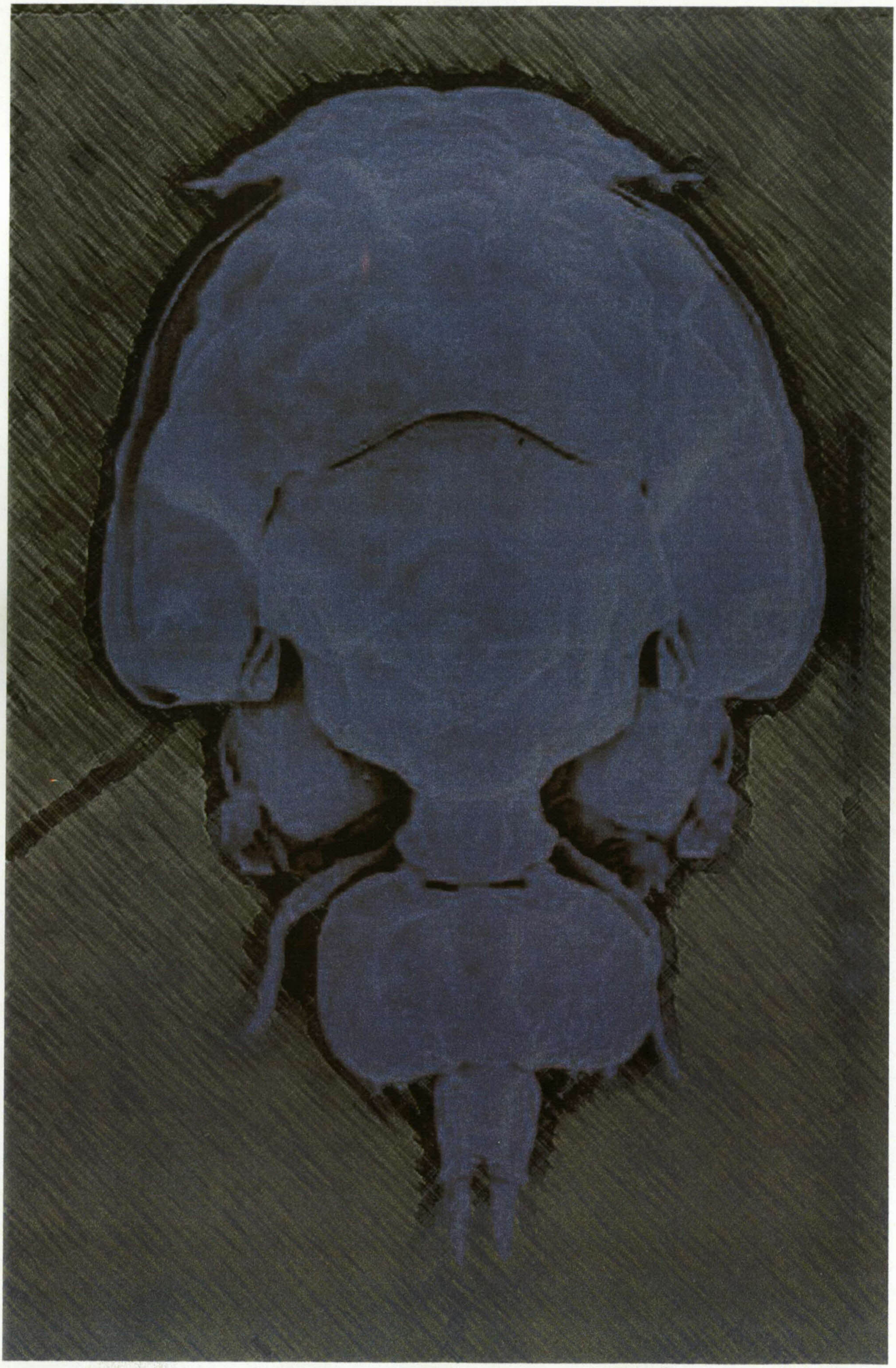

CALIGID FISH PARASITES FROM THE SOUTH AND EAST COAST OF SOUTH AFRICA

By

Nicolaas Johannes Grobler

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Magister Scientiae in the Faculty of Natural Sciences
Department of Zoology and Entomology
University of the Free State

