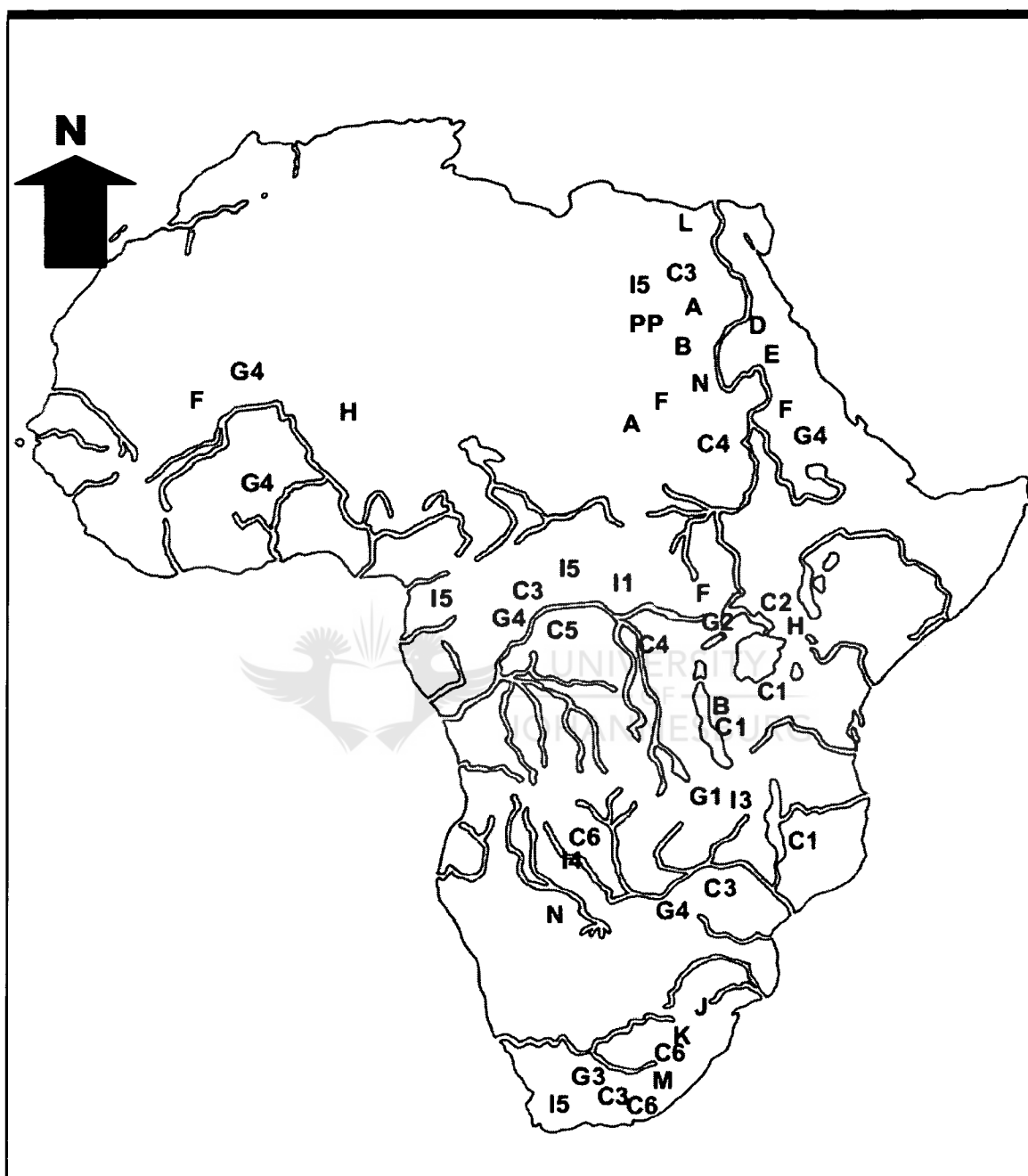
V	<sup>2</sup>	<i>Lamproglena compacta</i>	<i>Diptychus dybowskii</i>	Markewitsch (1936)	Kirgis (Mongolia)
W	<sup>2</sup>	<i>Lamproglena curta</i>	<i>Hemibarbus maculatus</i>	Gussev (1950)	China
X1	<sup>2</sup>	<i>Lamproglena cylindrata</i>	<i>Labeo calbasu</i>	Kumarie et al., (1989)	Sutlej River, Harike Pattan, Punjab, India
X2			<i>Spinibarbus sinensis</i>	Kumarie et al., (1989)	China
Y	<sup>2</sup>	<i>Lamproglena inermis</i>	<i>Barilius harmondi</i>	Kumarie et al., (1989)	Thailand
Z	<sup>2</sup>	<i>Lamproglena minuta</i>	<i>Puntius binotatus</i>	Kumarie et al., (1989)	Thailand
AA	<sup>2</sup>	<i>Lamproglena orientalis</i>	<i>Culter alburnus</i>	Kumarie et al., (1989)	Amur
BB	<sup>2</sup>	<i>Lamproglena robusta</i>	<i>Leiocassis bicolor</i>	Kumarie et al., (1989)	Thailand
CC	<sup>2</sup>	<i>Lamproglena yunnanensis</i>	<i>Schizothorax isolabius</i>	Kumarie et al., (1989)	China
DD	<sup>~2</sup>	<i>Lamproglena heterognatha</i>	<i>Xenocypris davidi</i>	Kuang and Qian (1991)	China
EE	<sup>~1</sup>	<i>Lamproglena cirrhinae</i>	<i>Cirrhina jullieni</i>	Ho and Kim (1997)	Thailand
FF	<sup>~2</sup>	<i>Lamproglena meridiona</i>	<i>Osteochilus vittatus</i>	Kuang and Qian (1991)	Guangdong
GG	<sup>~2</sup>	<i>Lamproglena cavasi</i>	<i>Labeo rohita</i>	Kumarie et al., (1989)	Chandigarh, India
HH	<sup>~1</sup>	<i>Lamproglena indica</i>	<i>Silundia gigantea</i>	Kumarie et al., (1989)	Sutlej River, Harike Pattan, Punjab, India
II	<sup>~1</sup>	<i>Lamproglena seenghala</i>	<i>Mystus seenghala</i>	Kumarie et al., (1989)	India
JJ	<sup>~2</sup>	<i>Lamproglena dibara</i>	<i>Zacco platypus</i>	Kuang and Qian (1985)	China
KK	<sup>~1</sup>	<i>Lamproglena forficata</i>	<i>Ophiocephalus striatus</i>	Ho and Kim (1997)	China
LL	<sup>~1</sup>	<i>Lamproglena chinensis sprostoni</i>	<i>Ophiocephalus striatus</i>	Mendis and Fernando (1962)	China
MM	<sup>~2</sup>	<i>Lamproglena semilabecola</i>	<i>Semi prochilus</i>	Liu and Wang (1991)	China
NN	<sup>~1</sup>	<i>Lamproglena aubentoni</i>	<i>Hydrocyon brevis</i>	Dollfus (1960)	Sudan
OO	<sup>~1</sup>	<i>Lamproglena gurayai</i>	<i>Mystus seenghala</i>	Battish and Brar (1993)	Ludhiana, Amritsar
PP	<sup>~1</sup>	<i>Lamproglena hospetensis</i>	<i>Silundia sykesi</i>	Manohar et al., (1992)	Karnataka, India
QQ	<sup>~2</sup>	<i>Lamproglena mongtinensis</i>	<i>Barilius guttatus</i>	Kuang (1977)	China
RR	<sup>~1</sup>	<i>Lamproglena markewitschi</i>	<i>Nemachilus cristatus</i>	Suchenko and Allanmuratov (1966)	Degrezskae Reservoir (Republic of Uzbekistan)
SS	<sup>~2</sup>	<i>Lamproglena krishnai</i>	<i>Channa striatus</i>	Thomas and Hameed (1984)	Cochin

Explanation of symbols. Letter in column 1 corresponds with symbols in Figure 4.

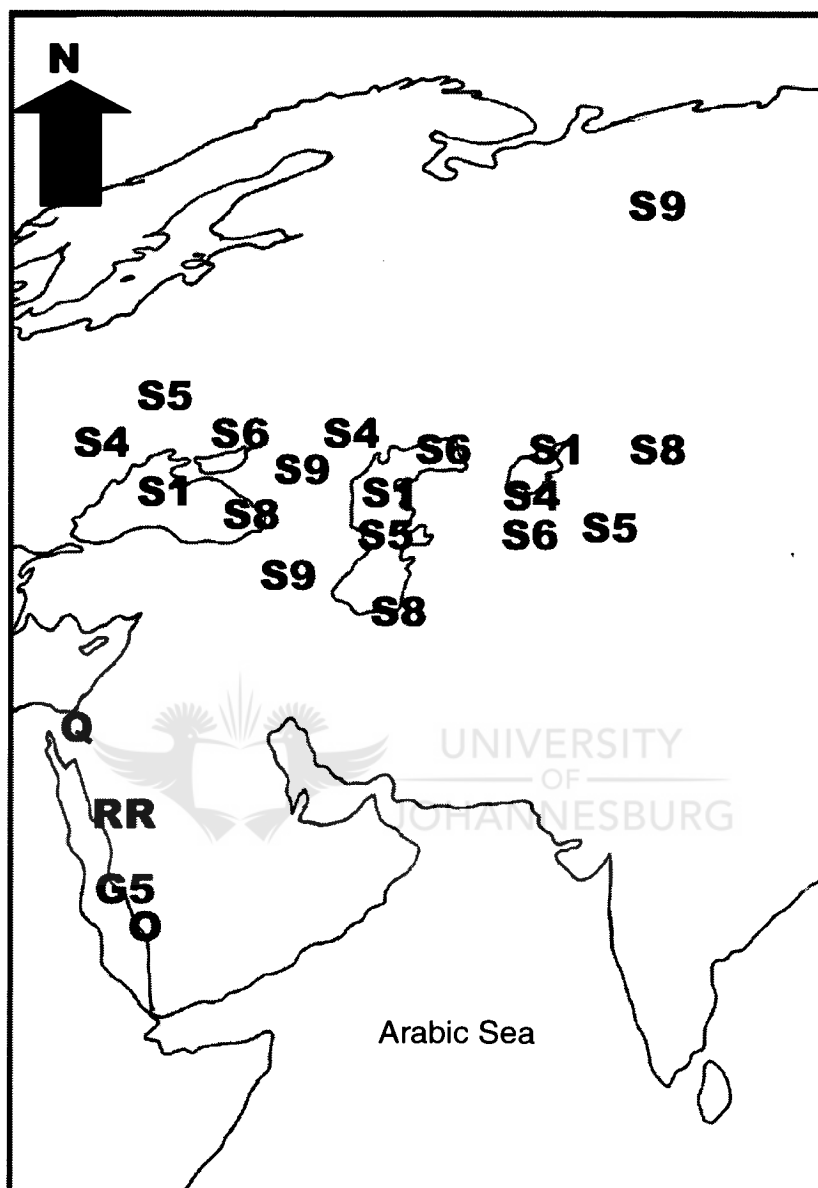
<sup>1</sup> indicates species in Group I according to Kumarie, et al., (1989)

<sup>~</sup> indicates species which has not yet been placed in a specific Group. Following Kumarie, et al., (1989) the ungrouped species were sorted into the two Groups.

[Group II = <sup>~2</sup>]

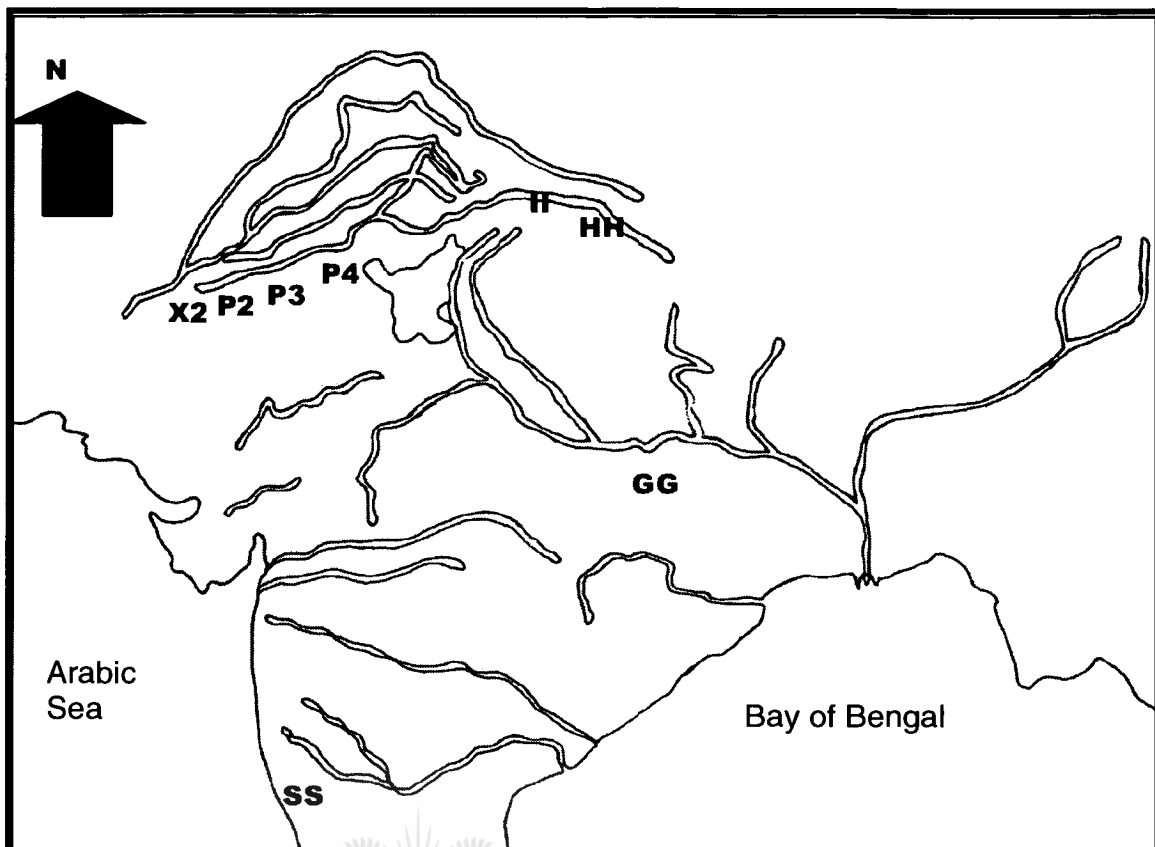


**Figure 2:** Map of the African continent, indicating localities where *Lamproglena* (as summarised in Table 2 and 3) was found. The symbols correspond with symbols in Table 2 and 3.

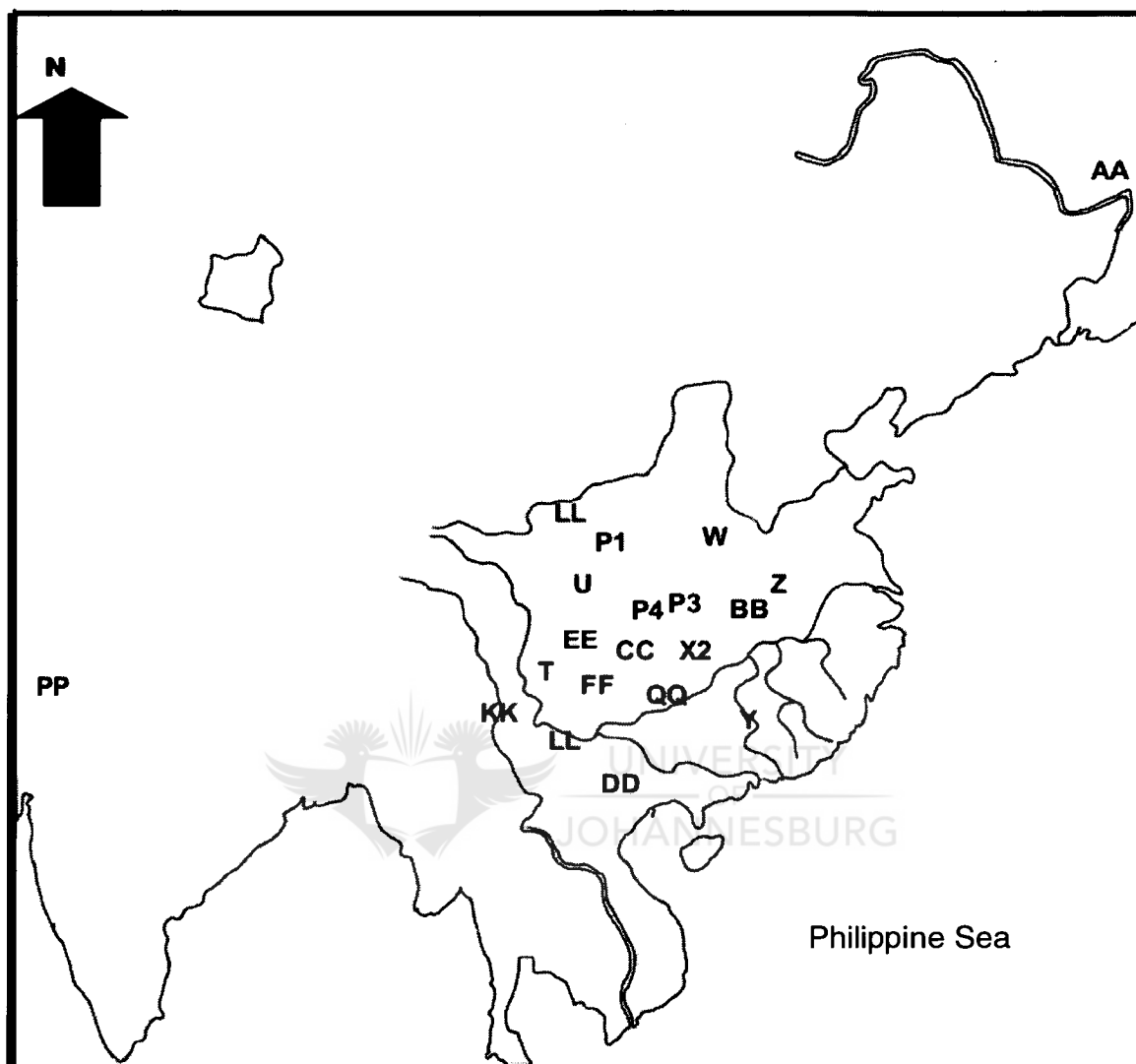


**Figure 3:** A map of the Palearctic region, depicting localities where *Lamproglena* has been found (summarised in Table 3). The symbols displayed on the map, correspond with symbols in Table 3.





