

CHAPTER 2

INTRODUCTION AND LITERATURE REVIEW



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

The discovery of the male and larval stages of the genus *Lamproglena* Von Nordmann, 1832 led to the transfer of this genus from Dichelesthiidae, and was therefore classified as follows:

PHYLUM ARTHROPODA

SUBPHYLUM CRUSTACEA

CLASS MAXILLOPODA

SUBCLASS COPEPODA

ORDER CYCLOPOIDA

FAMILY LERNAEIDAE Sproston et al., 1950

SPECIES *Lamproglena clariae* Fryer, 1956

2.1.1 A brief description of the female adult L. clariae

Morphological aspects of the adult female of this parasite have been extensively studied and described (Fryer 1956, 1961, 1964; Marx & Avenant-Oldewage 1996) and a brief description is as follows:

The body is elongated, widest at centre, tapering slightly anteriorly and posteriorly. Head as wide as the middle body region. Slightly transparent yellow body, digestive tract distinct, containing red blood cells. Cephalothorax, thorax and abdomen more distinctly demarcated from each other than the segmentation within these regions. Four pairs of biramous legs and fifth uniramous legs present on the thorax. Genital segment bearing two dorsal genital openings from where two uniseriate egg sacs extend. The abdomen made up of three distinct segments (Fig. 1).

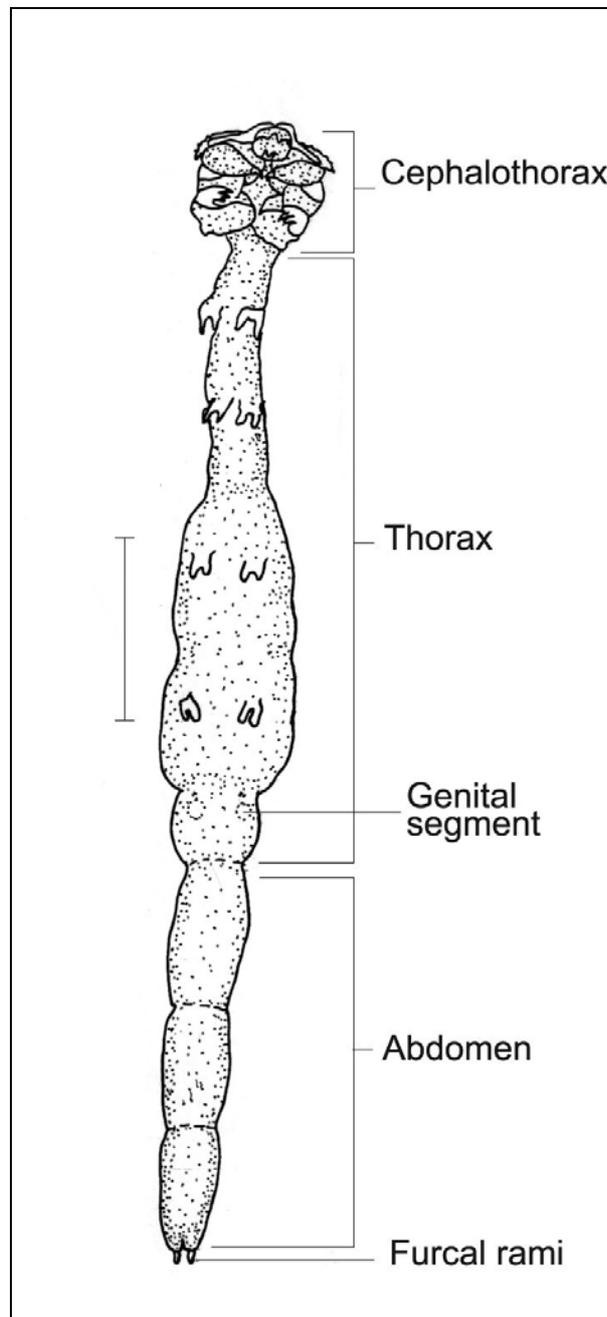


Fig. 1. *Lamproglena clariae*, adult female, ventral view, redrawn from Marx & Avenant-Oldewage (1996). Scale bar: 1mm.

Regarding the taxonomy of *Lamproglena clariae*, a general discussion on aspects from the subclass, order, family, genus to the species level is presented.

2.2 Occurrence of copepods

Copepoda is the largest subclass of small crustaceans and over 8500 species have been recorded. Most species are marine, but there are many freshwater species that live in moss, soil-water films and leaf litter. Also there are many that are parasitic (over 1000) on various marine and freshwater animals, especially fish. Most copepods range in length from less than 1mm to more than 5mm, although there are larger (17mm) free living species. Some copepods are ectoparasitic on fish and attach to the gill filaments, fins or the integument. Other copepods are commensals or endoparasites of polychaete worms, bivalves, echinoderms and tunicates. Many copepod species are also parasites of Cnidarians. All degrees of modifications from the free living copepod form are exhibited by these parasites. Ancestral forms are usually ectoparasites and resemble free living species. On the other hand some ectoparasites and endoparasites are so highly modified and bizarre that they no longer have any resemblance to the free living species. In most parasitic copepods the adults are adapted for parasitism, and the free swimming larval stages are usually similar to those of the free living copepods. Contact with the host occurs at various times during the life cycle of the copepod, and modifications appear with each molt (Ruppert & Barnes 1994).