Supervisor Prof J G Van As
Co-supervisor Prof PAS Olivier

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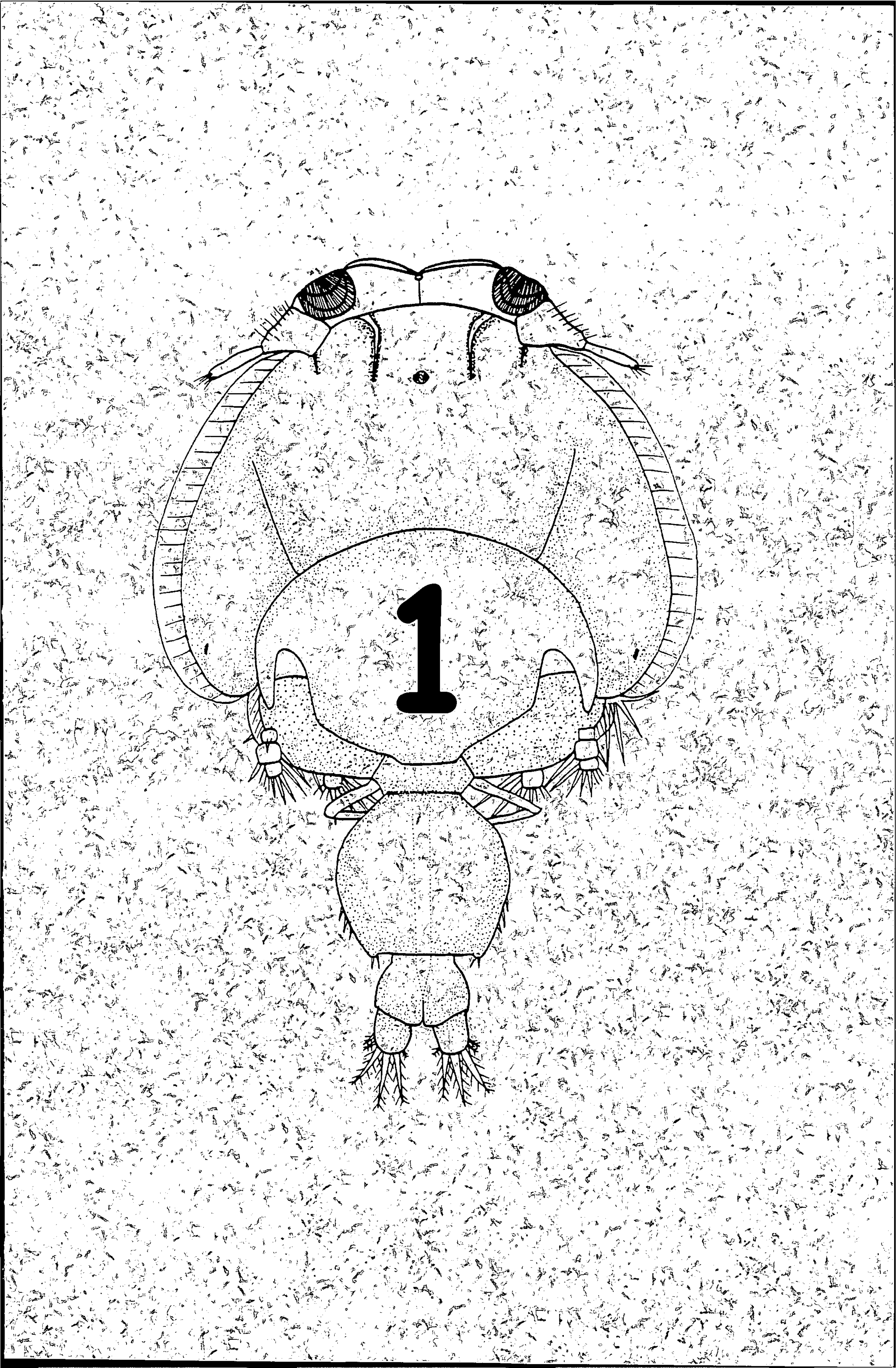
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Introduction