**Figure 4:** A map of the Oriental region, in particular China, indicating localities where *Lamproglena* sp. has (summarised in Table 3) been reported. The symbols correspond with symbols in Table 3.



**Figure 5:** Map of the Oriental region, specifically India, where *Lamproglena* spp. have been reported is depicted with symbols corresponding to symbols in Table 2 and 3.

#### **1.4.1 African distribution**

The majority of *Lamproglena* species have been described from the African continent, with the most in the Northern region. Specimens have been found as far North as the Red Sea, Nile River and Sudan. According to Fryer, 1964, *Lamproglena intercedens* (Fryer, 1964) have been found towards the west of Africa i.e. Ghana. This represents the most western record. To the east, they have been observed in Lake Albert, Lake Nyasa, Lake Victoria and Lake Tanganyika and south as far as the Vaal River System

#### **1.4.2 Oriental distribution**

As far as the Orient is concerned, it appears that the distribution of *Lamproglena* is concentrated in China, Japan and India.

#### **1.4.3 Palaeartic distribution**

In the Palaeartic region, only two species have been found on the European continent, i.e. *L. jordani* Paperna, (1964) and *L. pulchella* Nordmann, (1832).

#### **1.4.4 Synonyms**

*L. aubentoni* Dollfus, 1960 was synonymised with *L. hemiprichii* (cf. Fryer, 1964); *L. nyasae* Fryer, 1956 was synonymised with *L. monodi* (cf. Fryer, 1959) and *L. ophiocephali* Yamaguti, 1939 was synonymised with *L. chinensis* (cf. Sproston, Yin and Hu, 1950).

*L. intercedens* Fryer, 1964 was transferred to *Catlapphila* (cf. Ho, 1998) and *L. gurayai* Batish and Brar, 1989 was transferred to *Indolernaesa seenghalae* (cf.

Ho, 1998) and *L. seenghalae* Kumarie *et al.*, (1989) to *Indolerna* (cf. Ho, 1998).

### **1.5 Systematics**

Sproston *et al.*, (1950) was the first to consider the systematic position of *Lamproglena*. Since Wilson's (1922) monograph on the family Dichelesthiidae, the larvae and male of the genotype has been described by Filhol (1934). The significance of the predominant cyclopoid characteristics was not commented on by neither Monod (1932) nor Markewitsch (1936). It has been noted that the genus does not have any family relation with the Dichelesthiidae, and it was commented that the genus must be removed from the Caligiformes and placed within the Cyclopiformes. It was also suggested that the genus be placed within the family Lernaecidae (cf. Fryer, 1961).

Sproston *et al.*, (1950) reported great similarities between the males and larvae of *Lamproglena* and those of *Lerna* and the differences between *Lamproglena* and that of the other members of the Dichelesthiidae (cf. Fryer, 1961).

Both Sproston *et al.*, (1950) and Fryer (1960) advised that *Lamproglena* be removed from the Dichelesthiidae and the affinities with *Lerna* be recognised. They also advised that the two genera be placed within the same family (Fryer, 1960). This suggestion was followed in subsequent manuscripts.

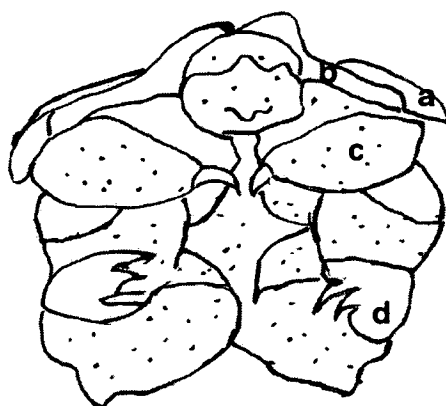
### 1.6. *Lamproglena clariae* Fryer, 1956

Classification of *Lamproglena clariae* according to Kabata (1979).

<b>PHYLUM</b>	Arthropoda
<b>SUBPHYLUM</b>	Crustacea
<b>CLASS</b>	Maxillopoda
<b>SUBCLASS</b>	Copepoda
<b>ORDER</b>	Cyclopoida
<b>FAMILY</b>	Lernaeidae Sproston <i>et al.</i> , 1950
<b>SPECIES</b>	<i>Lamproglena clariae</i> Fryer, 1956

#### 1.6.1 *Lamproglena clariae*

*Lamproglena clariae*, which belongs to Sproston's Group I, was described by Fryer (1956) from material collected from Lake Malawi. The description was adequate for the time, but was found wanting a number of morphological features. Fryer (1961; 1964), added additional morphological details, such as a description of the furcal rami and the number of setae which forms the armature of the legs. The description was done after discovery of specimens from Lake Victoria and the White Nile. In 1996 specimens collected in the Olifants River, Kruger National Park, South Africa and in the Cuando River, Caprivi strip, Namibia lead to a redescription of the species by Marx and Avenant-Oldewage with SEM which included the observation of only one claw on the maxilla, descriptions of the upper and lower lips, nuchal organ, fifth pair of legs and circular openings on all appendages, the redescription was accompanied by notes on its occurrence and distribution in southern Africa.



**Figure 6:** Ventral view of the head appendages; a, antennula; b, antenna c, maxilla; d, maxilliped. Redrawn from Tsotetsi (2004).

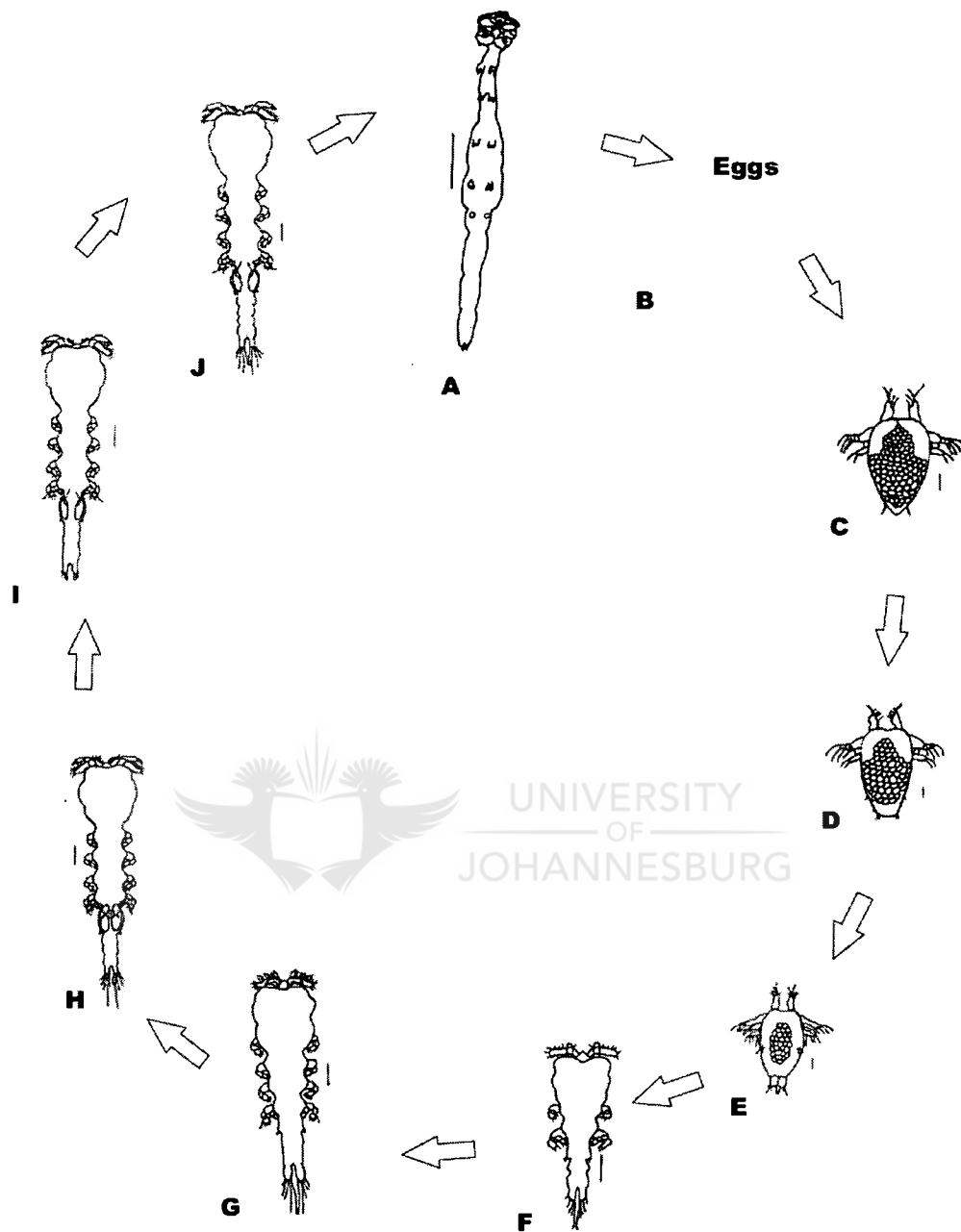
### 1.6.2 Host preference

According to Fryer (1968), the majority of members of this genus show strict host preference. Each species appears to be restricted to hosts of one family, except for *L. elongata* (Table 2) which has been recorded from hosts belonging to two closely related families, i.e. the Citharinidae and Characidae. On the other hand, the genus has undergone considerable radiation as far as host preference is concerned. *L. monodi* (Table 2) is specific to cichlid fishes, although it parasitises many genera and the widely distributed *L. hemiprichii* (Tables 2 and 3) is probably confined to characid fishes within the genus *Hydrocynus* (Fryer, 1968). *L. clariae* (Table 2) is host specific to the *Clariidae* and infects the gills of *Clarias gariepinus* (Burchell, 1822), *Clarias mossambicus*, *Heterobronchus longifilis*, *Clarias lazera* and *Clarias anguillaris* according to Fryer (1956; 1968), Shotton (1977), Marx and Avenant-Oldewage (1996) and Tsotetsi, Avenant-Oldewage and Masego (2005).

It is apparent that the different *Lamproglena* species have different host preferences. The Characidae are preferred by *L. hemiprichii* and *L. elongata*. Fish from the Malapteruridae are preferred by *L. angusta*. *L. monodi* prefers the Cichlidae and Hepsetidae families. The Cyprinidae are preferred by *L. cleopatra*, *L. barbicola*, *L. intercedens* and *L. hoi*. *L. intercedens* prefers Citharines from the Family Distichodontidae as well. *L. hepseti* prefers the Hepsetidae. The Clariidae are preferred by *L. cornuta* as well as *L. clariae*.

### **1.6.3 Biology**

*Lamproglena* has a direct life cycle. The male is cyclopoid in form and resembles the copepodid stages of the female (Fryer, 1968). The life cycle of *L. clariae* was described by Tsotetsi (2004). It consists of three naupliar stages followed by four copepodite stages. After copepodite stage four, the organism molts into the cyclopoid stage which is followed by the adult form after molting. During the naupliar stages, the organism is free-living and during the copepodite stages it is either loosely attached to a host or free-living. Only the adult females are found to be permanently attached to their hosts which induce proliferation of host tissue that may eventually encapsulates her.



**Figure 7:** Lifecycle of *Lamproglana clariae*, redrawn from Tsotetsi (2004).

**A** Adult female, **B** Eggs, **C** Nauplius stage 1, **D** Nauplius stage 2, **E** Nauplius stage 3, **F** Copepodite stage 1, **G** Copepodite stage 2, **H** Copepodite stage 3, **I** Copepodite stage 4, **J** Cyclopoid. Scale bar: **A** 1mm, **B-H** 0.001mm, **I, J** 0.002mm.



#### 1.6.4 Pathology

*Lamproglena* is commonly found concentrated at the ends of the gill arch and prefers the apex of the gill filament (Sproston *et al.*, 1950). However, Marx and Avenant-Oldewage (1996) mentioned that *L. clariae* attaches midway along the gill filament. Tsotetsi *et al.*, (2005) reported that the parasites preferred the median part of the fourth gill arch.

*Lamproglena* species attach themselves in general to the hosts' gills by way of spines which are situated on the maxillae and maxillipeds and which are particularly hook-like on the maxillipeds (Fryer, 1968). The adult female grips the gill filament (medium part of the fourth gill arch) with the strong maxillae and uses maxillipeds as both attachment and feeding appendages, penetrates the gill tissue with these appendages and consume blood (Marx and Avenant-Oldewage, 1996). The mouthparts are not fully understood as yet, but feeding presumably involves only two pairs of appendages as the maxillae are used for gripping the host (Fryer, 1968).

It has been noted by Fryer (1968) that *L. clariae* and *L. barbicola* both undoubtedly feed on blood as the gut is often filled with it. Tsotetsi *et al.*, (2005) found host tissue in the buccal cavity of *L. clariae* and in *L. monodi* red blood was never apparent in the gut (Fryer, 1968). This has lead to great confusion with regards to the food of *Lamproglena*.

Whilst feeding, the head of the parasite becomes embedded in host tissue (Marx and Avenant-Oldewage, 1996). The amount of damage caused by *Lamproglena* is variable (Fryer, 1968). *Lamproglena monodi* causes very little damage though; some proliferation of gill tissue is apparent (Fryer, 1968). *Lamproglena clariae* and *L. intercedens* are the cause of great proliferation of gill tissue which could lead to interference in respiration (Fryer, 1968). Tsotetsi *et al.*, (2005) noted that during the first phase of attachment, signs of acute inflammation occurred. The

proliferation of the host tissue observed in the second phase was caused by both attachment and feeding. The penetration of the feeding appendages and the consumption of blood induce hypertrophy of the connective tissue, with degradation of the blood capillaries in the filaments (Sproston *et al.*, 1950). In cases of heavy infections, respiratory problems arise, leading to oxygen deprivation, as the gills cannot function optimally (Marx and Avenant-Oldewage, 1996). Tsoetsi *et al.*, (2005) showed that there is no correlation between fish haematocrit values and moderate infestation intensity indicating that *L. clariae* does not cause anaemia in its host fish.

### **1.7 Crustacean Cephalon Morphology**

Dussart and Defaye (1995) mentioned that the nervous system morphology appears to be uniform throughout the copepod group. The nervous system consists of a central nervous system, which extends ventrally in a ventral nerve chord, and a sympatric system (Dussart and Defaye, 1995).

Literature regarding copepod cephalon morphology is very extensive, yet very little is known about the morphology of the lernaeid cephalon.

### **1.8 Crustacean feeding**

Kabata (1979) stated that it is extremely difficult to isolate mandibles and maxillules as they are covered by the well developed maxillula within the copepods. Literature regarding the mandibles of *Lamproglena* is very scant and vague.

## **1.9 Histo-morphology and digestion**

No information is available on the histo-morphology of this organism. Although there are numerous older studies describing the gut anatomy of Crustacea, only recent publications have detailed investigations into the regions of the gut, in particular, the foregut. In 1977, Briggs reported on the structural observations on the alimentary canal of *Paranthessius anemoniae*. The ultrastructure or histochemistry of the midgut of *Centropages typicus* (Copepoda, Calanoida) and *Hemidiaptomus ingens* (Copepoda, Calanoida) has been described by Arnaud, Brunet and Mazza (1987) and Arnaud, Brunet and Mazza (1991) respectively.

## **1.10 Objectives of the study**

As indicated there are a number of gaps in the knowledge concerning *Lamproglena*. Therefore, a study was planned to address the following research questions:

**1.10.1 How is the parasites digestive tract equipped to feeding?**

**1.10.2 Does *Lamproglena clariae* possess mandibles?**

The research hypothesis is:

**1.10.1.1** The parasite is superbly equipped to feeding on blood meals.

**1.19.2.1** The nerves that innervate the mandibles are not lost,  
the mandibles are rudimentary

### **1.11 An outline of the dissertation**

Different aspects of this study are discussed in different chapters. **Chapter 1** is a literature overview of the genus *Lamproglena* and has been submitted for publication in Suid-Afrikaanse Akademie vir Kuns en Wetenskap. Each chapter succeeding chapter 1 consists of an introduction, materials and methods, discussion and conclusion

These chapters are organised as follows:

- Chapter 2** contains the histological description of the alimentary tract of the mature female of *Lamproglena clariae*. This chapter is written according to the format of *Journal of Crustacean Biology* as it was prepared for publication in this journal.
- Chapter 3** deals with the nervous system of *Lamproglena clariae* and innervation of the mandibles. This chapter is written according to the format of *Journal of Morphology* as it was prepared for publication in this journal.
- Chapter 4** is a summative discussion of the study and gives suggestions for future research on *Lamproglena clariae*.
- Chapter 5** is a reference list of all the literature cited in the different chapters of the dissertation.

In addition to the prepared publications above, the following outputs were delivered.

#### Conference contributions

- 1) J.J. Moll and A. Avenant-Oldewage. 2006. Aspects of the feeding biology of *Lamproglena*. Post-graduate Project proposal symposium of the Department of Zoology at the University of Johannesburg. 29 May 2006. Provided as **Appendix A**.
- 2) J.J. Moll and A. Avenant-Oldewage. 2007. Aspects of the feeding biology of *Lamproglena clariae* Fryer, 1956. Poster presentation. 35th Congress of the Parasitological Society of Southern Africa. Windhoek. 24 – 27 September 2006. Abstract provided as **Appendix B**
- 3) J.J. Moll and A. Avenant-Oldewage. 2006. Aspekte van die voedingsbiologie van *Lamproglena clariae* Fryer, 1956. Poster presentation. Suid-Afrikaanse Akademie vir Wetenskap en Kuns. Afdeling Biologiese Wetenskappe. Bloemfontein, 8 September 2006. Abstract provided as **Appendix C**.
- 4) J.J. Moll and A. Avenant-Oldewage. 2007. Aspects of the feeding biology of *Lamproglena*. Post-graduate results symposium of the Department of Zoology at the University of Johannesburg. 7 November 2007. Provided as **Appendix D**.