2.2.1 Morphology of copepods

To appreciate the extent of morphological changes undergone by parasitic copepods for adaptation to their mode of life, one should be acquainted with the morphology of the free living copepod.

The body of a free living copepod is commonly tapered from anterior to posterior and is somewhat cylindrical. The trunk is composed of a thorax and abdomen. The head is either rounded or pointed. Compound eyes are absent, but the median naupliar eye is a typical and conspicuous feature of most copepods. Also conspicuous are the uniramous first antennae, which are generally long and held outstretched at right angles to the long axis of the body. The head is fused with the first of the six thoracic segments and sometimes with the second thoracic segment as well. The first pair of thoracic appendages has become modified to form maxillipeds used for feeding (Ruppert & Barnes 1994). The cephalothorax is followed by four free thoracic segments, each bearing a pair of swimming legs. These segments vary in proportion from species to species, but as a rule diminish from the second to the fifth leg bearing segment, the last of them being usually much reduced. This segment is followed by the genital complex, made up of two segments. The presence of vestigial pair of legs on the genital complex is an indication of the thoracic origin of the genital complex as no appendages are carried on the abdominal segments (Kabata, 1979). The abdomen is composed of five segments, which are commonly narrower than those of the thorax. There are no abdominal appendages, except for the anal segment bearing the two caudal rami (Fig. 2).

Adaptation to the parasitic mode of life, with fish as hosts, has led to substantial changes in the morphology of the copepods. Those changes took the form of addition of parasitic developmental stages to the free-swimming copepod life cycles and were directed towards the attainment of two main objectives: maintenance of secure hold on the host and accommodation of increased reproductive activity. The first resulted in the development of various prehensile mechanisms, in some instances

extensive metamorphosis has been adopted as the mechanism transforming free-swimming dispersal stages into sessile, parasitic adults (Kabata 1992).

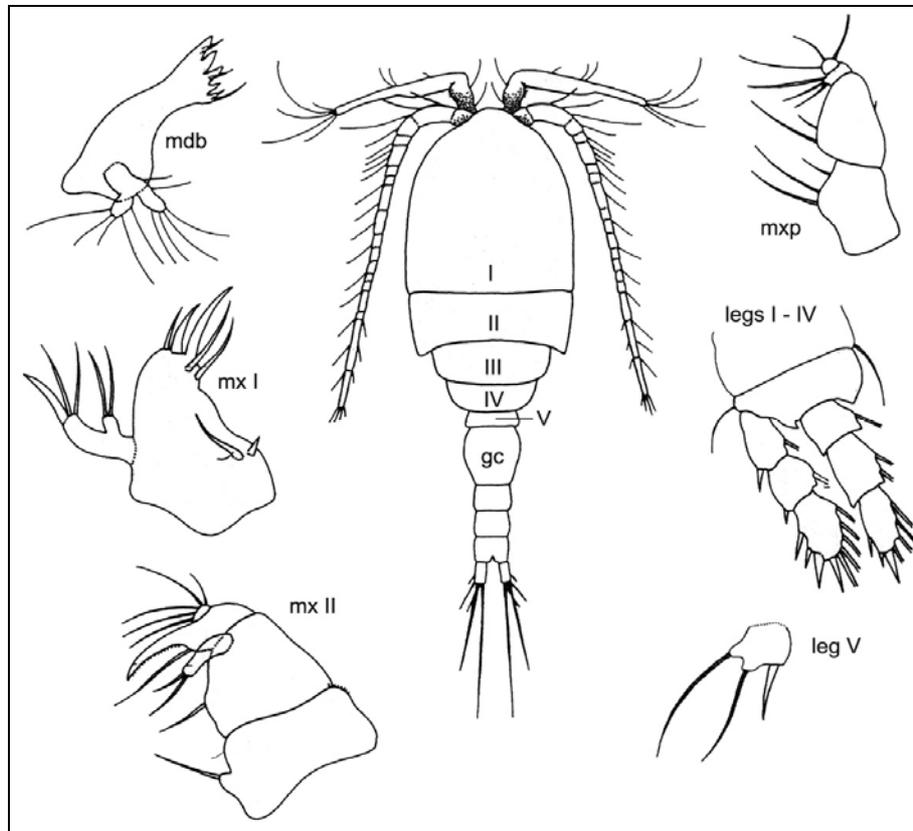


Fig. 2. Cyclops, free living cyclopoid copepod, redrawn from Ruppert & Barnes (1994).

More examples of modifications undergone by members of this taxon in order to adapt to the parasitic mode of life include:

Reduction in locomotory appendages; development of adaptations for adhesion, both by development of new structures and modification of appendages; increase in size and change in body proportions, caused by much greater growth of genital regions; fusion of body somites and loss of external evidence of segmentation; reduction of sense organs; and a reduction in numbers of instars that are free living, both through the passing of more stages before hatching and through larval instars

becoming parasitic (Roberts & Janovy 2005).