Copepod diversity

Copepods are small aquatic crustaceans, diminutive relatives of the crabs and shrimps. Copepods have successfully colonised all salinity regimes from freshwater, to marine and hypersaline inland waters and all temperature regimes from subzero polar waters to hot springs. In terms of their size, diversity and abundance they can be regarded as the insects of the seas (Huys & Boxshall 1991). The variety of free-living forms is only part of the copepod success story since copepods have become associates or parasites of virtually every animal phylum from sponges and cnidarians, up to the higher living species of chordates, including fish and mammals. At present there are approximately 12 000 known species of copepods. The number of species described during the past 27 years (1964-1991) is nearly two-thirds of all those described in the previous 100 years.

Approximately one-third of marine copepod species are parasites or associates, nearly equally divided between those on fishes and those on invertebrates. Copepods are extremely abundant, not only as free-living species or parasites of fishes, but as associates of invertebrates as well, especially in the tropical regions of the world (Humes 1994). An examination of the number of new families, new genera, and new species in the Zoological Record (Table 1.1) shows a sharp rise in the number of new species described since 1964. In the 27 years from 1964 to 1991, 37% of the species of copepods were described. If we accept the estimate of Raven and Wilson (1992) that roughly 1.4 million species of living animals known to date are probably far fever than 15% of the actual number, and apply it to copepods, then we have still a long way to go. On the basis that the figure of 11 302 copepod species represents 15% of all species in existence, we arrive at a hypothetical grand total of 75 347 species (Humes 1994). That should keep copepodologists busy for a considerable time.

Table 1.1 Comparison of numbers of new taxa of copepods according to Humes (1994).

	New families	New genera	New species	Number of species per year	Percentage of species
Prior to 1864	20	40	381		3%
1864 – 1963	131	1008	6780	68	60%
1964 – 1991	47	585	4141	153	37%
Total	**198**	**1633**	**11 302**		

The deep sea is very rich in new taxa, as many unknown species of copepods are still to be described from the oceans of the world. The number of copepod individuals in the world today make the statement true that copepods are the most plentiful multicellular animals on earth (Wiebe, Davis & Greene 1992), outnumbering the insects, which have more species but fewer individuals. Even among parasitic copepods of fishes the numbers of individual copepods on a host may be surprisingly large, as illustrated by Heinemann (1934) who found 5431 specimens of *Ergasilus sieboldi* in the gill chambers of a single fish (Kabata 1979).

Copepod parasitism – the family Caligidae Burmeister, 1835

Most parasitic copepods, especially those parasitic on fishes, have their origins among the representatives of cyclopoids. Parasitism is just one of the many trophic categories that copepods have successfully invaded. Parasitic copepods can have a devastating impact on the morbidity and mortality within fish populations, and these effects are usually disastrous under the confines of captive environments, especially the aquaculture industry. All siphonostomatoids are parasites or associates of other animals. In excess of 1550 species are known and, of these, about 1050 are parasites of fishes (and mammals such as dolphins and whales) and about 500 are parasites or associates of invertebrate hosts. The order is largely marine, although a small number of fish parasites are found in freshwater.

All members of the family Caligidae Burmeister, 1835 are parasites, clinging to their hosts' skin, fins or gills with the aid of prehensile appendages and capable of free movement over these surfaces. It is clear that maintenance of hold on a slippery surface swept by a current of water is best served by a low-profile shape, designed to disturb the water flow as little as possible. The flatness of caligids is the most striking feature of caligid morphology. In addition to its flatness, the body of the caligid copepod is characterised by being composed of four tagmata: the cephalothorax, fourth pediger, genital complex and abdomen (Kabata 1979). Reviewing the structure of the appendages of caligid copepods (Chapter 3), one becomes aware of their uniformity. The differences from genus to genus, and even more from species to species, are usually only in the proportions of the individual components of various appendages. Less frequently, one of the **secondary appendages** (lunules, postantennary process or sternal furca), or a part of the maxillule are suppressed due to parasitism. Not all caligid genera have all three secondary appendages, and some genera have none. The occurrence of the secondary appendages in caligid genera is shown in Table 1.2.