#### Published abstracts

- 1) Moll, J.J. en Avenant-Oldewage, A. (2007) Aspekte van die voedingsbiologie van *Lamproglena clariae* Fryer, 1956. Abstract published in *Suid-Afrikaanse Tydskrif vir Natuurwetenskap en Tegnologie* **26** (1): 70. (**Appendix B**).
- 2) Moll, J.J. and Avenant-Oldewage, A. (2008). Aspects of the feeding biology of *Lamproglena clariae* Fryer, 1956. Abstract published in *Journal of the South African Veterinary Association* **78** (2): 111. (**Appendix C**).

### Full length publications

- 1) Moll, J.J. and Avenant-Oldewage, A. (2008) 'n Oorsig oor die verspreiding, taksonomie en aspekte van die ekologie van die genus *Lamproglena* (Copepoda), 'n ektoparasiet op die kieu van visse. *Suid-Afrikaanse Tydskrif vir Natuurwetenskap en Tegniek*.



**ASPECTS OF THE  
ALIMENTARY  
TRACT OF  
*Lamproglena  
clariae*  
Fryer, 1956**

**2**  
*22*

## 2.1 INTRODUCTION

As far as the structure of the alimentary canal of the *Lernaeidae* (Copepoda) is concerned, the only literature available is a manuscript by Sabatini, Marini, Fratello, Gelosini, Mola and Benedetti (1987) which described the digestive tract of *Lernaea cyprinacea*. There still exists a need regarding the digestive tracts of many other parasitic copepods (Nylund, Økland and Bjørknes 1992). The crustacean digestive system is composed of a foregut, midgut with its accompanying caeca, glands as well as diverticula and ends in a hindgut (Dall and Moriarty, 1983).

Literature exists on the lifecycle; pathology as well as the ecology of the freshwater copepod *Lamproglena clariae* (Tsotetsi *et al.*, 2005), which is a known gill parasite of the sharp-tooth catfish, *Clarias gariepinus*. Marx and Avenant-Oldewage (1996), described the feeding behaviour of the organism. The maxillipeds are used as both attachment and feeding appendages that penetrates the gill tissue and the organism consumes blood (Marx and Avenant-Oldewage, 1996). Tsotetsi *et al.*, (2005) reported on the pathology, stating that severe tissue proliferation and inflammation surrounded the attachment site.

The food type on which copepod fish parasites feed seems to be uncertain (Bower-Shore, 1940). From the absence of a red coloured alimentary canal (an indication of blood), it has been concluded by some authors that the ectoparasites feed entirely upon mucus of the host's body (Bower-Shore, 1940; Johnson, Treasurer, Bravo, Nagasawa and Kabata, 2004).

Fryer, (1968) noted that *L. clariae* and *L. barbicola* undoubtedly feed on blood of which the gut is often full. Tsotetsi *et al.*, (2005) found also host tissue within the mouthparts of *L. clariae*. Whilst feeding, the head of the parasite becomes embedded in host tissue (Marx and Avenant-Oldewage, 1996). The amount of damage caused varies depending on the species of *Lamproglena* (Fryer, 1968).



*L. clariae* is the cause of severe proliferation of gill tissue; it is feared that it may lead to interference in respiration. Tsotetsi *et al.*, (2005) noted that during the first phase of attachment, signs of acute inflammation occurred. The proliferation of the host tissue observed in the second phase was caused by both attachment and feeding. Sproston *et al.*, (1950) reported degradation of the blood capillaries in *Clarias* species' gill filaments and that heavy infections lead to great blood loss, as the female feeds on it. Tsotetsi *et al.*, (2005) indicated no correlation between the haematocrit values and the intensity of infection, concluding that moderate infection in *L. clariae* does not cause anaemia.

Presently the mouthparts are not fully understood, but feeding presumably involves only two pairs of appendages i.e. the maxillae and maxillipeds as the maxillae are used for gripping onto the host (Fryer, 1968).

This paper studies the feeding by examining the morphology of the digestive tract and appendages using light and scanning electron Microscopy. It also reports on gut content.

## **2.2 MATERIALS AND METHODS**

*Lamproglena clariae* Fryer, 1956 specimens were collected from *Clarias gariepinus* (Burchell, 1822) in the Vaal Dam, Deneysville S 26° 52.249', E 28° 10.249', South Africa. Fish were killed by severing the spinal cord and the gills were removed. The samples were fixed in an aceto-formaldehyde alcohol solution and preserved in 70% ethanol prior to dehydration and embedding in resin. Serial sections were made at 5 µm and stained with a trichrome stain. A reconstruction according to the method of Pusey (1939) was made. Photographs of longitudinal sections were used to compile an image of the digestive tract.

The specimens were prepared for scanning electron microscopy by dehydrating in a series of increasing ethanol concentrations. Amyl acetate and liquid carbon dioxide successively replaced the ethanol prior to critical point drying. The sample was placed on carbon tape and gold coated using an Emscope SC 500 and scanning electron micrographs were obtained with a Jeol 5600 scanning electron microscope.

To establish the origin of the bolus found within the gut, a blood smear was made from *C. gariepinus* and stained using the same stain that was used with the serial sections.

## **2.3 RESULTS**

### **2.3.1 Gross morphology**

Observed live specimens showed peristaltic movement of the blood-filled digestive tract. In distressed specimens the formation of faecal pellets ceased. A graphic reconstruction (Figure 1), of the alimentary canal of *Lamproglena clariae*, comprised of the foregut, funnel-like structure, midgut and hindgut. A photographic compilation (Figure 2) revealed a foregut, midgut and a hindgut.

### **2.3.2 Foregut**

The anteroventral-situated mouth leads into the foregut. The oesophagus is 3.5  $\mu\text{m}$  in length in a 403.80  $\mu\text{m}$  specimen (0.75%), has a well-developed layer of circular muscle as well as a single pair of longitudinal muscles and is lined with cuboidal epithelium. It extends from the mouth to the funnel-like structure also covered by a cuticle (Figure 3). The foregut extends into the midgut via a funnel-like structure (Figure 4) consisting of two layers of cuboidal epithelial cells covered by cuticle (Figure 5). The two cell layers are 4.643  $\mu\text{m}$  and 2.289  $\mu\text{m}$

thick respectively, measured from the interior cell layer perpendicular to the basal layer.

### **2.3.3 Midgut**

The midgut is 393.30  $\mu\text{m}$  in length in a 403.80  $\mu\text{m}$  female specimen (97.4%). No caeca, glands or diverticula are found in *L. clariae*. *L. clariae* has a tubular shaped midgut. The midgut is divided into three regions based on the small differences in cellular appearance (Figure 1). The first region (anterior midgut) is situated posterior to the funnel-like structure which extends into the midgut (Figure 6). The region is characterised by cuboidal epithelium cells with centrally located, large nuclei and contains small vacuoles and is covered by cuticle. Microvilli are found scattered throughout the midgut.

The second region (median midgut) starts out triangular in shape (Figure 7) but takes a circular shape posteriorly (Figure 8). The region is characterised by vacuolated, club-shaped cuboidal cells, which protrude into the lumen. The nuclei of the cells are large and basally located.

The last region is the posterior part of the midgut. It is characterised by short, cuboidal cells, with a reduced number and size of vacuoles (Figure 9). Concentric rings are visible surrounding the bolus in the midgut, which would suggest the formation of a peritrophic membrane in this section (Figure 10). Throughout the midgut, cells are observed that are characterised by a centrally located nucleus and numerous vacuoles (Figure 14). These cells have a layer of minuscule microvilli.

### **2.3.4 Hindgut**

The hindgut is 0.030  $\mu\text{m}$  in a 403.80  $\mu\text{m}$  female specimen (0.007%) and is short in nature and characterised by a cuticle lining. The hindgut is surrounded by a

layer of circular muscle. The hindgut terminates in a dorsally located anus. The anus is a round aperture with a diameter of 2.27  $\mu\text{m}$ .

## **2.4 Gut content**

In Figure 12A, a longitudinal section through the foregut reveals a food bolus which consists of damaged cellular material. A comparison with host (Figure 12B) confirmed that the material was indeed host blood, but in an impaired state.

## **2.5 DISCUSSION**

With a few exceptions, the gut in crustacean copepods is basically a tube running virtually the length of the body (Dall and Moriarty, 1983). The fore and hindgut, which are derived from the ectoderm, are lined with cuticle (Dall and Moriarty, 1983). Storage, trituration and early digestion take place in the foregut. (Dall and Moriarty, 1983). The midgut, derived from the endoderm, has cells which are in direct contact with the lumen.

### **2.5.1 Foregut**

According to Ceccaldi (2006) the foregut of Crustacea comprises of a long, straight tube and the tract is covered by a single layer of cells. *Lamproglena clariae* does not possess a valve or partition separating the foregut from the midgut; instead, it possesses a funnel-like structure that functions as a partition separator. The funnel-like structure is characterised by two layers of epithelial cells and is covered by cuticle. It is the connection between the foregut and the midgut. The foregut is well equipped with circular dilator muscles in copepods (Dussart and Defaye, 1995). They reported that, especially in carnivorous copepods the mouth and oesophagus are provided with strong muscles which allows the ingestion of large prey.

In this study, the circular muscles present in the foregut serve as dilators-constrictors of the oesophagus. The longitudinal muscles assist with the contraction of the funnel-like structure, which facilitates closure of the lumen.

Boxshall (1992) stated that the function of the foregut in copepods is that of transport of ingested food material from the mouth opening to the midgut.

In both *L. clariae* and *L. cyprinacea* the mouth is part of the foregut that terminates in a funnel-like structure. In *L. cyprinacea* the structure has chitinous spurs, which are absent in *L. clariae*.

Sabatini *et al.*, (1987) observed that the funnel-like structure for the first time in Copepoda. He mentions that this structure plays a decisive role in the peculiar feeding mechanism of *L. cyprinacea*. Swimming *L. cyprinacea* attaches to the host, their maxillae open and the funnel-like portion of the foregut moves outward. The structure drags along the chitinous folds of the oral cavity. When comparing to *L. clariae*, the animal attaches to the host and the head becomes embedded within host tissue whilst the maxillae and maxillipeds are utilised in the feeding process, presumably also taking the cellular material in. Tsotetsi *et al.*, (2005) showed scraping of cellular material into the mouth cavity.

Both circular dilator muscles as well as longitudinal muscles were observed in the oesophagus of *L. clariae* and alternating constriction and dilation of these would assist in transport of food material.

### 2.5.2 Midgut

According to Nylund *et al.*, (1992) and Dussart and Defaye (1995) the gross morphology of the crustacean copepod midgut is variable; yet it is divided into three major parts. Dussart and Defaye (1995) noted that digestion occurs within

the first two regions and the posterior region is involved in the absorption of nutrients and faecal pellet formation. Nylund *et al.*, (1992) divided the midgut of *Lepeophtheirus salmonis* (Copepoda: Siphonostomatoida) into three regions and Avenant-Oldewage (1991) divided the midgut of *Chonopeltis australis*, a branchiuran, into two regions, based on the cellular structure and Tam and Avenant-Oldewage (2008) showed that in *Argulus japonicus* the cells found within the anterior midgut are primarily used for absorption of nutrients (lipids, amino acids and glycogen) due to their ultrastructural characteristics.

According to Dall and Moriarty (1983), the crustacean midgut is the site where most enzyme secretion and absorption takes place and consists of a single cell layer of glandular epithelium (Dall and Moriarty, 1983). This single cell layer is in direct contact with the blood internally, which enables rapid absorption of nutrients (Dall and Moriarty, 1983). This characteristic is followed by *L. clariae*, where limited storage takes place within the midgut.

As the midgut serves a dual role of secreting enzymes and absorption, it is expected that the epithelium in this region have differentiated into at least two cell types (Dall and Moriarty, 1983). This is dependent on two distinct cell types that occur in the digestive gland, within the midgut, which are of secretory and mucopolysaccharide-containing types, respectively, and of which the function is not yet clear (Dall, 1967b). Microvilli, suggesting absorptive functions, have been described in the Copepoda (Raymont, Krishnaswamy, Woodhouse and Griffin, 1974). Dussart and Defaye (1995) mentioned that the internal surface of the midgut is increased by the presence of microvilli; microvilli are present within the midgut of *L. clariae*. The minuscule microvilli suggest the presence of secretory cells that would aid in digestion. The cells are present in a mixture of cells characterised by a microvilli layer and those without. This is a general characteristic with parasitic copepods (Arnaud, Brunet and Mazza, 1980, Arnaud, Brunet and Mazza, 1984, Arnaud *et al.*, 1987, Arnaud *et al.*, 1991). Columnar shaped cells as well as amoeboid cells were described by Briggs (1977) in the

midgut of *Paranthessius anemoniae*. The columnar epithelium was described to have a brush border, whereas the amoeboid cells were reported to contain a large central vacuole and the cells protrude into the lumen, much in the same manner as the club-shaped cells of the midgut in *L. clariae*. According to Tam and Avenant-Oldewage (2008) these cells would have the function of absorption of waste materials. Avenant-Oldewage and Van As (1990) reported on the cuboidal cells found in the midgut of *Dolops ranarum*. These cuboidal cells were found to possess elongated nuclei as well as numerous vacuoles, which suggested absorption within the midgut. Briggs (1977) reported on amoeboid cells of *Paranthessius anemoniae* and speculated that their function is that of taking up food material. Similarly cuboidal cells are also found within the midgut of *L. clariae* suggesting that the club-shaped cells may aid in absorption.

Sabatini *et al.*, (1987) found two types of vacuolar cells in the midgut of *L. cyprinacea* and these cells were grouped depending on size and granule distribution. The majority of cells had granules of varying sizes, which were often so abundant that they masked the cytoplasm completely. The other group of cells are characterised by either discrete or very large granules. The cells were found to be in the minority and were only present in the lateral pouches of the midgut. No pouches were observed in *L. clariae*. The histological preparations of *L. clariae* revealed only two types of vacuolated cells. The cells differed on grounds of the amount of vacuoles they possessed. One type of vacuolated cell protruded into the lumen and the other was normal cuboidal cells. Some cells only contained a single vacuole, whereas others contained numerous.

The peritrophic membrane, in Copepoda, is known to build an envelope around what is to become the faecal pellet (Ceccaldi, 2006). It is secreted by the midgut of copepods such as some calanoids, cyclopoids and a harpacticoid respectively according to Gould (1957) and Yoshikoshi & Kô (1988).

### 2.5.3 Hindgut

According to Boxshall (1992) the short copepod hindgut is separated from the midgut by a valve. It opens posteriorly or post dorsally via the anus (Boxshall, 1992). In *L. clariae*, no valve was observed separating the mid and hindgut from each other.

Yoshikoshi (1975) and Briggs (1977) showed that the hindgut in copepods is usually a simple, cuticle lined tube, with the function of defecation. The muscular hindgut has also been found to pump water into the gut (Dall and Moriarty, 1983). Anal uptake of water has been observed in many Crustacea (Fox, 1952; Pillai, 1960; Dall, 1967a; b). It was suggested by Fox (1952) that this aids in defaecation as it acts like an enema, but Dall (1967a) proposed it could assist in electrolyte removal after numerous hypo-osmoregulatory experiments were conducted.

### 2.5.4 Mouthparts

According to Ceccaldi (1989) the mouth of the decapod crustacean is surrounded by specialised appendages such as the maxillulae, maxillae, mandibles and maxillipeds.

The form and functions of the anterior pairs of appendages depend on the alimentary specialisations of the copepod group at issue (Ceccaldi, 2006) and Copepoda comprise numerous morphological types.

Comparing *Lamproglena clariae* with *Lernaea cyprinacea*, it was found that the buccal cavity of *L. cyprinacea* is delimited by a labrum, mandibles, maxillulae, and a lower lip (Sabatini *et al.*, 1987) in *L. cyprinacea*. They found the oral



opening covered by the large maxillae, which terminate in non-motile hooks with secondary motile hooks. The mouth had chitinous foldings and possessed two rows of triangular teeth. This study shed light on the feeding mechanism of *L. clariae* females. The parasite is superbly equipped to attach herself to the host fish and to obtain food from the gills utilising her robust mouthparts, as described by Marx and Avenant-Oldewage (1996) and Tsotetsi *et al.*, (2005). The funnel-like structure acts as a valve, whilst the peristaltic motion promotes the intake of host blood. The long midgut aids in absorption as a result of the abundant club shaped cells protruding into the lumen, which increases the absorption surface. No valves are found within the alimentary tract. The circular muscles found around the tract aid the peristaltic movement.

## **2.6 Feeding mechanism**

*Lamproglena clariae* specimens possess extremely well-developed robust maxillae and maxillipeds (Figure 11). These appendages scrape tissue from the host's gill. Whilst feeding capillaries and cellular membranes of erythrocytes presumably break. This leads to haemorrhaging of host tissue. A schematic representation of the feeding mechanism is illustrated in Figure 15 and is explained as follows: It is suggested that the lumen fills up with host's blood during the feeding process after dilation of the muscle surrounding the funnel (Figure 13) and oesophagus (Figure 3) and simultaneous contraction of the pair of longitudinal muscles, forces constriction of the funnel, thereby forming a plug at the end of the funnel. As the circular muscles dilate a vacuum is formed, promoting the intake of cellular material through the slit like mouth. Contraction of the circular muscles and relaxation of the longitudinal muscles will release the funnel plug; it will extend and allow the content of the foregut to move into the midgut (Figure 15).

Kabata (1974) presented a new concept of the mode of feeding of *Caligidae* (Copepoda). He stated that the fish tissues are scraped off by the movements of the strigil and the mandibles then picked up the debris by initiating the passage thereof into the buccal cavity.