Out of ten Copepod orders; Calanoida, Platycopioidea, Misophrioida, Harpacticoida, Mormonilloidea, Gelyelloidea, Monstrilloidea, Cyclopoida, Poecilostomatoida and Siphonostomatoida, only the latter three orders are parasitic on fishes; about 75% of parasitic species belong to Siphonostomatoida, about 20% to Poecilostomatoida and only some 5% to Cyclopoida (Ho 1990). According to Kabata (1970) classification of the three parasitic orders of Copepoda is partly based on morphology of their mouthparts (Fig. 3).

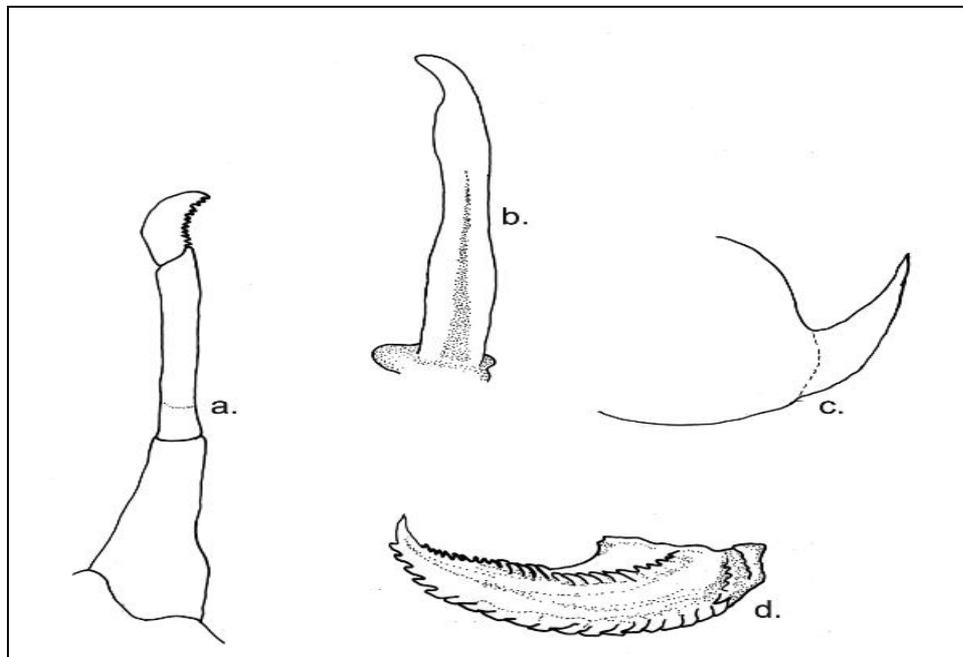


Fig. 3. Three parasitic orders, subclass copepoda, morphology of the mandibles, A, B = Siphonostomatoida, C = Cyclopoida, D = Poecilostomatoida, redrawn from Kabata (1988).

Members of the suborder Cyclopoida of which *L. clariae* is a member, have the buccal orifice not projecting much above the surface of the body. It is usually a partly uncovered hole, anteriorly overhung by the flap of the upper lip. The cyclopoid mandible consists of two parts; the basal part is short and stocky. The distal part is

falciform, long and pointed with rows of small denticles running along the entire or almost entire lengths of both its margins. This is apparently the ancestral condition and is possessed by several copepod suborders (Kabata 1970). Unlike the other two suborders, Cyclopoida has no authenticated records of species parasitic on marine fishes. A large proportion of cyclopoid species parasitic on freshwater fishes belongs to the family Lernaeidae (Kabata 1992).

Association between the morphology of the parasite and the type of host-parasite relationship determine the extent of the deleterious impact exerted by copepods on their fish hosts. A wide range of effects have been observed, from relatively innocuous to lethal. Generally speaking, the damage caused to the fish by copepods is directly proportional to the degree of closeness of this relationship. Mobile ectoparasites tend to be less harmful than sessile, mesoparasitic species penetrating host tissue and in some cases invading vital internal organs. The final effects depend, however, on more than one factor and are influenced by the intensity of infection, the site infected and often by environmental parameters such as temperature, oxygen content or salinity level of water (Kabata 1992). If the dissolved oxygen drops at night in a river/any water body the fish that appear healthy during the day may die at night because copepods and other gill parasites would have reduced their respiratory capacities (Thatcher 1998). Definitive evaluation of the possible impact therefore must not be generalised (Kabata 1992).

2.3 The family Lernaeidae

2.3.1 Distribution and occurrence of species of the family Lernaeidae

Lernaeidae is a major family of cyclopoid copepods parasitic on freshwater fishes. Some of them are among the most harmful parasites of cultured fishes;

consequently they have become the target for extensive studies (Ho & Kim 1997). In 1979, Kabata stated that the family Lernaecidae contains genera, displaying a broad range of morphological differences (Fig. 4).