The history and systematics of the family Caligidae Burmeister, 1835

The history and systematics of the family Caligidae is mostly based on the work done by Kabata (1979). The concept of the familial unity of Caligidae was only slowly arrived at in the course of a long and complicated process, contributed to the work of many authors. As is usual in the development of taxonomic understanding, the blurred outlines of a taxon, at times grossly inclusive, at others too restrictively exclusive, cleared only gradually. It is, therefore, virtually impossible to grant credit for the establishment of the family Caligidae to any single author.

The roots of the family reach back into the eighteenth century, to the date on which Müller (1785) established the genus *Caligus* for the parasite with a rather complicated and obscure earlier history. It is, however, in the early nineteenth century that one must seek the initial attempts for placing *Caligus* in a larger taxon. In an early work of Leach (1816) we find *Caligus* and a spurious genus *Binoculus*, placed with all copepods equipped with a flat dorsal shield in a tribe of Entomostraca named Thecata, family Pseudonura.

Table 1.2 Occurrence of secondary appendages in caligid genera according to Kabata (1979).

	Lunule	Postantennary process	Sternal furca
Abasia	a	a	a
Alicaligus	+	+ (m) a (f)	a
Anuretes	a	+	+ a
Caligodes	+	+	+
Caligopsis	?	?	?
Caligulina	+	+	a
Caligus	**+**	**+ a**	**+ a**
Dartevellia	a	+(v)	a
Diphyllogaster	a	?	+ a
Echetus	+	a	a
Haeniochophilus	a	a	+
Hermilius	a	+ a	+ a
Lepeophtheirus	a	+	+
Mappates	a	a	a
Parapetalus	+	+	+
Parechetus	+	+	+
Pseudanuretes	a	a	a
Pseudocaligus	+	+ a	+ a
Pseudolepeophtheirus	a	+	+
Pseudopetalus	+	+	+
Pupulina	a	+	a
Sciaenophilus	+	+	+ a
Synestius	+	+	+

(+) = present; (a) = absent; (m) = male; (f) = female; (v) = vestigial

Later, Leach (1819) elaborated and modified his scheme. Division I of Entomostraca, identified only by the numeral, contained all species equipped with flat, horizontal dorsal shields and sessile eyes. The nature of the shield was used as the next discriminant, with the present-day caligids belonging to a subgroup with shields consisting of a single part. This subgroup was, in turn, divided into species with jaws (*Apus*) and those without jaws but with a "rostrum". The latter fell into two groups again: those with four antennae (*Argulus*) and those with two (*Cecrops*, *Caligus*, *Pandarus*, *Anthosoma*). With the exception of *Anthosoma*, all these genera were to be placed subsequently in Caligidae and remained in that family for some time.

Contemporaneous with the work of Leach (1819) was that of Lamarck (1818) in which *Caligus*, *Cecrops*, *Argulus* and *Dichelesthium* were placed in "Branchiopodes parasites", a branch of the entomostracan division of "Branchiopodes". Although the name would suggest that the morphology of swimming legs was decisive in ascribing species to this division, it is worth noting that all genera in it possess a flat dorsal shield, smaller in *Dichelesthium*, larger in the remaining genera.