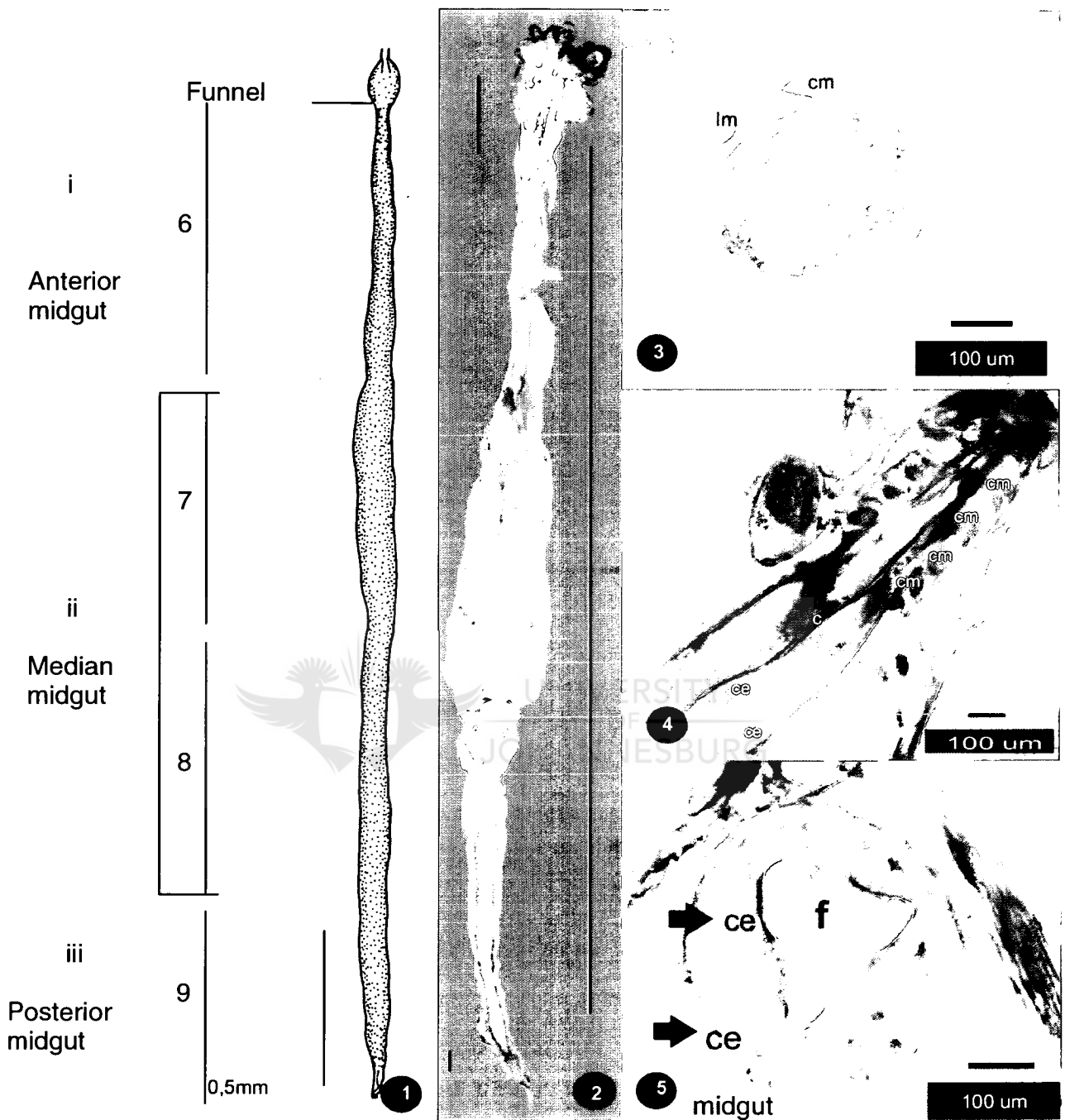
## **2.7 Gut content**

Einszporn (1965) stated that red blood cells undergo decomposition after consumption by organism and that the cell membrane of the red blood cell is deformed and disappears, thus resulting in the appearance of haemolysed blood cells. The cytoplasm disappears due to the intestinal enzyme actions.

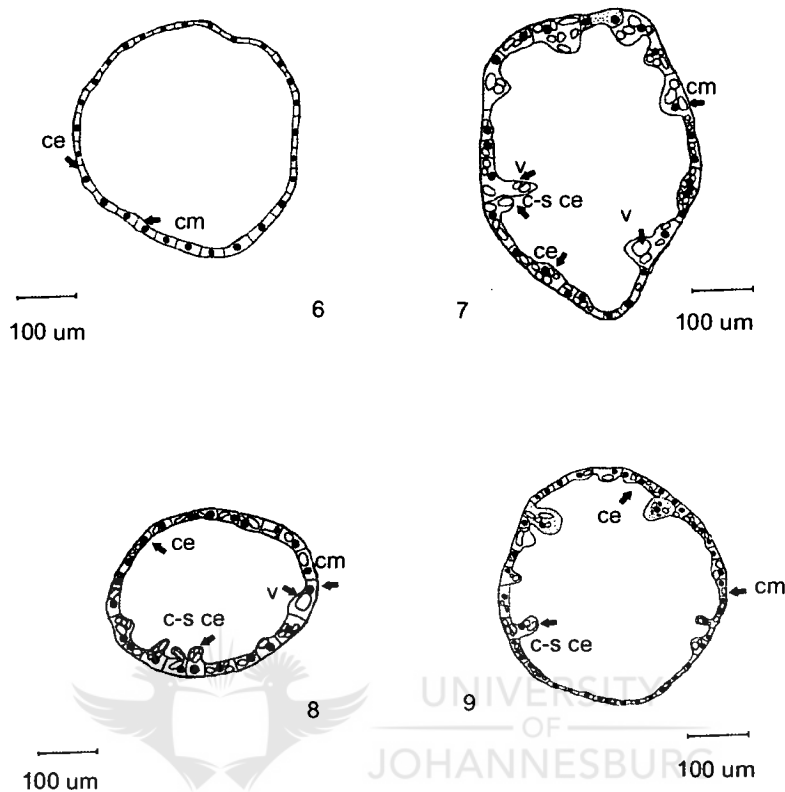
As previously mentioned by Marx and Oldewage (1996), feeding in *Lamproglena* leads to severe tissue proliferation, which creates a lumen in which the head of *Lamproglena* is then embedded.

## **2.8 GENERAL CONCLUSION**

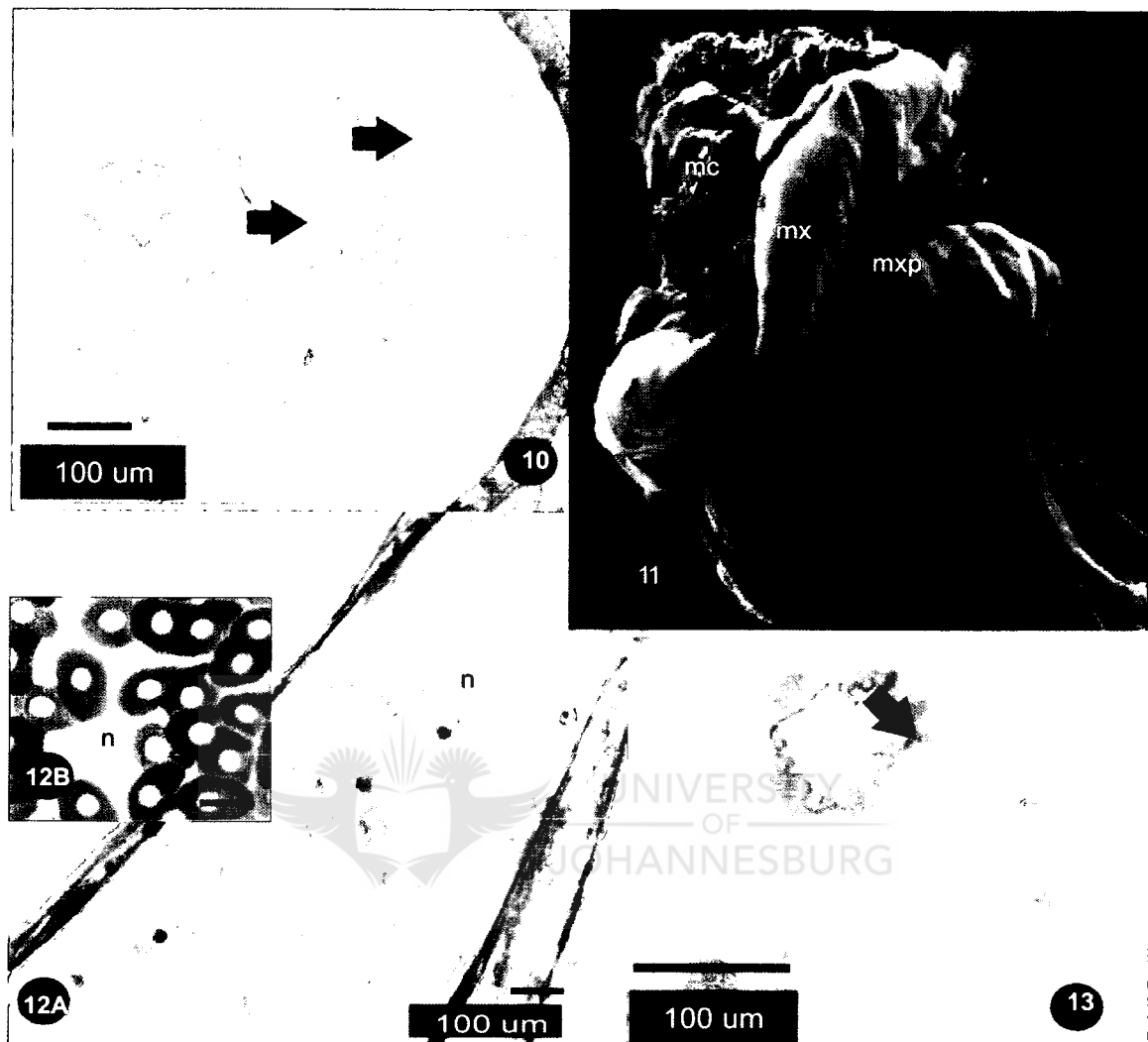
It has been established that *Lamproglena clariae* has a tube-like alimentary tract, which consists of a foregut, an extensive midgut and a very short hindgut. The midgut is divided into three zones. After host blood was compared to the parasite's tissue, it was confirmed that haemolysed blood is present in the digestive tract of *L. clariae*. Thus, confirming that *L. clariae* feeds on the host fish's blood.



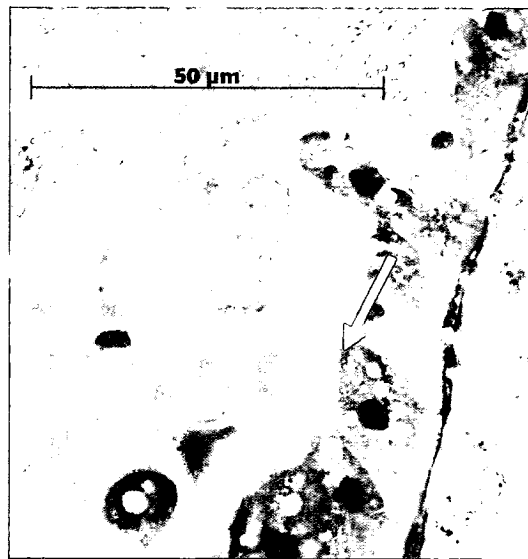
**Figures 1- 5:** 1: Graphic reconstruction of the dorsal view of the digestive tract of *Lamproglena clariae*. The numbers allocated to the figure refers to Figures 6 - 9. 2: Graphic compilation of photographs of longitudinal sections through the digestive tract. The lines divide the digestive tract into the different parts. 3: Light micrograph of a cross section through the esophagus, showing longitudinal muscles as well as circular muscles. 4: Light micrograph of a longitudinal section through the funnel-like structure indicating the circular muscles surrounding the esophagus, the presence of a cuticle layer and cuboidal epithelial clearly visible. 5: Light micrograph of a cross section through the funnel-like structure at the terminal end of the esophagus. Two layers of cuboidal epithelial cells can be seen as indicated by the arrows. Abbreviations: **lm**: longitudinal muscles, **cm**: circular muscles, **f**: funnel-like structure, **c**: cuticle, **ce**: cuboidal epithelium. The roman numerals i-iii depict the regions allocated for the midgut.



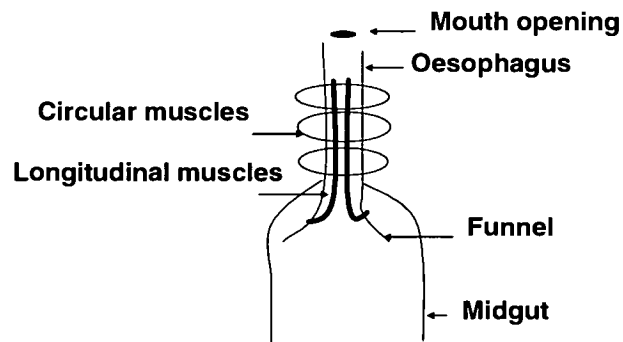
**Figures 6 - 9:** (Numbers allocated to diagrams correspond with reconstruction region numbers) **6:** Region I, characterized by cuboidal epithelial cells containing basally located nuclei: The tract is ventrally flattened. **7:** Region II is characterized by a large lumen within the tract. The tract is found to be egg-shaped. Flattened cuboidal epithelial cells are found with a combination of non-, uni- and multi-vacuolated cells. **8:** Elongated flat cuboidal epithelial cells containing many vacuoles as well as small cuboidal epithelial cells with no vacuoles are present. The tract has a condensed appearance. 7 and 8 are part of region II. **9:** Region II, the lumen is here found to be at its widest, containing multi-vacuolated cuboidal epithelial cells with scattered club-shaped cuboidal epithelial cells. Circular muscles are observed, yet they are in such close proximity to the tract that they are not visible. Abbreviations: ce: cuboidal epithelium, v: vacuole, c-s ce: club-shaped cuboidal epithelium



**Figures 10-13:** 10: Light micrograph of a cross section through the midgut, clearly showing concentric rings (arrows), suggesting the presence of a peritrophic membrane. 11: Scanning electron micrograph showing the mouthparts, mouth cone (mc), maxillae (mx) and maxillipedes (mxp). 12A: Light micrograph of a longitudinal section through the foregut, showing a bolus containing the remains of nuclei (n) found within damaged cells and nuclei. 12B: Comparison done with host blood, indicating compact nuclei. 13: Cross section through anterior midgut, revealing circular muscles (arrow) aiding in peristaltic contractions in the digestive tract.



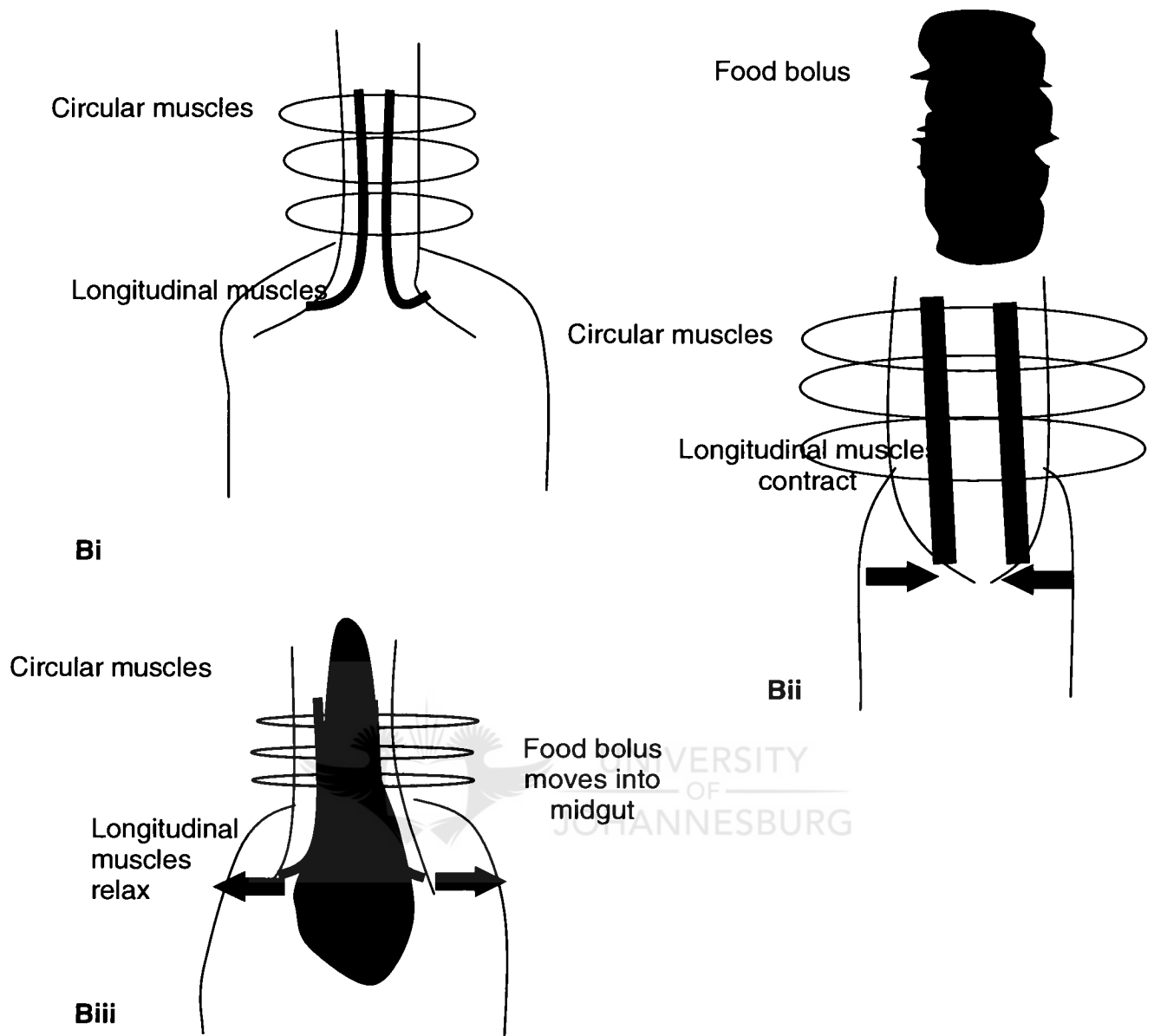
**Figure 14:** Light micrograph of a secretory cell found within the digestive tract of *Lamproglena clariae*. A layer of minuscule microvilli is present (arrow). The vacuoles observed within the cell normally would be lipid filled, but the staining method dissolves the lipids. Scale bar: 50 µm



**A**

**Figure 15: A:** Graphic representation of the anatomy of the funnel-like structure found within the foregut of *L. clariae*.





**Figure 15: B:** (i) The funnel-like structure is dilated, the circular muscles as well as the longitudinal muscles are in the relaxed position. (ii) The circular muscles dilate, the longitudinal muscles contract, forcing the funnel-like structure to close (arrows) creating a vacuum and the meal is sucked towards the slit-like mouth opening. (iii) The circular muscles contract, the longitudinal muscles dilate and the funnel structure extends (arrows) forcing the meal into the midgut.