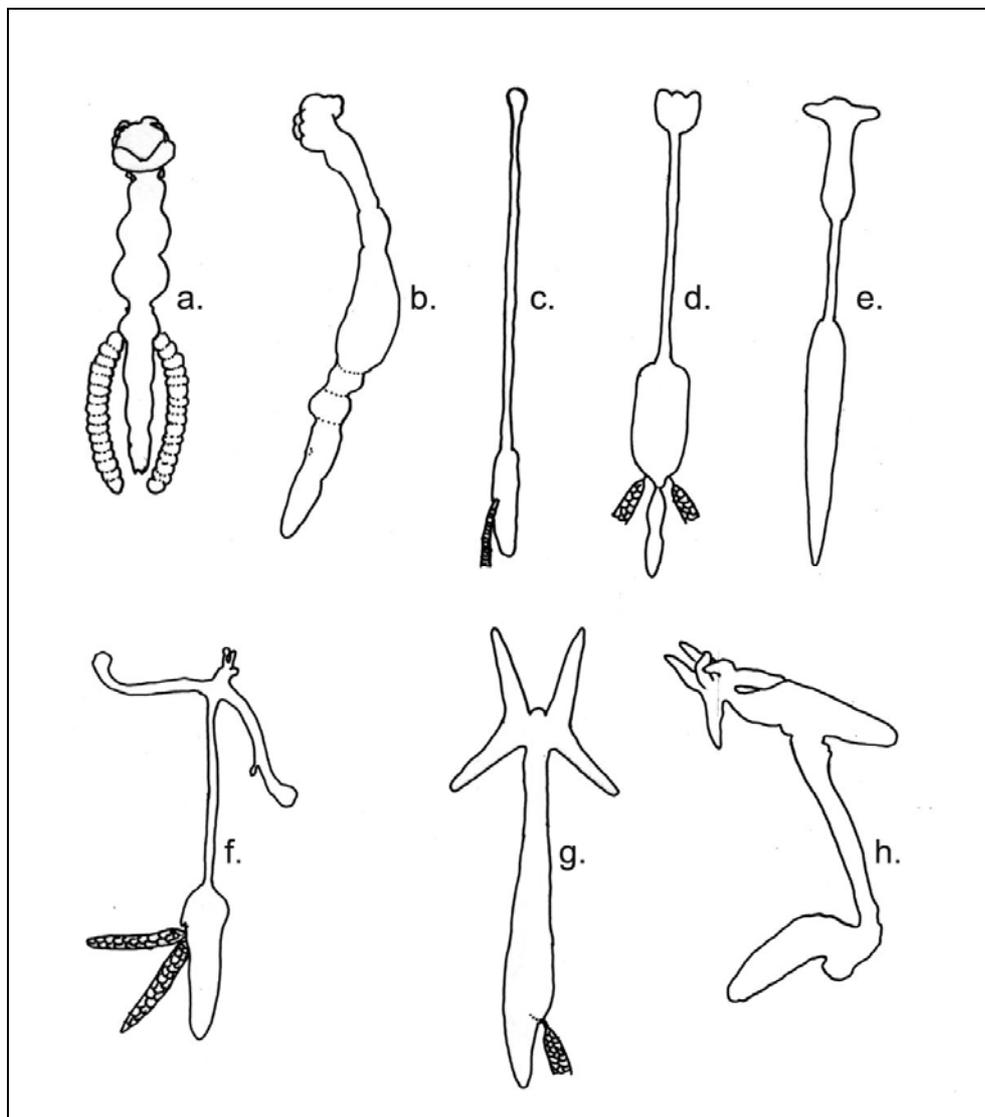


Fig. 4. Morphological differences of the members of the family Lernaecidae to show total body morphology of *Lamproglena* **a**, *Lamproglenoides* **b**, *Afrolernaea* **c**, *Lernaegarriffa* **d**, *Areotrachelus* **e**, *Taurecheros* **f**, *Lernaea* **g** and *Opistholernaea* **h**, redrawn from Kabata (1979).

At one extreme are species of *Lamproglena* Von Nordmann, 1832 whose morphology bears many traces of its free living ancestry; at the other are members of

Lernaea L., the notorious ‘anchor worm’ that has been metamorphosed to the point of losing, at first sight, all indication of its kinship with Crustacea (Kabata 1983). The genus *Lamproglena* is the most primitive member of the family Lernaeidae. Following attainment of maturity, the females increases in size only moderately and, though their external segmentation is at least partially lost, do not show any significant tagmosis. All segments present following the moult of the last copepodid stage are still more or less recognisable and their proportions have been largely retained. The genital segment is usually separated from the segments anterior to it by the small fifth leg bearing segment that forms a waist like constriction. This condition resembles the exclusion of the genital segment from the poecilostome pregenital trunk, such as exists in Chondracanthiidae. It is at odds however, with the aberrant developments in that part of the body exhibited by the metamorphosing genera of its own family (Kabata, 1979).