The first more precise definition of the genus *Caligus* was given by Von Nordmann (1832), who framed it as follows: "Body consists of two main parts, the larger shield-like head and the narrower, either quadrate or heart-shaped hindbody, connected to each other by means of a short and narrow breast-piece, to which the seventh pair of feet is attached. Of the seven pairs of feet, the three anterior ones are jaw-like, the fourth and the seventh are simple, the fifth and the sixth are cleft and provided with plumose setae." Failing to recognise the difference between the thoracic legs and the appendages borne upon segments anterior to the first leg-bearing segment, this definition recognised that the genus *Caligus* has only one independent thoracic segment between the cephalothorax and the genital complex. This fact continued to be disregarded for some time after Von Nordmann's work, in assessment of relationships among species with superficially similar morphology. Another fact pointed out by the same author remained unrecognised for some time: the existence of the genus *Lepeophtheirus*, based on its lack of lunules as a distinguishing feature. This was perhaps due to the fact that Von Nordmann (1832) made a conspicuous error in describing them as the eyes and confused the issue. In spite of this error, his work was of high quality for the period.

Burmeister (1835) described a new family, Caligina, and defined it as being equipped with feelers and jointed legs. Burmeister (1835) believed that his Caligina were related to Ergasilina, a group characterised by the possession of multisegmented "inner feelers" (antennules), while the corresponding appendages of caligids are composed of only two or three segments. Burmeister's work is of particular interest because of his attempt at intrafamilial taxonomy, presented in the form of a key. Caligina are divided into two groups by the presence or absence of eyes. The eyeless group included the genus *Cecrops*. The group equipped with eyes is divided into two by the structure of the "last legs of hindbody" (fourth thoracic legs): uniramous or biramous. The former group includes the genera *Chalimus* (a juvenile stage of several caligid genera), *Caligus* and *Lepeophtheirus*; in the latter are *Pandarus* and *Dinematura*. It is interesting to note that all copepods presently still in the family Caligidae (*Caligus* and *Lepeophtheirus*) are grouped together in this system and thus the first tentative lines of division between them and other caligoid genera begin to be timidly drawn.

Edwards (1840) clearly did not recognise the taxonomic importance of lunules and disregarded Von Nordmann's (1832) genus *Lepeophtheirus*. Although numbers of thoracic segments were used in his system, he did not use the single independent thoracic segment of caligids as a noteworthy distinguishing mark. On the other hand he accepted the genus *Chalimus*. At this junction Baird (1850) produced his major work, the first monograph on British Crustacea published by the Ray Society. Of interest here is Baird's order Siphonostomata. Baird is the first one to use the familial endings "idae" for his family group taxa, and the Peltocephala consisted now of four families: Argulidae (*Argulus*), Caligidae (*Caligus*, *Lepeophtheirus*, *Chalimus* and *Trebius*), Pandaridae (*Pandarus*, *Dinemoura*) and Cecropidae (*Cecrops*, *Laemargus*).

The next important work on copepod taxonomy in which Caligidae were dealt with, was that of Dana (1852). Dana's Caligidae were a part of the tribe Caligacea which also contained the families Argulidae, Dichelesthiidae, Ergasilidae and Nicothoidae. Three subfamilies were recognised in 1852, the Caliginae, Pandarinae and Cecropinae. Dana's work marked an important stage in the shaping of Caligidae as he was the first to divide them into subfamilies, using subfamilial names ending in "inae".

Steenstrup and Lütken (1861) divided copepods, both free-living and parasitic, into three parallel rows of species, depending on the nature of their egg sacs. Wilson (1905, 1907a, 1907b) revised the family at greater length and recognised five subfamilies (Caliginae, Pandarinae, Cecropinae, Euryphorinae and Trebinae). In the later work of Wilson (1932), he upgraded the status of the subfamilies by giving familial rank to Cecropidae, Pandaridae, Euryphoridae and Trebiidae.

Having reviewed the rather tortuous course travelled by the concept of Caligidae as a family unit, one becomes aware of a conflict between two tendencies. The first is to group all species with flat, horizontal dorsal shields and similar mouthparts. The second tendency is to bring into the definition more structural features and, with the increased precision of definition, to make the concept a more restrictive one. The introduction of the number of segments fused with the cephalothorax and of the absence of even rudimentary elytra as diagnostic features, has gained general acceptance and is now shared by many authors.