# MANDIBLES IN *Lamproglena clariae*

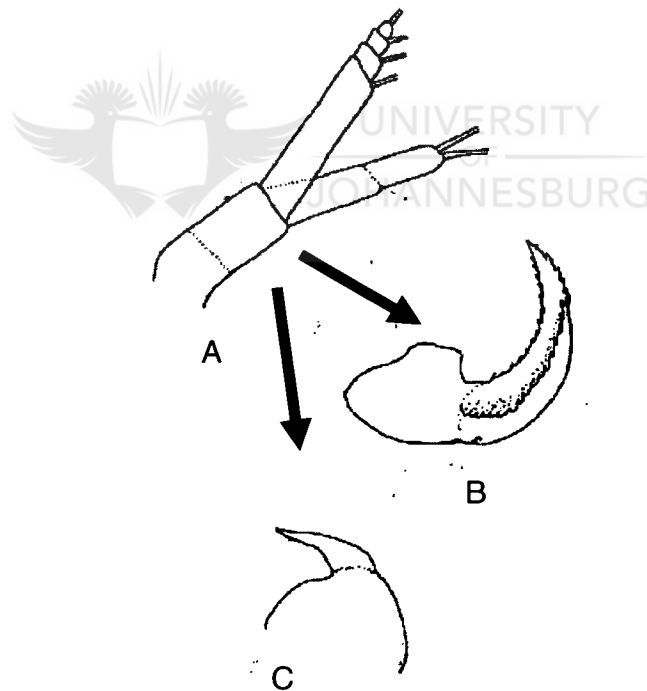


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### 3.1 Introduction

A remarkable variety of structural and functional adaptations is shown by crustacean ectoparasites of fishes (Kabata, 1984). The transformation that copepods undergo from a free living existence to that of a parasitic existence with the host organism has a weighty effect on the appendages of the copepods (Kabata, 1984). Previous functions provided by these appendages are no longer carried out. As the appendage function changes, new functions arise. The structure of the appendage might have to transform, although the transformation does not cause the appendage to lose any importance (Kabata, 1979). The amount of structural modification depends on the amount of functional change (Kabata, 1979). Examples of this transformation can be seen in Figure 1.



**Figure 1:** Types of mandibles. **A:** Nauplii of parasitic copepods. **B:** The mandible to some adult poecilostomes. **C:** Mandible to adult *Lernaean* (which is closely related to *Lamproglena*). Redrawn from Kabata (1979).

The mouth parts that are the cause of the controversy in the copepods are the mandible and the maxillulae. In a copepod these are well separated from each other but they are situated in close proximity to each other. Lang (1946) stated that in the Poescilostomes, the mandibles have either disappeared or have been displaced together with the maxillulae so that they partly cover each other. Only Thorell (1859) and Sars (1913, 1918, 1921) have substantiated their opinions by referred to the great resemblances between the first pair of mouth parts found in the Poescilostomes and the maxillulae within the other copepods (Lang, 1946).

In 1946 Lang entered into the debate surrounding the presence of mandibles in the poescilostomes and stated that many authors were of the opinion that the group lacks mandibles (Thorell, 1859 and Sars, 1913, 1918, 1921). Whereas some authors are of the opinion that they do indeed have mandibles [Claus, (1863), Brady (1880), Aurivillius (1882), Gurney (1913, 1927, 1933) and Monod and Dollfus, (1932)] Lang, (1946). Lang (1946) does not believe that the Poescilostomes are in possession of mandibles. Authors, who were of the opinion that copepods have both mandibles and maxillulae, do not provide any arguments to support their view (Lang, 1946).

Among the cyclopoid copepods parasitic on fishes, the highest degree of adaptation to parasitism has been reached by a small group of about 50 species belonging to the family Lernaeidae (cf. Kabata, 1979). The genus *Lamproglena* is the most primitive member to this family as they have undergone the least amount of adaptation towards their way of living (Kabata, 1979).

### **3.1.1 Mandibles**

Schram (1986) described the food processing appendages of the crustaceans as the mandibles, maxillules or first maxillae and maxillae or second maxillae. One of the characteristics of these appendages is that the distal elements of the limb

are generally reduced to 'palps'. The proximal protopodal elements are developed specialised endites, which handle the food (Schram, 1986).

The majority of parasitic copepods feed by using their mandibles to rasp the surface of the host. The dislodged host tissue fragments are then directly taken into the mouth and carried into the digestive tract for digestion (Boxshall, 1990).

The mandibles can exhibit great variation in form (Schram, 1986). Dussart & Defaye (1995) described the mandibles as generally biramous and are situated on either side of the mouth; the endopodite and exopodite often reduced.

The smallest and least well known lernaeid appendage is the mandible. It is often left out of descriptions, or passed over in brief and imprecise statement, without accompanying illustrations. It has been referred to as 'vestigial' or 'hook-like' and consists most commonly of a squat, small segment, bearing an equally small claw (Kumarie *et al.*, 1989).

From the 39 known *Lamproglena* species, only eight species were described to possess mandibles. Sproston *et al.*, (1950) mentioned that *L. carassi* possess mandibles and they were short and did not enter the mouth cavity except at their dorsally bent tips. They were described as being broadly triangular, with the distal half divided into what appears to be four closely parallel setae (Table 1).

Fryer (1964) described the mouth region of *L. cornuta* as being surrounded by fleshy lobes that were of an uncertain homology. He speculated that they were derived at least in part from the labrum (Fryer, 1964). There was no mention of mandibles.

Kuang (1977) stated that *L. mongtinensis* possessed a star-shaped structure which was the lips and mandibles. No figures accompanied this description. Kuang (1977) noted that *L. brevis* possess mandibles (Table 1).




Furthermore, in a redescription of *L. ophiocephali* by Kumarie *et al.*, (1989) it is said that “the mouth is surrounded dorsally and laterally by fleshy lobes, lateral lobes project forwards and median lobe along mandibles”. Unfortunately this description was not accompanied by drawings. There was no mention of mandibles.

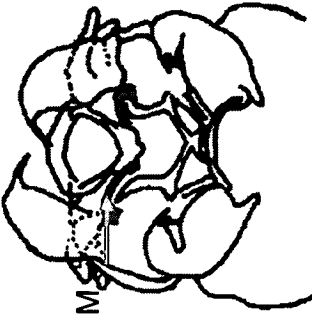



Kuang and Qian (1991) described the mandibles of *L. heterognatha* as needle-like and Kuang (1991) mentioned that *L. dibara* possess mandibles (Table 1). Liu and Wang (1991) described *L. semilabecola* as a new species resembling *L. brevis* and the description is accompanied by sketches of the mandibles (Table 1).

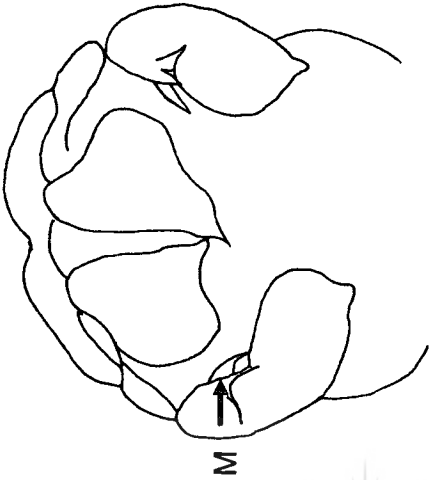



There is no further mention of the mandibles of any of the other 31 species of *Lamproglena*.

In 2004 the life-cycle of *L. clariae* was studied by Tsotetsi (2004), who found that the mandibles were present in the naupliar stages but were apparently absent in the copepodite stages. Although Sproston *et al.*, (1950) described the life cycle of *L. carassi* the mandibles were not described apart from noting that the young male of this species had visible mandibles and first maxillae at the sides of the mouth but they were obscured by the massive second maxillae.

**Table 1:** Frontal drawings of adult females, as well as larval stages were available of species with mandibles (M) indicated in blue (when illustrated) accompanied by drawings of the mandibles.

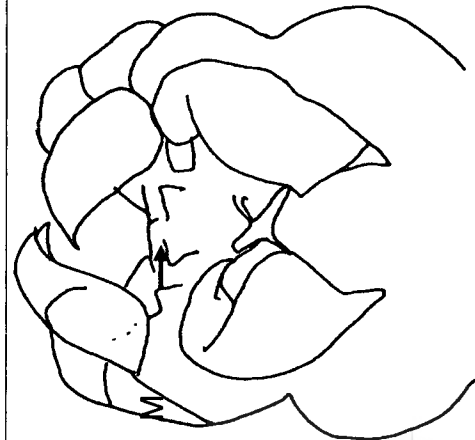
Species	Larval stage	Adult stage	Mandible
<i>Lamproglena carassi</i>	 <p>Redrawn from Sproston <i>et al.</i>, (1950). Scale bar: 100um.</p>	 <p>Redrawn from Sproston <i>et al.</i>, (1950). Scale bar: 100um</p>	 <p>Mandible and First Maxilla. Redrawn from Sproston <i>et al.</i>, (1950). Scale bar: 50um</p>

<i>Lamproglena brevis</i>		 <p>Redrawn from Kuang (1977). Scale bar: 0, 3 um</p>
<i>Lamproglena pulchella</i>	 <p>Mandibles not visible in drawing.</p>	 <p>Redrawn from Kumarie et al., (1989) Scale bar: 0, 5 um</p>

<i>Lamproglena heterognatha</i>		 <p>Redrawn from Kuang (1991). Scale bar: 0, 3um</p>
<i>Lamproglena dibara</i>	 <p>Mandibles not visible in drawing.</p>	 <p>Redrawn from Kuang (1991). Scale bar: 0, 3um</p>



*Lamproglena semilabecola*.



15

Redrawn from Liu and  
Wang (1991).  
Scale bar: 0, 5 um.

In the Copepoda, all the appendages are innervated individually by a cephalic nerve (Dussart and Defaye, 1995). To establish the true nature of the existence of a mandible in *Lamproglena clariae*, a study must be undertaken to explore the cephalic morphology of *L. clariae*.

### **3.2 Crustacean Cephalon Morphology**

The central nervous system in Crustacea consists of a large brain or cerebrum, which is merged with several paired ganglia. These paired ganglia are situated dorsally in front of the oral aperture (Dussart and Defaye, 1995). The cerebrum comprises of three parts: the protocerebrum, deutocerebrum and tritocerebrum (Boxshall, 1992) (Figure 2).

#### **3.2.1 The Protocerebrum**

The morphology of the protocerebrum is uniform throughout the copepod group (Dussart and Defaye, 1995) and is located anterior to the rest of the cephalon. It is also bilobed (Dussart and Defaye, 1995). It innervates the rostrum, the frontal organ and the eye (Gicklhorn, 1930). From the protocerebrum, the optic nerve arises to the tripartite nauplius eye as well as the paired nerves of the organ of Bellonci (Boxshall, 1992).

#### **3.2.2 The Deutocerebrum**

The deutocerebrum is typically the widest part of the cerebrum in Copepoda and gives origin to large antennular nerves (Boxshall, 1992; Dussart and Defaye, 1995). These are laterally directed to the antennules. The sensory roots form a bipolar, dorsal ganglion (Dussart and Defaye, 1995). The deutocerebrum innervates the labrum by a single nerve (Dussart and Defaye, 1995).

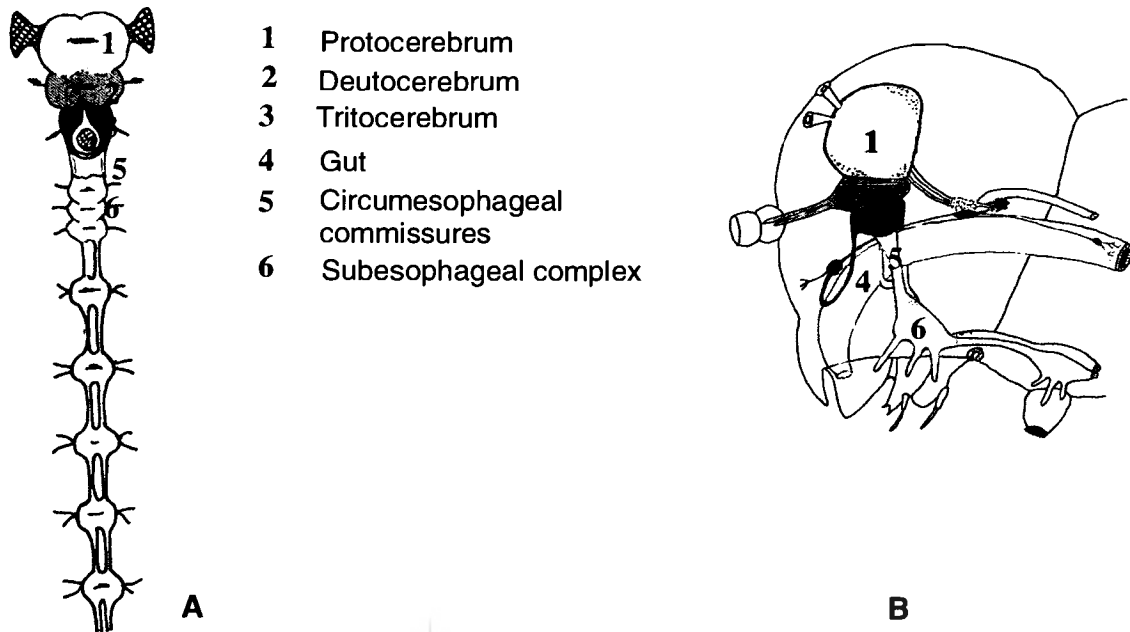
### **3.2.3 The Tritocerebrum**

The tritocerebrum in Copepoda includes the circumesophageal commissure and innervates the antennae (Dussart and Defaye, 1995). According to Boxshall, (1992), its precise anterior and posterior boundaries are difficult to define.

### **3.2.4 The Ventral Nerve Chord**

The chord commences where the circumesophageal commissures (both the double circumesophageal commissure and postesophageal commissure) come together (Boxshall, 1992). The region which is often referred to as the subesophageal ganglion is the widest part of the nerve cord (Boxshall, 1992).

The widest part of the chord includes ganglia for the mandibles, maxillules and maxillae (Dussart and Defaye, 1995). The ganglia following the previously mentioned, serve the thoracic appendages as well as the transverse and longitudinal trunk muscles via dorsolateral nerves (Dussart and Defaye, 1995).



**Figure 2 A:** Schematic representation of the copepod cephalon. Redrawn from [www.mbscientific.com](http://www.mbscientific.com). **B:** Lateral view of the arthropod brain. Redrawn from Remane, Storch and Welsch (1978). The Deutocerebrum is indicated in blue, the Protocerebrum in green and the Tritocerebrum in purple. The circumesophageal commissures are in orange. The gut is in yellow and the subesophageal complex is red.

### 3.3 Materials and Methods

*Lamproglena clariae* specimens were collected from *Clarias gariepinus* in the Vaal Dam, Deneysville, South Africa, after the fish were killed and the gills removed. The samples were fixed in an acetoformaldehyde alcohol solution and preserved in 70% ethanol prior to dehydration and imbedding in resin. Serial section were made at 5µm and stained with a trichrome stain. A graphic

reconstruction of the cephalon, showing the nerve that innervates the mandibles, were done.

The specimens were prepared for scanning electron microscopy by dehydration in a series of increasing ethanol concentrations. Amyl Acetate and liquid carbon dioxide replaced the ethanol prior to being placed in a critical point drier. The sample was placed on carbon tape and gold coated using an Emscope SC 500. Scanning Electron micrographs were obtained with a Jeol 5600 Scanning Electron Microscope.

### **3.4 Results**

The cerebrum consists of a small protocerebrum, large deutocerebrum and large tritocerebrum. Two commissures are found as well as a ventral nerve cord.

The cerebrum is located in the mouth cone of *L. clariae* with the rest of the cephalon found within the anterior part of the cephalothorax (Figures 3 and 4).

#### **3.4.1 The Protocerebrum**

The protocerebrum in *L. clariae* is a bilobed cylindrical part of the cephalon. It does not have any nerves originating from it (Figures 3 (1) and 4 (1)).

#### **3.4.2 The Deutocerebrum**

The deutocerebrum is the middle part of the cephalon and is bilobed (Figure 3 (2) and Figure 4 (2)). The deutocerebrum innervates the antennae of *L. clariae*. The nerve leaves the deutocerebrum from the both the anterior proximal and anterior distal parts of the deutocerebrum. The nerve runs along the proximity of the body wall towards the antennae. The precise starting and end points of the deutocerebrum are difficult to ascertain, as the deutocerebrum and tritocerebrum overlap each other constantly (Figures 3 (7) and 4 (7)).