The genus *Lamproglenoides* bridges the morphological gulf separating the genus *Lamproglena* from other lernaeid genera. This copepod can be seen as an intermediate between metamorphosed and non-metamorphosed lernaeids. Though its segmentation is partially retained, the extension in length, with distinct evidence of differential growth, disturbs the cyclopid body proportions. The mesoparasitic lernaeid genera have adult females profoundly modified as the result of metamorphosis. The essence of morphological changes imposed upon them by their mode of life consists in: development of a holdfast intended to secure the position of the head within the host, elongation of the body necessary for the penetration of the host and retention of contact with the external environment, and expansion of the genital region to accommodate increased reproductive efforts. In consequence of these changes the original segmentation and appearance are lost and the body of the

female becomes roughly divisible into three regions: the cephalothorax (with more or less prominent holdfast), elongated neck, cylindrical or gradually expanding posteriorly, and the posterior part of variable structure.

The Lernaecidae predominate in the Old World. Although some genera have American representatives (*Taurocheros* Brian, 1924, and *Areotrachelus* Wilson, 1924, are known from America only), the majority of the lernaecid species occur in Eurasia or Africa. These vast continental masses continue to yield records of new genera and species of Lernaecidae (Kabata 1983). About 110 species of lernaecid copepods are known from 332 species of freshwater fishes belonging to 161 genera in 41 families. They are mostly known from females, which are highly modified and parasitic on freshwater fishes. Some of them are mesoparasites anchoring to their hosts with the transformed cephalothorax (bearing holdfast), but others are ectoparasites attaching to hosts by means of the enlarged, powerful maxillae. From the works of the lifecycle of *Lamproglena chinensis* Yu by Kuang (1962) and *Lernaea cyprinacea* Linnaeus, by Grabda (1963) it is understood that the adult male lernaecids are not as transformed as their opposite sex, and they die soon after mating. *Lamproglena* and *Lernaea* are the two largest genera of the Lernaecidae, they together account for more than two thirds of the known species of the family. Species of *Lamproglena* are not as widely distributed as those of *Lernaea*; they are absent from the new world and South Pacific including Australia and New Zealand (Ho 1998).

2.3.2 Biogeography of the family Lernaecidae

Asia and Africa have the largest number of lernaecids (about 89%) and species of *Lamprogleninae* are confined to Africa and Asia. This peculiar pattern of lernaecid distribution seems to have resulted from an explosive cladogenesis on the mobile

'Indian Raft'. According to the Plate Tectonic Theory, India separated from Gondwana in the late Cretaceous, moved northwards and collided with Laurasia in the Middle Eocene. This piece of Gondwana-originated subcontinent carries nine of 14 lernaeid genera (*Afrolernaea*, *Catlaphilla*, *Indolernaea*, *Indopeniculus*, *Lamproglena*, *Lamproglenoides*, *Lernaea*, *Pillainus* and *Pseudolamproglena*) including all seven genera of the Lamprogleninae. Since species of *Afrolernaea*, *Lamproglena*, *Lamproglenoides* and *Lernaea* are known from both Africa and India, it is logical to assume that these four genera originated within Gondwana before the separation of India from Africa. Then, the remaining five must have evolved through an explosive cladogenesis of this Indian Raft. This historic event explains why the occurrence of *Indopeniculus* is seen in Thailand and *Pseudolamproglena* is seen in China, but not in Africa. It also explains why the modern Lamproglenids are restricted to Africa and Asia with more than half of them occurring in Asia (Ho 1998; Fryer 1968).

2.3.3 Systematics of the family Lernaeyidae

Lernaeyidae are parasitic on freshwater teleosts and because of their morphological plasticity, their systematics are only too often beset with uncertainties, spurious taxa and confused synonyms. They are characterised by pronounced sexual dimorphism because their males do not undergo metamorphosis and retain a similarity to their free living cyclopod relatives, as well as to the unmetamorphosised females. The familial diagnosis based on metamorphosised female and adult male is as follows:

Female: Body divided into cephalothorax, long subcylindrical thoracic neck and more or less distinct trunk like posterior section. Cephalothorax with holdfasts of various types. Neck with or without secondary holdfast. Posterior section either

containing indistinguishable fused genital segment and abdomen or indistinctly divided in their two components. Antenna absent or present, other appendages cyclopoid. One to four pairs of biramous legs, fifth and sixth legs also present or absent.

Male: Cephalothorax without holdfast, well delimited. Four free leg-bearing segments diminishing in size from first to fourth. Genital segment small, subspherical. Abdomen of fewer than four segments. Appendages as in unmetamorphosed female, but antennae always present (Kabata 1992).

Very few families of parasitic copepods have a history as confused as Lernaevidae. When families began to be established, the group accommodating *Lernaeva* became a composite taxon, including at various times, and under various names, quite diverse and unrelated copepod species. A clear concept of the family did not emerge until Sproston et al. (1950) transferred to it *Lamproglena*, hitherto classified with a siphonostome family Dichelesthidae. Most members of the family Lernaevidae resemble members of the siphonostomatoid Pennellidae, with which they were confused for a large part of their history. Each has an anterior extremity typically provided with a well developed holdfast, often deeply embedded in the tissues of the host. Their bodies are more or less elongated, trunk-like, and have lost external segmentation and all resemblance to the crustacean habitus. The similarity however is only superficial. While in members of Pennellidae, the comparatively gigantic trunk is formed by the genital segment only, in those genera of Lernaevidae that undergo metamorphosis it also consists of all but the first leg-bearing segments. Extensive morphological modifications in all genera of this family except *Lamproglena* and *Lamproglenoides* Fryer, 1964 make the morphology of fully adult females difficult to understand, and also tend to obscure the phylogenetic affinities of