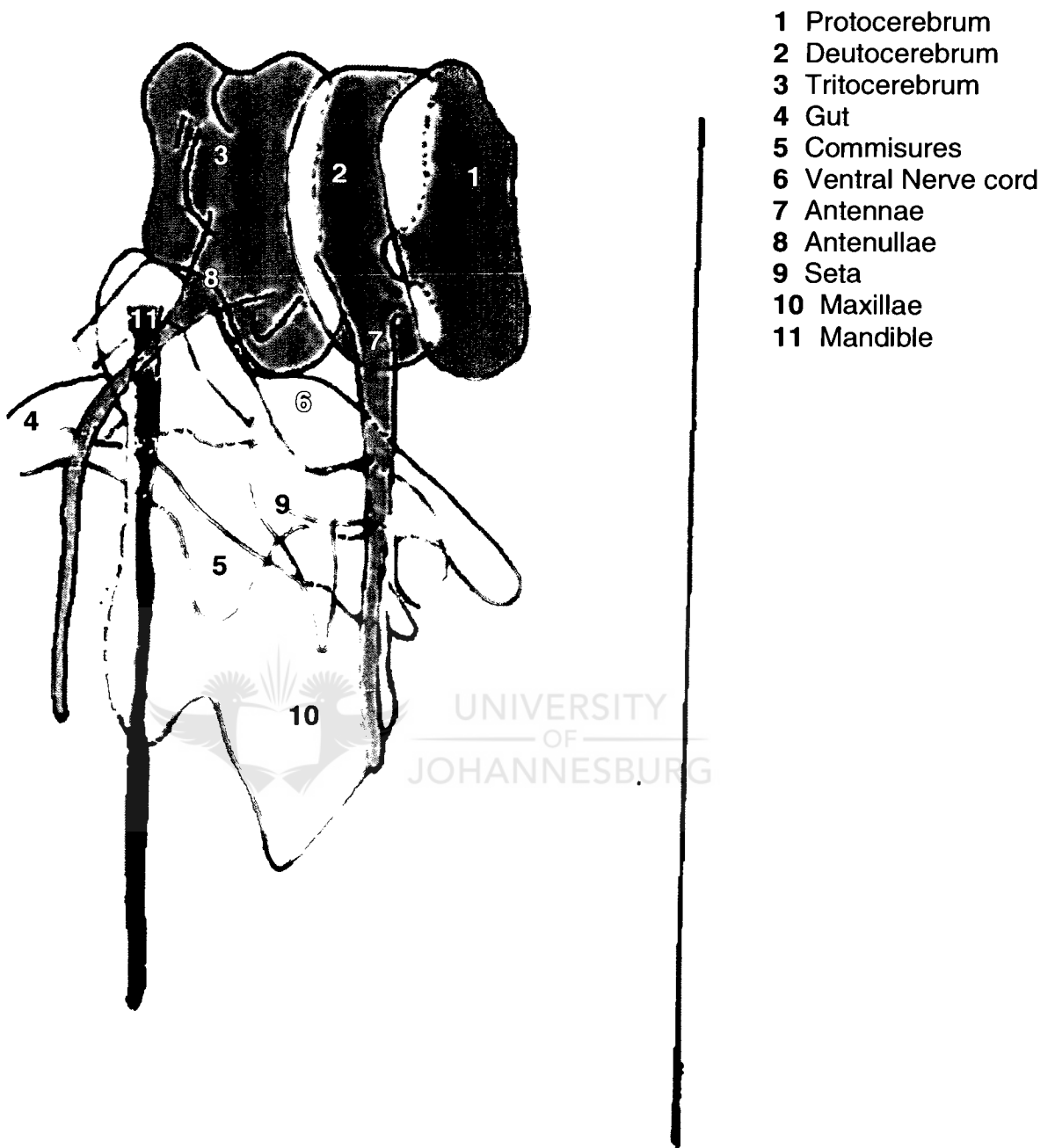
### **3.4.3 The Tritocerebrum**

The tritocerebrum is positioned behind the deutocerebrum (Figure 3 (3) and Figure 4 (3)). The tritocerebrum was observed to consist of two lobed parts and innervates the nerve for the antennulae (Figures 3 (8) and 4 (8)). The nerves leave the tritocerebrum from anterior distal position and median proximal position respectively from a dorsal view point. The nerves run parallel to that of the antennae towards the antennulae (Figure 4 (8)).

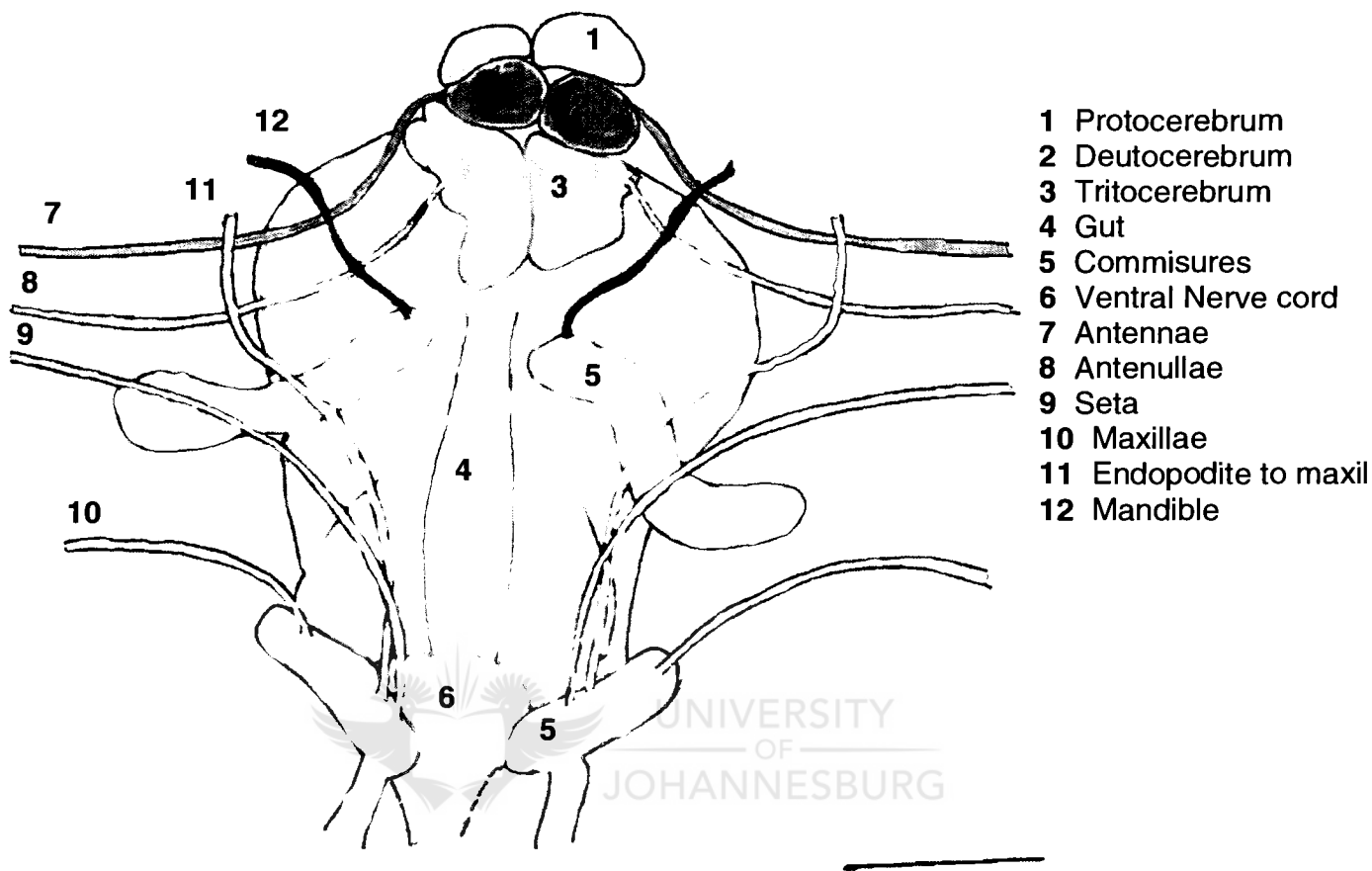
### **3.4.4 The Ventral Nerve Chord**

The ventral nerve cord is situated posterior to the cephalon of *L. clariae* (Figure 3 (6) and Figure 4 (6)). The nerve cord runs ventrally along the cephalon. It surrounds the commissures and the alimentary tract. A protrusion is visible from the anterior side of the ventral nerve cord (Figure 4 (6)). It is from this protrusion that the posterior commissures innervate. The nerves that innervate the seta, that are positioned between the antennae and antennulae, are located distally and proximally on the commissures respectively (Figure 4 (9)), (Figure 3 (9)). The nerves for the maxillae innervate from the proximal and distal parts of the posterior commissures respectively (Figure 4 (10)), (Figure 3 (9)). From the median parts of the posterior commissures the nerves for the endopodite to the maxillae innervate respectively (Figure 4 (11)). The anterior commissures innervate closer anteriorly to the tritocerebrum.

The nerves lending to the mandibles are innervated from the distal and proximal sides of the anterior commissure from a dorsal view point respectively (Figures 3 and 4 (12)).



**Figure 3:** The graphic reconstruction of the cephalon of *Lamproglena clariae*. The nerve that innervates the mandibles is indicated. Scale bar: 0.01mm

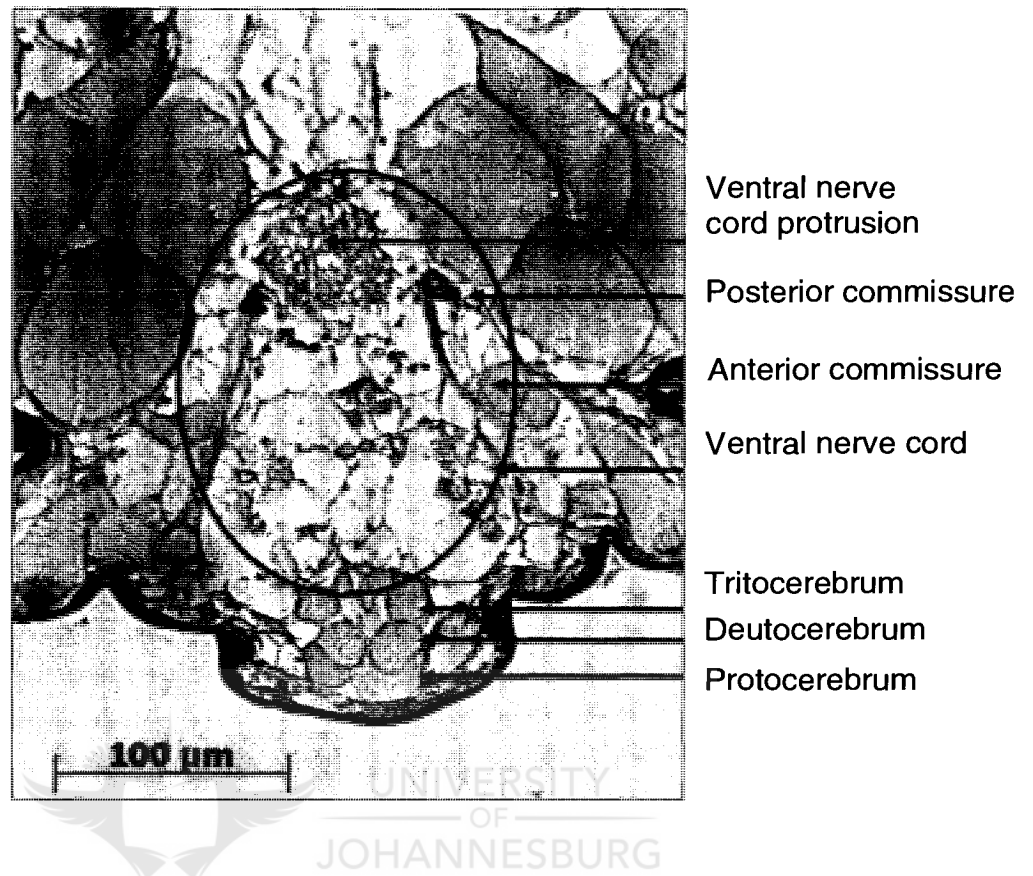


**Figure 4:** Dorsal view of the cephalon of *Lamproglena clariae*. Scale bar 100µm.

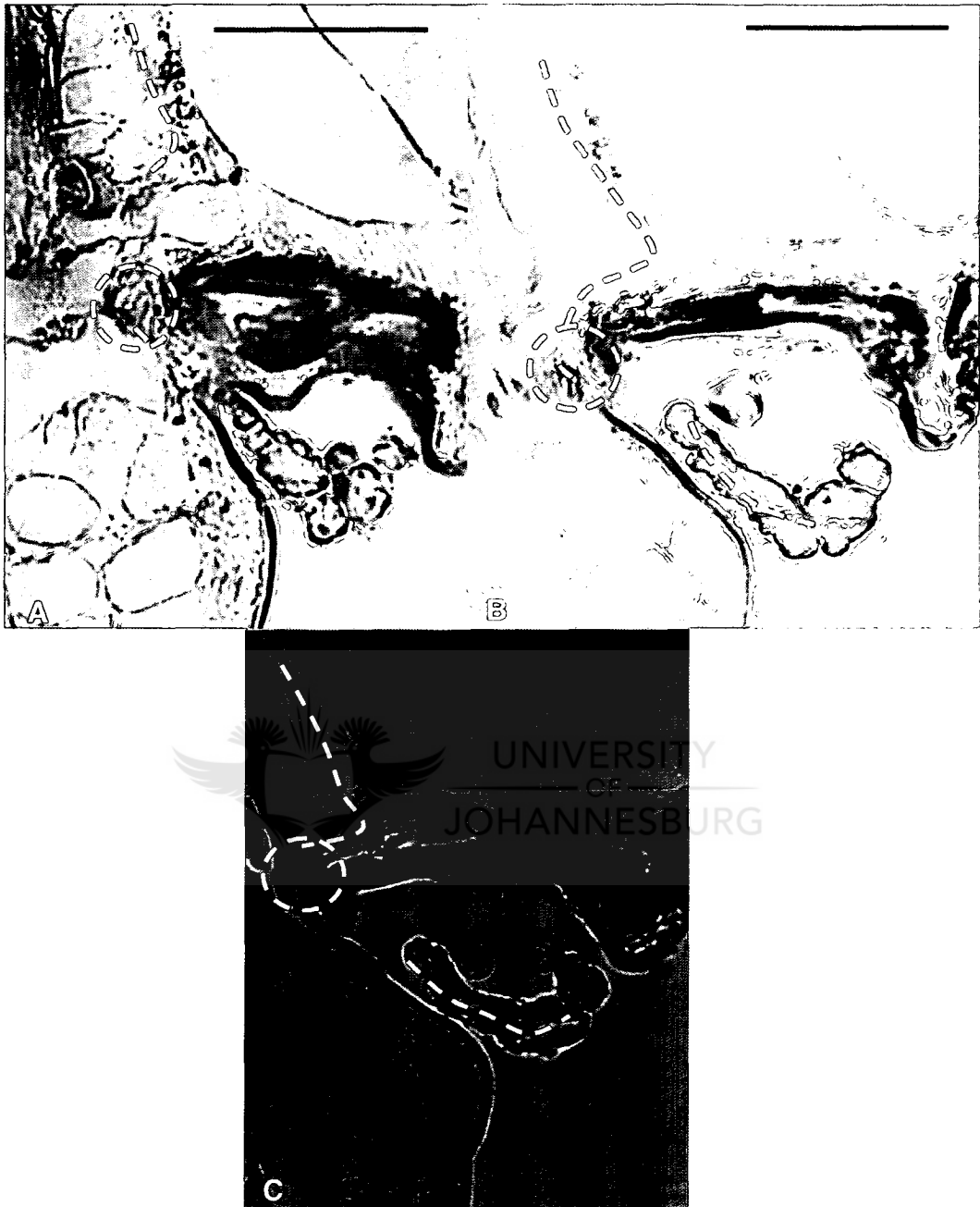




**Figure 5:** Scanning electron micrograph of the frontal view of *Lamproglena clariae*. The mouth cone that contains the cephalon is indicated by the arrow. The reduced mandibles are indicated by the white ovals.



**Figure 6:** Sagittal section through the cephalon of *Lamproglena clariae* indicating the protocerebrum, deutocerebrum, tritocerebrum, nerve cord as well as the commissures. Scale bar: 100μm.



**Figure 7:** A series of light micrographs depicting the path of the mandibular nerve. **A.** The nerve can be seen (indicated as dotted white line) in the direction of the nodule (indicated by the circle), which leads to the mandible. **B.** The nerve (indicated by the white line) is closer to the nodule (white circle). The mandibular nerve is visible in the protruding mandible (white line). **C.** The nerve reached the nodule. Scale bar: 50  $\mu\text{m}$ .

### **3.5 Discussion**

In 1996, Marx and Avenant-Oldewage found what they described as 'papillated structures', located in close proximity to the mouth of *L. clariae* and noted that mandibles were absent. The papillated structures are the reduced mandibles of *L. clariae*.

When examining the cephalic morphology of *L. clariae*, it is clear that the nerves that are innervated by the protocerebrum are absent. In *L. clariae* no eyes are present.

The deutocerebrum constitutes a large portion of the cephalon and innervates the nerves to the antennae.

The tritocerebrum constitutes a larger portion of the cerebrum than the deutocerebrum and innervates the antennules.

The anterior located commissure innervates the rudimentary nerve to the mandible and the posterior located commissure innervates the seta, maxillae as well as the endopodite to the maxillae.

The seta was observed in the scanning electron micrographs for the first time as it is located in an obscure position, covered by the antennulae.

In 1962, Kabata re-examined the structures of the buccal tube, the mandibles and the maxillae as it was suggested that previous investigators had incorrectly described the mentioned structures. Kabata speculated that due to the inability to view the entire mandible the previous examiner could mistakenly observe 'two rows of chitinous teeth' as there are no such structures within the buccal cone or buccal tube.

It is speculated that the reason why mandibles were left out of species descriptions of *L. clariae* is a result of their size. The other descriptions of *L.* species, which had accompanying sketches of the mandibles, revealed slender-looking mandibles located in close proximity to the mouth opening. The mandibles of *L. clariae* structure do not resemble a similar structure as those described in other species. It is very robust, in contrast to the slender mandibles found on the other species.

The function of the mandibles is uncertain as their locality is not suitable for food collection.

### **3.6 Conclusion**

Kabata stated in 1984 that the presence of mandibles in all copepods has been proven convincingly. This statement included the Poescilostomes (cf. Kabata, 1984). In adult stages of heavily adapted species where no mandibles can be found, the earlier stages in ontogeny have been shown to possess it. *L. clariae* does indeed possess mandibles; the modification that they have undergone has resulted in failure to identify them as mandibles.

# **GENERAL DISCUSSION AND FUTURE RESEARCH**



**4**  
*Part*

All of the objectives of this study were set out in chapter 1 have been achieved. The digestive tract of *Lamproglena clariae* was examined and the position of the mandibles located. The following was achieved:

In Chapter 1, a species distribution list compiled by Piasecki (1993) was updated and it was concluded that the genus consisted of 39 valid species and subspecies. This chapter included a review of the genus and the information is organized into three comprehensive tables listing the species name, the author, the host list and distribution. A discussion of synonymised species is included in the text. Furthermore, an accompanying sketch of each species and information regarding the distribution is provided. This parasite genus occurs throughout Asia and Africa with only *L. pulchella* recorded outside of these two continents. In Africa, *Lamproglena* has been recorded mainly in the big lakes and as far south as the Vaal River in South Africa. The species exhibit narrow host specificity and is limited to one host species in the majority of cases with *L. elongata* an exception occurring on representatives from two closely related families. *Lamproglena* has been recorded as parasites of the Characidae, Cichlidae, Citharinidae, Clariidae, Cyprinidae, Distichodontidae, Hepsetidae and Malapteruridae fish families. As far as the pathology of the genus is concerned the parasites' feeding behaviour was described in *L. clariae* and *L. intercedens* which are both blood feeders. Blood was, however, not present in the digestive system of *L. monodi* and it is therefore not conclusively proven that specimens in this species are blood feeders.