the family. The true nature of the lernaeid copepods can be revealed only through knowledge of their developmental stages, currently either unknown or known very imperfectly. A notable exception to this unfortunate rule is provided by the genus *Lernaea* L. which, because of its economic importance, has been studied probably more extensively than most parasitic copepods. The life cycle of its type and best known species *L. cyprinacea* is known in detail. Since it is very probable that most Lernauids do not differ greatly from one another as far as ontogeny is concerned, a brief account on the life stages of *L. cyprinacea* might be useful as an introduction to life cycle of members of Lernauidae (Kabata 1979).

2.3.4 *Life history of the family Lernauidae*

The first three stages of the life cycle are nauplii, slightly differing from each other by the progressive increase in length. The third nauplius at the latest phase contains the first copepodid stage within its cuticle. There are five copepodid stages resembling those of other cyclopoid families. At the copepodid V stage, the sex of the parasite is distinguishable. This stage is succeeded by the young adult male and female stages, sometimes referred to as cyclopoids (Grabda, 1963). On seeking its host, the larva (cyclopoid) uses the second antennae and maxillipeds for prehension. After settling on the gills it continues to use these appendages. Males use this method, as they are not permanently parasitic, but the female when searching for the host burrow or push the cephalothorax into the host's tissue until it is completely buried and only the genital segment and the abdomen are left on the outside. The females become fixed parasites, and consequently there is a loss or reduction in locomotory appendages and there is great diversity in the means of prehension. The male does not finally become a fixed parasite, but swims about freely until his death, and it is only

after the female has become a fixed parasite and the male has perished that the former increase enormously and becomes transformed (Paperna 1996). The body of the female is always a little longer than that of the male, and just before as well as for some time after fertilization the genital segment increases greatly in length, but remains of the same width, thus giving the larva destined to become a female an exceptionally elongated form. The only dimorphism is one of length and not of structure, a difference which is common to all copepods, but is here carried a little farther than usual (Kabata 1971).

The environment of adult female copepods is fish tissue and they can modify this habitat by means of their attachment and feeding strategies (Thatcher 1998).

2.3.5 Pathology caused by members of the family Lernaeidae

According to Kabata (1981) initial mechanical disruption of the gill epithelium is a result of penetration by the second antennae, which are characteristically used for primary attachment in parasitic copepods, however there are exceptions to this statement as other copepods such as members of the genus *Lamproglena* use second maxillae (Sproston et al. 1950) and maxillipedes (Marx & Avenant-Oldewage 1996) for attachment, whilst second antennae are sensory in function (Sproston et al. 1950). Lernaeids feed directly on blood and can cause primary anaemia in fish. Those that produce hyperplasia and metaplasia in gill filaments can reduce respiratory capacity in fish (Thatcher 1998). Infection with lernaeids may be very detrimental to the fish. The point of attachment of the adult female to the host integument (skin, buccal or branchial mucosa or the gills) shows a typical inflammatory reaction, being hyperemic or swollen. A fibrotic capsule is eventually formed around the embedded head and neck, alternatively the area around the attachment site may ulcerate with

resulting focal necrosis and in skin infection also loss of scales. In lernaeids more selective in site preferences, relatively fewer numbers of parasitic females, if aggregated into a limited attachment zone such as the gills or the fins may cause severe damage to their host. The entire attachment zone will ulcerate and undergo necrosis. The resulting lesion may become secondarily infected by bacteria, fungi or epizoic protozoans. In juvenile fish species infection by a single parasitic female may cause damage and eventual death. For example, heavy infections with copepodites of *L. cyprinacea* on the gills caused death of *Gambruna affinis* and juvenile carp and *Tilapia spp.* However, mature specimens of *Bagrus docmac* appeared to be tolerant even to infections as heavy as 1000 copepodites (Paperna 1996). However, many studies report pathology associated with heavy infestations. Some of the *Lamproglena* species found on older *Ophiocephalus* were found to have induced a distorted growth on the tip of the gill filament in such a way that there was hypertrophy of connective tissue and a local degeneration of the capillaries. The head of the copepod became deeply embedded and it was suggested that this was not the result of active burrowing of the parasite, but of tissue growth around it, stimulated by irritation set up by the head-appendage, perhaps after more than a season sojourn (Sproston et al. 1950).

2.4 The genus *Lamproglena* Von Nordmann, 1832

The genus *Lamproglena* has no need of the profound modification common to the rest of its family. Attached to the gills of the host, *Lamproglena* preserves a recognisable copepod habitus, with partially retained external segmentation and absence of gigantic hypertrophy of the genital region. To add to the difference between members of the genus *Lamproglena* and other members of the family Lernaeidae, the eggs of its species are partly flattened and their egg sacs are

uniseriate. It consists of species living on the gills or in the branchial cavity of fishes similar to copepods such as caligids, ergasilids and dichelesthiiids. *Lamproglena* is so much like some dichelesthiiids that it was classified under the family Dichelesthiiidae. The discovery of the male and the developmental stages of this species were necessary, before its true affinities became understood (Kabata 1970). The attachment of members of the genus *Lamproglena* to their hosts is by the second maxilla. The prehensile maxillipeds with their palmate claws are probably ancillary to feeding, grasping the gill filament to within reach of the mouth. The second antennae are relatively feebly developed, reduced and purely sensory in function (Sproston et al. 1950).

2.4.1 *Distribution and occurrence of species of the genus Lamproglena Von Nordmann, 1832*

Members of the genus *Lamproglena* is mostly found in Africa but some species are also known in Palearctic and Oriental regions. In 1993, Piasecki mentioned a total of 41 species that he at the time considered as valid species of *Lamproglena*. However, Dippenaar et al. (2001) stated that this genus comprises of 38 nominated species and suggested that the number of species mentioned by Piasecki (1993) possibly includes species that have been synonymised or transferred to other lernaeid genera. For example, *L. abentoni*, Dollfus, 1960 was synonymised with *L. hemiprichii* Fryer, 1964; *L. nyasae* Fryer, 1956 was synonymised with *L. monodi*, Capart, 1944 and *L. opiocephalus* Yamaghuti, 1939 was synonymised with *L. chinensis* (Sproston, Yin and Hu, 1950). *Lamproglena intercedens* Fryer, 1964 was transferred to *Catlaphilla* (Ho, 1998). *Lamproglena surayai* Battish and Brar, 1989 was transferred to *Indorlerna* *seengalae* (Ho, 1998). Therefore, it seems that the

species complex of the genus is still confusing because of the very scanty and incomplete descriptions of many of the existing species (Dippenaar et al. 2001).

Of 38 species 16 have been recorded in Africa, of which five (*L. monodi* Capart, 1944; *L. clariae* Fryer, 1956; *L. barbicola* Fryer, 1961; *L. cornuta* Fryer, 1964; and *L. hoi* Dippenaar *et al.*, 2001) were recorded from southern Africa (Dippenaar et al. 2001).

2.5 Occurrence and distribution of *Lamproglena clariae*

Adult female specimens of *Lamproglena clariae*, an ectoparasitic copepod attach to the gill filaments of the freshwater fish of the family Clariidae, such as *Clarias mossambicus*, *C. lazera*, *C. anguillaris* and *C. gariepinus* (Marx & Avenant-Oldewage 1996). In South Africa it has been found attached to the gills of *C. gariepinus*. Specimens of this parasite were generally found on either extremity of the gills and attached midway along the gill filament and on the apex. Lesions caused by the parasite were haemorrhaged and hyperplasia was frequently observed around the site of attachment. The adult female grips the gill filament with the strong maxillae using maxillipeds as attachment and feeding appendages, penetrates the gill tissue with these appendages and consumes blood, the head then becomes embedded in the host tissue. *Lamproglena clariae* can be regarded as an apomorphous parasitic species, which shows secondary reductions in segmentation, development of a neck and reduction of swimming appendages, antennules, antennae and furcal rami (Marx & Avenant-Oldewage 1996).

The parasite *L. clariae* is endemic to Africa, although not regarded as pan African by Fryer (1968). It was subsequently found in the East, West, Southern, and

Central Africa (Marx & Avenant-Oldewage 1996). The distribution of this parasite is depicted in Table 1 and Fig. 5.

Table 1: Occurrence and distribution of *Lamproglena clariae* Fryer, 1956 according to Marx & Avenant-Oldewage (1996).

Numbering on map	Reference	Location	Host species
1	Fryer, 1956	Lake Malawi,	Clariid species
2		Banga River tributary of Luweya	<i>Clarias mossambicus</i> Peters, 1852
3	Fryer, 1961	Lake Victoria,	<i>Clarias mossambicus</i>
4		Iragalla, Malagarassi swamps	<i>Heterobronchus longifilis</i> Valenciennes, 1840
5	Fryer, 1964	White Nile near Khartoum	<i>Clarias lazera</i> Cuvier and Valenciennes, 1840
1	Fryer, 1968	Lake Malawi,	Clariid species
3		Lake Victoria/Albert, Lower Nile	
6	Thurston, 1970	Edward-George Lake System, Kazinga Channel, Uganda	<i>Clarias lazera</i>
7	Schotter, 1977	Galma River, lakes around Zaria in Nigeria	<i>Clarias anguillaris</i> Linnaeus, 1758
8	Marx and Avenant-Oldewage, 1996	Cuando River Namibia	<i>Clarias gariepinus</i> Burchell, 1822
9	Euler and Avenant-Oldewage, 1992	Olifants River South Africa	<i>Clarias gariepinus</i>