In Chapter 2, a reconstruction and histological examination of the alimentary tract of *L. clariae* was performed. It was shown that the digestive system is tube-like and consists of three predominant parts; fore, mid and hindguts. It was confirmed by histology that *L. clariae* does indeed feed on haemolysed blood as reported by Fryer (1968) and Tsoetsi *et al.*, (2005) from observations *in situ*. Scanning electron microscopy revealed unknown papillary structures surrounding the mouth, which were investigated in the study recorded on in chapter 3.

After a graphic reconstruction of the cephalon of *L. clariae*, it was established that the ventral nerve cord innervates the nerves that lead to the mandibles and that the papillary structures mentioned in Chapter 2 are indeed rudimentary mandibles. Feeding in *L. clariae* is assisted by the maxillae and the maxillipedes, the function of mandibles is unknown. This is discussed in Chapter 3.

Based on the findings of this study the following future research possibilities regarding *Lamproglena* became apparent:

Other *Lamproglena* species should be studied by scanning electron microscopy to disclose the structure of minute morphological structures that are not visible with a light microscope. Specific attention should be paid to structures such as mandibles that were previously taken as absent. With the aid of SEM used in conjunction with histology, it is possible that previously described species can be redescribed and previously overlooked structures added.

As far as the alimentary tract of *L. clariae* is concerned, the study has proven that the tract consists of a short foregut, an extended midgut and a very brief hindgut. A bolus was observed in the foregut; containing cells that was identified as blood cells, indicating that the parasite does feed on blood of which the gut is obviously full (Fryer, 1968). The midgut was divided into regions according to the cellular structure as well as the tract structure. Sabatini *et al.*, (1987) conducted a study on *Lernaea cyprinacea* where the digestive tracts of the different life stages were examined. Studying the alimentary tracts of the different life stages within the life cycle of *L. clariae* would show the adaptative changes allowing for the change in diet from the nauplii which feeds off yolk, to the free living copepodite stages terminating in blood feeding parasitic adults.

Earlier researchers have produced literature regarding the digestive tracts of crustaceans. Digestive cells of crustaceans have been categorised into different



classes depending on their cellular components and functions with transmission electron microscopical (TEM) studies (Brunet *et al.*, 1994). These cells are identified as R-, F-, B-, E-, and S- cells and are found within the gut of decapods, amphipods and mysids. Lower crustaceans (Calanoida, Ostracoda and Harpacticoid Copepoda) have also been studied for the occurrence of these cells (Arnaud *et al.*, 1978, Arnaud *et al.*, 1980, Arnaud *et al.*, 1984, Arnaud *et al.*, 1987, Arnaud *et al.*, 1991). Ceccaldi (2006) described these cells in the digestive tracts of both free-swimming as well as parasitic copepods. The cellular components and functions of the cells found within the digestive tract of *L. clariae* unknown.

Tsotetsi *et al.*, (2004) described the pathology caused by this parasite as the result of tissue proliferation and haemorrhage. The robust, maxillae and maxillipeds are responsible for the pathology as *Lamproglena* uses these appendages to hold on to the gill filament and scrape the tissue, thus tearing the blood capillaries which enable feeding on the blood.

Conducting histological, TEM and SEM studies on the ontogenetic development of *Lamproglena* would reveal the morphological, histological and functional changes of the digestive cellular components as well as the mouth appendages that occur during development in order to follow the transition from free-living organism to that of a parasite.

# REFERENCES



**5** *Life*

**Arnaud, J., Brunet, M. and Mazza, J. (1978)** Studies on the midgut of *Centropages typicus* (Copepod, Calanoida). I. Structural and ultrastructural data. *Cell and Tissue Research* **187**: 333-353.

**Arnaud, J., Brunet, M. and Mazza, J. (1980)** Structure et ultrastructure comparées de l'intestin chez plusieurs espèces de Copépods Calanoides (Crustacea). *Zoomorphologie* **95**: 213-233.

**Arnaud, J., Brunet, M. and Mazza, J. (1984)** Détection d'une activité arylsulfatasique dans les cellules B de l'intestin moyen de *Centropages typicus* (Copépode, Calanoïde). *Comptes rendus des Seances Academie de Sciences (Paris) Serie 3 Science de la vie* **17**: 499-502.

**Arnaud, J., Brunet, M. and Mazza, J. (1987)** Rôle des cellules B de l'intestin moyen chez *Centropages typicus* (Copepoda, Calanoida). *Reproduction Nutrition Développement* **27** (4): 817-827.

**Arnaud, J., Brunet, M. and Mazza, J. (1991)** Données ultrastructurales démontrant le caractère sélectif de l'endocytose par les cellules intestinales de type B chez *Hemidiaptomus ingens* (Copepoda, Calanoida). *Comptes rendus des Seances Academie de Sciences (Paris) Serie 3 Science de la vie*: 469-501.

**Aurivillius, C.W.S. (1882)** Bidrag till kännedomen om Krustaceer, som lefva hos Mollusker och Tunikater. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*. **39**: 31-67 & 41-117.

**Avenant-Oldewage A (1991)** A new species of *Chonopeltis* (Crustacea: Branchiura) from the Kruger National Park, Southern Africa. *Journal of African Zoology* **105**: 313 - 321.

**Avenant-Oldewage, A. and Oldewage, W.H. (1993)** The occurrence of fish parasites in the Kwando River, Caprivi, Namibia. *Madoqua* **18** (2): 183-185.

- Avenant-Oldewage, A. and Van As J.G. (1990)** The digestive system of the fish ectoparasite *Dolops ranarum* (Crustacea: Branchiura). *Journal of Morphology* **204**: 103-112.
- Battish, S.K. and Brar, M. (1993)** A new copepod parasite *Lamproglena gurayai* (Family: Lernaeidae) infecting *Mystus seenghala* (Sykes). *Himalain Journal of Environmental Zoology* **3**:193-198.
- Bower-Shore, C. (1940)** An investigation of the common fish louse, *Argulus foliaceus* (Linn.) *Parasitology* **32**: 361-371.
- Boxshall, G.A. (1990)** Siphonostome copepods associated with sponges from Hong Kong. In: Morton, B.S. (Ed.) *Proceedings of the Second International Workshop Marine Flora and Fauna of Hong Kong and South China* **2**: 523-547.
- Boxshall, G.A. (1992)** Copepoda. Chapter 7. In: *Microscopic Anatomy of Invertebrates*. Volume 9: Crustacea. Wiley-Liss, Inc. pp.347-384.
- Brady, G.S. (1880)** A monograph of the British free and semi-parasitic Copepoda. Vol. 3. Ray Society, London. pp. 1–83.
- Briggs, R.P. (1977)** Structural observations on the alimentary canal of *Paranthessius anemoniae*, a copepod associate of the snakelocks anemone *Anemonia sulcata*. *Journal of Zoology* **182**: 353-368.
- Brunet, M., Arnaud, J. and Mazza, J. (1994)** Gut structure and digestive cellular processes in marine Crustacea. *Oceanography and Marine Biology: an Annual Review* **32**: 335-367.
- Bykhovskaya-Pavlovskja, I. E., Gussev, A. V., Dubinina, M. N., Izyumova, N. A., Smirnova, T. S., Sokolovskaya, I. L., Shtein, G. A., Shulman, S. S., Epshtein, G. A. (1964)** Key to parasites of freshwater fish of the USSR. *Academy of Sciences of the U.S.S.R. Zoological Institute. Israel Program for Scientific Translation, Jerusalem* pp. 919.

- Capart, A. (1943)** Notes Sur Les Copepodes parasites. 1.- Quelques Copépodes parasites des poissons d'eau douce de Thaïlande. *Bulletin du Musée royal d' Histoire naturelle de Belgique* **19** (8): 1-12.
- Capart, A. (1944)** Notes sur les Copépodes parasites. III. Copépodes parasites des poissons d'eau douce du Congo Belge. *Bulletin du Musée royal d' Histoire naturelle de Belgique* **20** (24): 1-24, Figs 1-4.
- Capart, A. (1956)** Quelques Copépodes parasites de poissons du Niger (Gourao) récoltés par Th. Monod. *Institut Fondamental d'Afrique Noire, Dakar., sér. A* **18** (2): 485-494.
- Ceccaldi, H.J. (1989)** Anatomy and physiology of digestive tract of Crustaceans Decapods reared in aquaculture. *Advances in Tropical Aquaculture, Tahiti. Aquacop Ifremer. Actes de Colloque* **9**: 243-259.
- Ceccaldi, H.J. (2006)** The digestive tract: Anatomy, Physiology, and Biochemistry. Chapter 10. *In: Treatise on Zoology – Anatomy, Taxonomy, Biology The Crustacea*. Volume 2. Revised and updated form the *Traité De Zoologie* (Forest and von Vaupel Klein eds). Brill London. pp.522.
- Claus, C. (1863)** *Die frei lebenden Copepoden mit besonderer Berücksichtigung der Fauna Deutschlands, der Nordsee und des Mittelmeeres.* Verlag von Wilhelm Engelmann, Leipzig. pp. 230.
- Dall, W. (1967a)** Hypo-osmoregulation in Crustacea. *Comparitive Biochemistry and Physiology* **21**: 653-678.
- Dall, W. (1967b)** The functional anatomy of the digestive tract of a shrimp, *Metapenaeus bennettiae* Racek & Dall (Crustacea: Decapoda: Penaeidae). *Australian Journal of Zoology* **15**: 699-714.

- Dall, W. and Moriarty, D.J. (1983)** Functional aspects of nutrition and digestion. In: *The Biology of Crustacea Volume 5* (Mantel ed). Academic Press, New York, U.S.A. pp. 215-261.
- Dippenaar, S.M., Luus-Powell, W.J. and Roux, F. (2001)** *Lamproglena hoi* n.sp. (Copepoda: Lernaecidae) from two yellow fish hosts, *Barbus marequensis* and *Barbus polylepis*, caught in a river in Mpumalanga, South Africa. *The Onderstepoort Journal of Veterinary Research* **68**: 209-215.
- Dollfus, R.P. (1960)** Mission M. Blanc, F. d' Aubenton (1954) VII. Copépodes parasites de Téléostéens du Niger. *Bulletin de l'Institut Français d'Afrique Noire Serie, A*, **22**: 170–192.
- Douëllou, L. and Erlwanger, K.H. (1994)** Crustacea parasites of fishes in Lake Kariba, Zimbabwe, preliminary results. *Hydrobiologia* **287**: 233-242.
- Dussart, B.H. and Defaye, D. (1995)** Copepoda. Introduction to the Copepoda. Guides to the Identification of the Micro-invertebrates of the Continental Waters of the World. (Dumont ed). SPB Academic Publishing, Netherland. pp. 277.
- Einszporn, T. (1965)** Nutrition of *Ergasilus sieboldi* Nordmann.II. The uptake of food and the food material. *Acta Parasitologica Polonica* **13** (37): 373-380.
- Euler, C. and Avenant-Oldewage, A. (1992)** Die Biologie van verteenwoordigers van die genus *Lamproglena*. *Suid Afrikaanse Tydskrif vir Natuurwetenskap en Tegnologie* **11** (2): 72-73.
- Filhol, J. (1934)** Embrjologja i rozwój gatunku *Lamproglena pulchella* Nordmann. – Embryologie et développement de *Lamproglena pulchella* Nordmann, description du mâle. *Bulletin de l'Academie Polonaise des Sciences Ser. B II*: 225–232.
- Filhol, J. (1936)** Nouvelles observations sur le développement et la biologie du *Lamproglena pulchella* Nordmann. *Annales de parasitologie T. XIV* (3):246-255.

**Fox, H.M. (1952)** Anal and oral intake of water by Crustacea. *Journal of Experimental Biology* **29**: 583-599.

**Fryer, G. (1956)** A report on the parasitic Copepoda and Branchiura of the fishes of Lake Nyasa. *Proceedings of the Zoological Society of London* **127**: 293–344.

**Fryer, G. (1959)** A report on the parasitic Copepoda and Branchiura of the fishes of Lake Bangweulu (Northern Rhodesia). *Proceedings of the Zoological Society of London* **132**: 517–550.

**Fryer, G. (1960)** Studies on some parasitic crustaceans on African freshwater fishes, with descriptions of a new copepod of the genus *Ergasilus* and a new branchiuran of the genus *Chonopeltis*. *Proceedings of the Zoological Society of London*, **133**: 629–647.

**Fryer, G. (1961)** The parasitic Copepoda and Branchiura of the fishes of Lake Victoria and the Victoria Nile. *Proceedings of the Zoological Society of London* **137**: 41-60.

**Fryer, G. (1964)** Further studies on the parasitic Crustacea of African Freshwater Fishes. *Proceedings of the Zoological Society of London* **21** (143): 79-102.

**Fryer, G. (1965)** Crustacean parasites of African Freshwater fishes mostly collected during the expeditions to Lake Tanganyika and to Lakes Kivu, Edward and Albert by the Institut Royal des Sciences naturelles de Belgique. *Institut Royal des Sciences naturelles de Belgique. Bulletin Part XLI* (7): 1-22.

**Fryer, G. (1968)** The parasitic Crustacea of African freshwater fishes; their biology and distribution. *Journal of Zoology* **156**: 45-95.

**Gicklhorn, J. (1930)** Notiz über die sogenannten “Cornealinsen” von *Cyclops strenuus* Fisher. *Zoologischer Anzeiger* **90**: 250-258.

**Gould, D.T. (1957)** A peritrophic membrane in Calanoid copepods. *Nature* **179**: 325-326.

- Gurney, R. (1913)** Some notes on the parasitic copepod *Thersitina gasterostei*, Pagenstecher. *Annals and Magazine of Natural History* **12**: 415-424.
- Gurney, R. (1927)** Zoological results of the Cambridge Expedition to the Suez Canal, 1924. 33. Report on the Crustacea: Copepoda (littoral and semi-parasitic). *Transactions of the Zoological Society* **22**: 453-557.
- Gurney, R. (1933)** Notes on some copepoda from Plymouth. *Journal of the Marine Biological Association of the United Kingdom*, **19** (1):299-304.
- Gusseu, A.B. (1950)** New type of parasitic copepods of the family Dichelesthidae. *Doklady Akademij Nauk SSSR* **71**: 1167-1170.
- Ho, J-S. (1984)** Phylogeny of Cyclopoida. In: *Proceedings of the 2nd Conference on Copepoda* (Schriever, Schminke, and Shih, eds.). Ottawa, Syllogeus **58** : 539-546.
- Ho, J-S. (1994)** Chondracanthid copepods (Poecilostomatoida) parasitic on Japanese deep-sea fishes, with a key to the genera of the dracanthidae. *Journal of Natural History* **28**: 505-517.
- Ho, J-S. (1998)** Cladistics of the Lernaeidae (Cyclopoida), a major family of freshwater fish parasites. *Journal of Marine Systems* **15**: 177-183.
- Ho, J-S. and Kim, I.H. (1997)** Lernaeid copepods (Cyclopoida) parasitic on freshwater fishes of Thailand. *Journal of Natural History* **31**: 69-84.
- Humes, A.G. (1957)** Two New Caligoid Copepods from Egyptian Fishes. *The Journal of Parasitology* **43** (2): 201-205.
- Huys, R. and Boxshall, G.A. (1991)** Copepod Evolution. Ray Society, London, Great Brittan. pp. 469.



- Jirsa, F., Zitek, A. and Schachner, O. (2006)** First record of *Lamproglena pulchella* Nordmann 1832 in the Pielach and Melk Rivers, Austria. *Journal of Applied Ichthyology* **22**(5): 404-406.
- Johnson, S.C., Treasurer, J.W., Bravo, S., Nagasawa, K., and Kabata, Z. (2004)** A Review of the Impact of Parasitic Copepods on Marine Aquaculture. *Zoological Studies* **43**(2): 229-243.
- Kabata, Z. (1979)** *Parasitic Copepoda of British Fishes*. Ray Society, London, Great Brittan. pp. 468.
- Kabata, Z. (1984)** Diseases caused by metazoans: crustaceans. *In: Diseases of marine animals*. Vol IV, part 1: *Introduction: Pisces* (Kinne, ed.). Biologische Anstalt Helgoland, Hamburg. pp. 374-378.
- Kirtisinghe, P. (1950)** Parasitic Copepods of fish from Ceylon. *Parasitology* **40** (1-2): 77-86.
- Kuang, P. (1977)** Parasitic Copepods from freshwater fishes of China I on the genus *Lamproglena* (Lernaeidae) with description of five new species. *Acta Zoologica Sinica* **23** (3): 290-302.
- Kuang, P. (1991)** Parasitic crustacea on fishes from Yunnan, China, with description of a new species. *Zoological Research* **12** (4): 343-347.
- Kuang, P. and Qian, J. (1985)** Three new species of the genus *Lamproglena* from China (Copepoda:Cyclopoida, Lernaeidae). *Acta Zootaxonomica Sinica* **10** (4): 363-369.
- Kumarie, P., Khera. S. and Gupta, N. K. (1989)** On six species of the genus *Lamproglena* Nordmann (Copepoda: Eudactylinidae), ectoparasitic on freshwater fishes of India. *Research Bulletin (Science) of the Punjab University* **40**: 9-23.
- Lang, K. (1946)** A contribution to the question of the mouthparts of the Copepoda. *Arkiv för Zoology* **38** A (5):1-24.