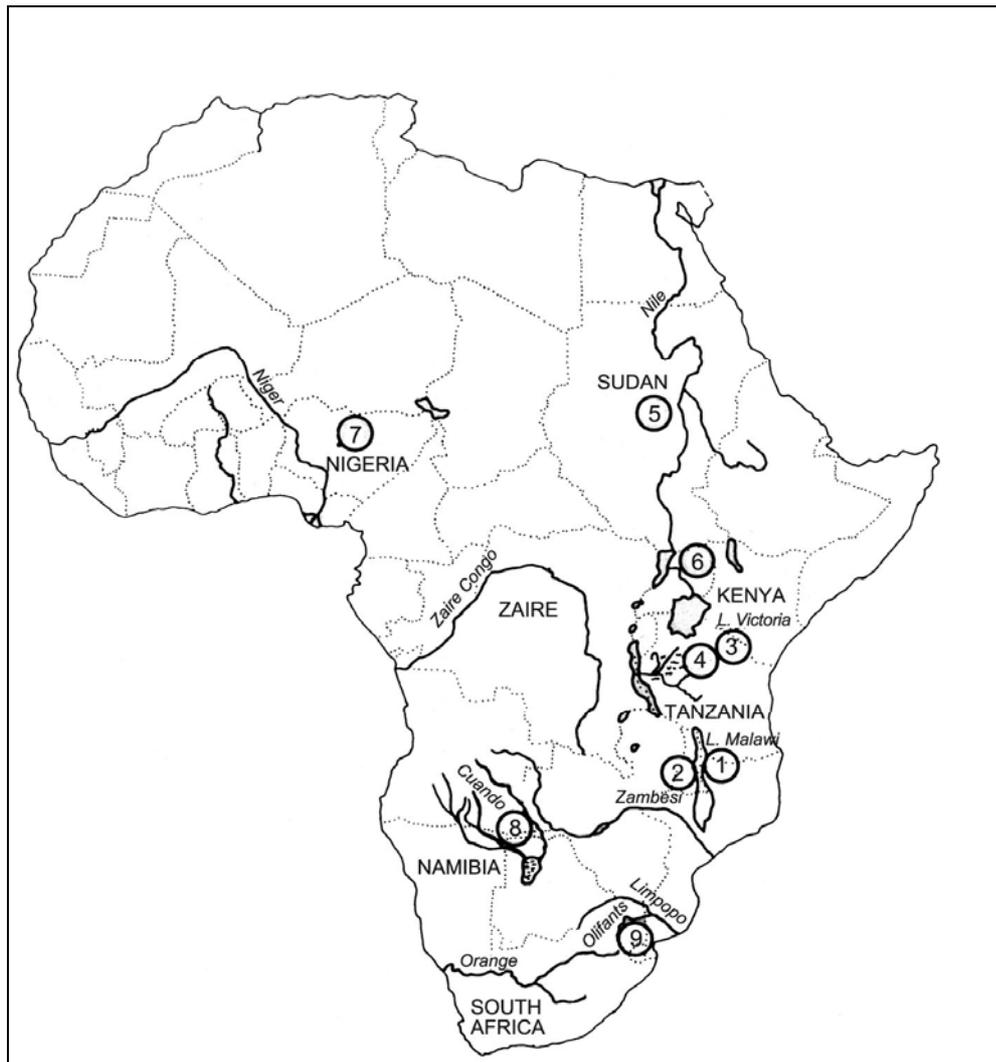


Fig. 5. Map of Africa depicting the distribution of *Lamproglena clariae*, redrawn from Marx & Avenant-Oldewage (1996).

2.6 Description of the attachment site of *L. clariae*

Clarias gariepinus as a catfish, have four pairs of gill arches, from each gill arch are two hemibranchs that consist of a row of primary lamellae. Secondary lamellae are found on each primary lamella. The purpose of this structure is to establish a large surface area that supports respiratory and excretory functions. The gill epithelium is thin to allow gas exchange and therefore is particularly vulnerable to pathogen invasion or irritation. Gills are also responsible for regulating the exchange of salt and water and play a major role in the excretion of the nitrogenous waste

products ammonia and urea. Even slight structural damage can render a fish very vulnerable to osmoregulatory as well as respiratory difficulties (Hughes & Morgan 1973). The gill arch is a curved osseous structure from which radiate the bony supports of the primary lamellae. The gill arch is covered by typical teleost epidermal tissue, but at the origin of the primary lamellae the epidermis is much thicker and usually extremely well endowed with mucus cells. The primary lamella is covered by a mucoid epidermis which may have within it pale staining saline, or salt secreting chloride cells. These chloride cells are most numerous at the basal part of the lamellae. They function in ionic transport with a possible role in detoxification (Roberts & Ellis 2001). Gaseous exchange takes place across the surface of the secondary lamellae. This surface consists of overlapping or interdigitating squamous epithelial cells, usually one layer thick, supported and separated by pillar cells. The pillar cells have primarily a support function. Since the blood entering the lamellar blood spaces comes directly from the ventral aorta at high pressure the presence of contractile elements in the supports of these spaces serve to resist their distension under normal circumstances. The surface of the lamellar epithelium is thrown into microvilli. These serve to aid attachment of the cuticular mucous, which in addition to its role in reducing infection and abrasion, has a significant role in regulating the exchange of gas, water and ions. Goblet cells are found scattered among the squamous epithelial cells of the gill lamellae, as well as in the basal region of the lamellae (Ferguson 1989).