- Liu, J.X. and Wang, W.J. (1991)** A new species of the genus *Lamproglena* from freshwater fishes of China (Copepoda: Cyclopoida, Lernaedidae). *Acta Hydrobiologica Sinica* **15** (3): 271-273. (In Chinese)
- Manohar, L., Seenappa, D. and Venkateshappa, T. (1992)** *Lamproglena hospetensis* n. sp. from the fish *Silundia sykesi*. *Indian Journal of Parasitology* **16** (2): 127-130.
- Markewitsch, A.P. (1936)** Lamproglenae Z.S.R.R i ich rozmieszczenie geograficzne. Lamproglenae der Sowjetunion und ihre geographische Verbreitung. *Annales Musei Zoologici Polonici* **23**: 387-401.
- Marx, H.M. and Avenant-Oldewage, A. (1996)** Redescription of *Lamproglena clariae* Fryer, 1956 (Copepoda, Lernaedidae) with notes on its occurrence and distribution. *Crustaceana* **69**: 509-523.
- Mendis, A.S and Fernando, C.H. (1962)** A guide to fresh water fauna of Ceylon. *Bulletin of the Fisheries Research Station. Ceylon* **12**: 1-160.
- Mhaisen, F.T., Al-Salim, N.K. and Khamees, N.R. (1986)** The parasitic fauna of two cyprinid and a mugilid fish from Mehaijeran Crek, Basrah. *Journal of Biological Sciences Research, Baghdad*, **17** (3): 63-71.
- Monod, T. (1932)** Contribution à l'étude de Quelques Copépodes parasites de poissons. I. Description d'une espèce nouvelle du genre *Lernaea* Linné 1758. II. Liste des espèces connues du genre *Lernaea*. III. Sur Quelques copépodes parasites provenant du Haut-Nil . *Annales de Parasitologie* **10**: 345-378.
- Monod, T. and Dollfus, R. (1932)** Les copepodes parasites de mollusques. *Annales de Parasitologie* **10**: 129-204.
- Nordmann, A. (1832)** Mikrographische Beiträge zur Naturgeschichte der wirbellosen Thiere. Berlin. Heft 2: 1-50.

- Nylund, A., Økland, S. and Bjørknes, B. (1992)** Anatomy and Ultrastructure of the Alimentary canal in *Lepeophtheirus salmonis* (Copepoda: Siphonostomatoida). *Journal of Crustacean Biology* **12** (3): 423-437.
- Paperna, I. (1964)** Parasitic Crustacea (Copepoda and Branchiura) from inland water fishes of Israel. *Israel Journal of Zoology* **13**: 58-68.
- Pesce, G.L. (1995)** Checklist of the Italian Copepods. An electronic update to the Checklist delle specie della fauna Italiana. Copepoda Calderini ed. Italy and to the checklist of the species of the Italian fauna by F.Stoch. (<http://www.faunaitalia.it/checklist/>)
- Piasecki, W. (1993)** Comparative morphology of the three species of *Lamproglana* (Copepoda, Cyclopoida, Lernaedidae) described by von Nordmann, based on re-examination of the types. *Mitteilng Zoologica Museum auf Berlin* **69**: 307-315.
- Pillai, R.S. (1960)** Studies on the shrimp *Caridina laevis* (Heller). I. The digestive system. *Journal of Marine Biology Association of India* **2**: 57-74.
- Ponyi, J. and Molnár, K. (1969)** Studies on the Parasite Fauna of Fish in Hungary V. Parasitic Copepods. *Parasitologia Hungarica* **2**: 137-148.
- Pusey, K.H. (1939)** Methods of reconstruction from microscope sections. *Journal of the Royal Microscopical Society* **59**: 232-251.
- Raymont, J.E.G., Krishnaswamy, S., Woodhouse, M.A. and Griffin, R.L. (1974)** Studies on the fine structure of Copepoda. Observation on *Calanus finmaarchicus* (Gunnerus). *Proceedings of the Royal Society. London, Series B* **185**: 409-424.
- Remane, A., Storch, V. and Welsch, U. (1978)** "Kurzes Lehrbuch der Zoologie" Gustav Fisher Verlag, Stuttgart, 3. Auflage. (<http://www.ginko-web.de/streifzug/pyrrhocoris/bilder/gehrin1.gif>)

- Sabatini, M.A., Marini, M., Fratello, B., Gelosini, C., Mola, L. and Benedetti, I. (1987)** The digestive apparatus of the parasitic copepod *Lernaea cyprinacea* L. during development and in the adults. *Acta Embryologiae et Morphologiae Experimentalis* n.s. **8** (2-3): 389-409.
- Sağlam\*, N. (1992)** Some external Parasites on Cyprinids in Keban Dam Lake. Master Dissertation Firat University, Science Institution, Firat. pp.50.
- Sağlam, N. (1998)** Investigation of *Lamproglana pulchella* (Nordmann 1832) on *Capoeta trutta* and *Chondrostoma regium* caught in Keban Dam Lake (Elaziğ, Turkey). *Journal of Applied Ichthyology* **14**: 101-103.
- Sars, G.O. (1913)** An Account of the Crustacea of Norway VI. Copepoda Cyclopoida pts. I & 11. Oithonidae, Cycloidinidae, Cyclopidae (part). The Bergen Museum. Christiania: Alb. Cammarmyer's Forlag. pp.225.
- Sars G.O. (1918)** Copepoda Cyclopoida: An account of the Crustacea of Norway. Volume VI. The Bergen Museum, Bergen, Norway. pp. 225
- Sars G.O. (1921)** An account of the Crustacea of Norway, with short descriptions and figures of all the species. Vol. VII. Copepoda Monstrilloida & Notodelphyoida. The Bergen Museum, Bergen pp. 91, fig 1-37.
- Schram, F.R. (1986)** Crustacea. Oxford University Press. New York. Chapter 1. pp.606.
- Shotter, R.A. (1977)** Copepod parasites of fishes from northern Nigeria. *Bulletin de l'Institut Francais d'Afrique Noire, Serie A* **39** (3): 583-600.
- Skelton, P. (2001)** A complete guide to freshwater fishes of Southern Africa. Struik Publishers, Cape Town, South Africa. pp. 395.
- Soylu\*, E. (1990)** Surveys on the parasitic Fauna of Fishes in Mogan Lake. Master Dissertation, Ankara University, Science Institution, Turkey. pp.73.

**Sproston, N.G., Yin, W.Y. and Hu, T. (1950)** The genus *Lamproglena* (Copepoda Parasitica): The discovery of the life-histories and males of two Chinese species from food fishes, revealing their relationship with *Lernaea*, and of both to the cyclopoidea. *Sinensia* n.s. 1: 51-84.

**Stojanovski, S., Hristovski, N., Cakic, P. and Baker, R.A. (2006)** Preliminary Investigations on the Parasitic Crustacea of Freshwater Fishes from Macedonia. BALWOIS 2006, International Conference on Water Observation and Information System for Decision Support Ohrid, Macedonia, Full Paper, 8pp. [http://balwois.mpl.ird.fr/balwois/administration/full\\_paper/ffp-497.pdf](http://balwois.mpl.ird.fr/balwois/administration/full_paper/ffp-497.pdf).

**Suchenko, G.E and Allanmuratov, B. (1966)** *Lamproglena markewitschi* sp. nov., Novii vid parazit icheskikh veslonogikh. *Lamproglena markewitschi* sp. nov., A new species of parasitic copepods (Copepoda Parasitica). *Gidrobiologicheskii Zhurnal* 2 (6): 64-65, fig.1. (22-xii-1966).

**Tam, Q. and Avenant-Oldewage, A. (2008)** The ultrastructure of the digestive cells of *Argulus japonicus*, Thiele 1900 (Crustacea: Branchiura) *Arthropod Structure and Development* 38:45-53.

**Thomas, S. and Hameed, S. (1984)** Description of a new sp. of *Lamproglena* (Copepoda: Lernaeidae) from Kerala. *Indian Journal of Fisheries* 31: 223-227.

**Thorell, T. (1859)** "Bidrag till Kannedomen om Krustaceer, som lefva i Arter af Slagtet Ascidia L." Kongliga Svenska Vetenskaps-Akademiens Handlingar, ns, 3(8): 1–84.

**Thurston J.P. (1970)** The incidence of Monogenea and parasitic Crustacea on the gills of fish in Uganda. *Revue de Zoologie et de Botanique Africaines* 82: 111-130.

**Tsotetsi, A.M. (2004)** Aspects of the biology of *Lamproglena clariae* (Copepoda: Lernaeidae) from the Vaal River System, South Africa. Unpublished thesis, Rand Afrikaans University, Johannesburg. pp.109.

- Tsotetsi, A.M., Avenant-Oldewage, A. and Mashego, S.N. (2005)** Aspects of the pathology of *Lamproglena clariae* (Copepoda: Lernaeidae) on gills of *Clarias gariepinus* from the Vaal River System, South Africa. *African Zoology* **40**(2): 169-178.
- Van As, L.L. and Van As, J.G. (2007)** *Lamproglena hepseti* n. sp. (Copepoda: Lernaeidae), a gill parasite of the African pike *Hepsetus odoe* (Bloch) from the Okavango River and Delta, Botswana. *Systematic Parasitology* **67**: 19-24.
- Wilson, C.B (1922)** North American parasitic copepods belonging to the family Dichelesthidae. *Proceedings of the United States National Museum* **60**: 1-100.
- Wilson, C.B. (1924)** New North American parasitic copepods, new hosts and notes on copepod nomenclature. *Proceedings of the United States National Museum* **64** (17) (2507):1-22, pls. 1-3.
- Yamaguti, S. (1939)** Parasitic copepods from fishes of Japan. Part 4. Cyclopoida, II. Vol. Jub. Yoshida, 2: 391 – 414, plates 1-4, 7-13. Volumen Jubilare Professor Sado Yoshida.
- Yoshikoshi, K. (1975)** On the structure and function of the alimentary canal of *Tigriopus japonicus* (Copepoda: Harpacticoida). I. Histological structure. *Bulletin of Japanese Society of Fisheries* **41**: 929-935.
- Yoshikoshi, K. and Kô, Y. (1988)** Structure and Function of the Peritrophic membranes of copepods. *Nippon Suisan Gakkaishi* **54** (7): 1077-1082.
- Yü, S.C. (1937)** Synopsis of the genus *Lamproglena* Nordmann with description of a new species from North China. *Bulletin of the Fan Memorial Institute of Biology* **7**: 131-139.

**Zimmermann, F. (1922)** Wissenschaftliche Ergebnisse der mit unterstützung der Akademie der wissenschaften in wien aus der erbschaft treitl von F. Werner unternommenen zoologischen expedition nach dem Anglo-Ägyptischen Sudan (Kordofan) 1914. IX Bearbeitung der parasitischen Copepoden von Fischen; Denkschriften der Akademie der Wissenschaften Wien Mathematische.-Naturwissenschaftlichen Klasse, **98**: 101-111, Taf. I-II.

\* Original literature not seen

Chapter 3 Figure 2A: [www.mbscientific.com/KnowEvol/cns1.gif](http://www.mbscientific.com/KnowEvol/cns1.gif)



## Appendix A

### Aspects of the feeding biology of *Lamproglena*.

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The copepods are the largest and most diverse animal group. A major family of cyclopoid parasitic copepods is the Lernaeidae and comprises of 10 genera and subgenera of which *Lernaea* and *Lamproglena* contains 77% of the known species of this family. The genus *Lamproglena* (Nordmann, 1832) is a broad-based ecto-parasite which currently comprises of 37 nominated species. *Lamproglena* are most abundant in Africa, Palaertic and Oriental regions. Kumarie, *et al.*, 1989 placed the species within two groups. Group I, consisting of eighteen species, includes species with an elongated, cylindrical body, whereas Group II, having ten species has short and compact bodies. The first description of *Lamproglena* by Fryer, 1956 was adequate for the time, but lacked detail of certain morphological features. Marx and Avenant-Oldewage (1996) redescribed *Lamproglena clariae* with notes of its occurrence and distribution. Tsotetsi, *et al.* 2004 mentioned that *Lamproglena clariae* (Fryer, 1956) is an ecto-parasite infecting the gills of the sharptooth catfish, *Clarias gariepinus* (Burchell, 1822). The species of *Lamproglena* attach themselves to the gills of the host by means of the spines on the maxillae and maxillipeds. *Lamproglena* mouthparts are not fully understood but it is known that feeding presumably involves only two pairs of appendages, as the maxillae are also used for gripping host tissue. *Lamproglena clariae* has been noted to be the cause of extensive gill tissue proliferation, which may have interfered with host respiration according to Tsotetsi, A., Avenant-Oldewage, A., Mashego, S.N (2005). Tsotetsi, *et al.* (2005) established the pathology of *Lamproglena clariae* specifically on *Clarias gariepinus*. A study into the structural morphology of the organisms' digestive system and mouthpart morphology will be undertaken to ensure a better understanding of the pathology caused by this fish parasite.



## Aspekte van die voedingsbiologie van *Lamproglena*

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### *Aspects of the feeding biology of Lamproglena*

*Lamproglena clariae* is a gill parasite of *Clarias gariepinus*. The digestive tract and mouthpart's morphology was studied from specimens collected from the Vaal Dam. The tract consists of a fore-, mid-, and hindgut. The morphology indicates that it is able to suck blood.

*Lamproglena clariae*-individue is bekende kieuparasiete van *Clarias gariepinus*-eksemplare en gebruik hul maksillae en mandibels om vas te heg aan die kieu van hul gasheer. Dit word algemeen aanvaar dat die verkryging van voedsels net die maksillae en maksillipe betrek. Onsekerheid oor die weefsel tipe waarop eksemplare van *Lamproglena* voed, bestaan. Bloed is nooit in die spysverteringstelsel van eksemplare van *L. monodi* aanwesig nie maar in die geval van *L. clariae* en *L. barbicola*-individue is die spysverteringstelsel met bloed gevul. 'n Studie om die morfologie van die spysverteringstelsel en die monddele deur middel van lig- en skandeerelektronmikroskopie te bestudeer, is aangepak. *Lamproglena clariae*-individue is versamel van *C. gariepinus*-eksemplare in die Vaaldam, nadat die visse gedood en die kieu verwyder is. Die eksemplare is in 'n ys-asyn-formaldehiedalkoholoplossing gefikseer en gepreserveer in 70% etanol voordat dit gedehidreer en in hars ingebed is. Seriesneë is gekleur en 'n grafiese rekonstruksie van die spysverteringstelsel het gevolg. Die spysverteringstelsel bestaan uit 'n voor-, middel- en agterderm. Die esofagus is uitgevoer met selle wat bedek is met kutikula en dit word omring deur 'n spierlaag. Die esofagus is verleng tot 'n tregtervormige struktuur wat tot binne-in die middelderm verloop. Die middelderm bestaan uit drie dele, naamlik die anterior-, mediane en posteriorsones wat gekenmerk word deur verskillende epiteellae. Die agterderm is 'n eenvoudige, gekutiniseerde buis. Die morfologie dui daarop dat eksemplare van *L. clariae* in staat is om bloed te suig. Die struktuur van die patologies-veroorsakende monddele steun die aanname.

## APPENDIX C

### Aspects of the feeding biology of *Lamproglena clariae*

Fryer, 1956

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*Lamproglena clariae* is a well-known gill parasite of *Clarias gariepinus* attaching to the gills of the host using the maxillae and mandibles. Even though the mouthparts are not fully understood, it is generally accepted that feeding involves only the maxillae and maxillipeds. It is uncertain on which tissue type *Lamproglena* feeds, as blood is never apparent in the gut of *L. monodi*, whereas in the case of *L. clariae* and *L. barbicola* the gut is blood-filled. Therefore a study was conducted to examine the morphology of the digestive tract and the structure of the mouthparts using light and scanning electron microscopy.

*Lamproglena clariae* specimens were collected from *C. gariepinus* in the Vaal Dam after the fish were killed and the gills removed. The samples were fixed in an acetoformaldehyde alcohol solution and preserved in 70 % ethanol prior to dehydration and imbedding in resin. Serial sections were stained and a graphic reconstruction of the digestive tract followed. The digestive system consists of a fore, mid- and hindgut. A cuticle-lined, muscularised oesophagus extends into the midgut via a funnel-like structure. There are 3 zones within the midgut, namely the anterior, median and posterior zones characterised by the epithelial lining. The hindgut is a simple, cuticle lined tube. The digestive system morphology suggests that *L. clariae* is able to suck blood and this deduction is supported by the structure of the wound-inflicting appendages.

## APPENDIX D

### The digestive system of *Lamproglena clariae* Fryer, 1956

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*Lamproglena clariae* is a gill parasite of *Clarias gariepinus* attaching to the gill of the host using the maxillae and maxillipeds. Even though the mouthparts are not fully understood, it is generally accepted that feeding involves only the maxillae and maxillipeds. It is uncertain on which tissue type *Lamproglena* feeds, as blood is never apparent in the gut of *L. monodi*, whereas in the case of *L. clariae* and *L. barbicola* the gut is often blood-filled. Therefore a study was conducted to examine the morphology of the digestive tract and the structure of the mouthparts using light and scanning electron microscopy. *Lamproglena clariae* specimens were collected from *C. gariepinus* in the Vaal Dam after the fish were killed and the gills removed. The samples were fixed in an acetoformaldehyde alcohol solution and preserved in 70% ethanol prior to dehydration and imbedding in resin. Serial sections were stained and a graphic reconstruction of the alimentary tract followed. The alimentary tract consists of a fore, mid – and hindgut. The foregut is well equipped with circular muscles that act as dilator muscles. A cuticlerised, muscularised oesophagus extends into the midgut via a funnel-like structure. Strong muscles surround the entire tract. The midgut is lined by cuboidal cells lined with a varying number of large vacuoles. In some regions club-shaped cells are present containing numerous vacuoles. These multi-vacuolated cells protrude into the lumen. No specific zonation is observed, however, the midgut is divided into regions of transition marked by a changing cellular appearance. The hindgut is a simple, cuticle lined section. A longitudinal section through the foregut revealed a bolus which consisted of damaged cellular material. After a comparison with host blood was performed, it was confirmed that the material was indeed host blood, but in a damaged state. Red blood cells undergo decomposition relatively quickly and the cell membrane of the red blood cell is deformed and disappears rather quickly, resulting in haemolysed blood cells. It is speculated that the reason for the intake of haemolysed blood could be the absence of piercing mouthparts. *Lamproglena's* feeding leads to severe tissue proliferation, which creates a chamber in which the head of *Lamproglena* is then embedded. It is speculated that the chamber contains blood during the feeding process. The circular muscle layer that is observed surrounding the funnel and oesophagus dilate to create a vacuum while the funnel flaps block the posterior end, promoting the intake of cellular material through the slit-like mouth opening. A peristaltic like action maintains the vacuum. The digestive tract morphology suggests that *L. clariae* is able to suck blood, released by the wound-inflicting appendages.