Yamaguti's (1963a) proposal of new subfamilies for Caligidae has not yet been commented upon. It seems, however, that it will not gain general acceptance, based as it is in part on faulty information. Ho (1966) pointed out, for example, that *Echetus* does possess lunules, contrary to Yamaguti's key and that it should, therefore, be included in Caliginae.

To date, Caligidae are represented by three genera in the South African coastal waters. The key does not distinguish between indistinguishable males of *Caligus* and *Sciaenophilus* (Kabata 1979). No record of *Pseudocaligus* in African coastal waters exists. It is included in the key for identifying *Caligus* species:

1. Lunules absent..***Lepeophtheirus***
   Lunules present..**2**
2. Abdomen in female equal to, or more than half of body length........***Sciaenophilus***
   Abdomen in female less than half of body length.......................................**3**
3. Fourth leg well developed, two to four segments..............................***Caligus***
   Fourth leg vestigial, one-segmented......................................***Pseudocaligus***

Notes on the genus *Caligus* Müller, 1785

Caligus is the most abundant copepod genus parasitic on fishes. Since its foundation in the late eighteenth century more than 300 species have been assigned to it, validly or otherwise (Kabata 1992). It is not an exaggeration to say that hardly any part of the world`s oceans is without some *Caligus* species living on the outer surfaces, within buccal cavities, or on the gills of their hosts. Occasionally they can be found penetrating the lower reaches of rivers. One species, *Caligus lacustris* Steenstrup & Lütken, 1861, has become widespread in the freshwater habitats of Eurasia. Some, at least, cause a good deal of damage to their fish hosts by their feeding activities. Fishes harbouring *Caligus* belong to very diverse groups, from the primitive elasmobranchs to highly advanced teleosts. Some hosts are commercially important, so the ravages of these small crustacean parasites have economic repercussions.

Most of the work done along the South African coastline is largely due to the work of Basset-Smith (1898), Barnard (1948, 1955a, 1955b, 1957), Kensley (1970) and Kesley and Grindley (1973). Oldewage (1987) completed his Ph.D on *Ergasilus* and *Caligus* parasites found along the South African coastline. A synopsis of host- and distribution records of *Caligus* parasites found in South African coastal waters is given by the author of this thesis in chapter 4, which is a combination of all the work done by the above mentioned authors. As many of the research were done in the middle of the twentieth century, a new look will be given to the genus *Caligus*, as it is the most widespread and abundant parasitic copepod found.

The Aquatic Parasitology Research Group in the Department of Zoology and Entomology at the University of the Orange Free State has been involved in studying parasites and symbionts of aquatic organisms since 1980. Most of their research has been devoted to freshwater organisms, but also included studies on intertidal species. Currently, most freshwater research in the Group forms part of the Okavango Fish Parasite Project. Since 1994 the Foundation for Research Development (FRD), now referred to as the National Research Foundation (NRF), has been supporting their research project entitled: **Intertidal Symbionts of the South African coast**. This project falls within the realm of the Coastal Resources Program of the NRF. Within the context of this research program, one Ph.D. and five M.Sc. students have already completed their research on aspects of intertidal parasites and symbionts. Van As (1997) studied ciliophoran parasites of limpets (Patellogastropoda). The M.Sc. works are that of Botha (1994) who studied ciliophoran symbionts of *Oxystele* Philippi, 1847 species; Loubser (1994) studied the ciliophorans of intertidal fishes; Molatoli (1996) investigated the symbionts of red bait, *Puyra stolonifera* (Heller, 1878); Smit (1997) who studied gnathiid isopods of intertidal fishes and Botes (1999) who studied sessiline ciliophorans associated with *Haliotis* Linnaeus, 1758 species. Currently other projects within this program are also being carried out, i.e. on the myxosporideans, ciliophorans, isopods and caligid copepods of intertidal fishes, turban gastropods, polychaetes and echinoderms.

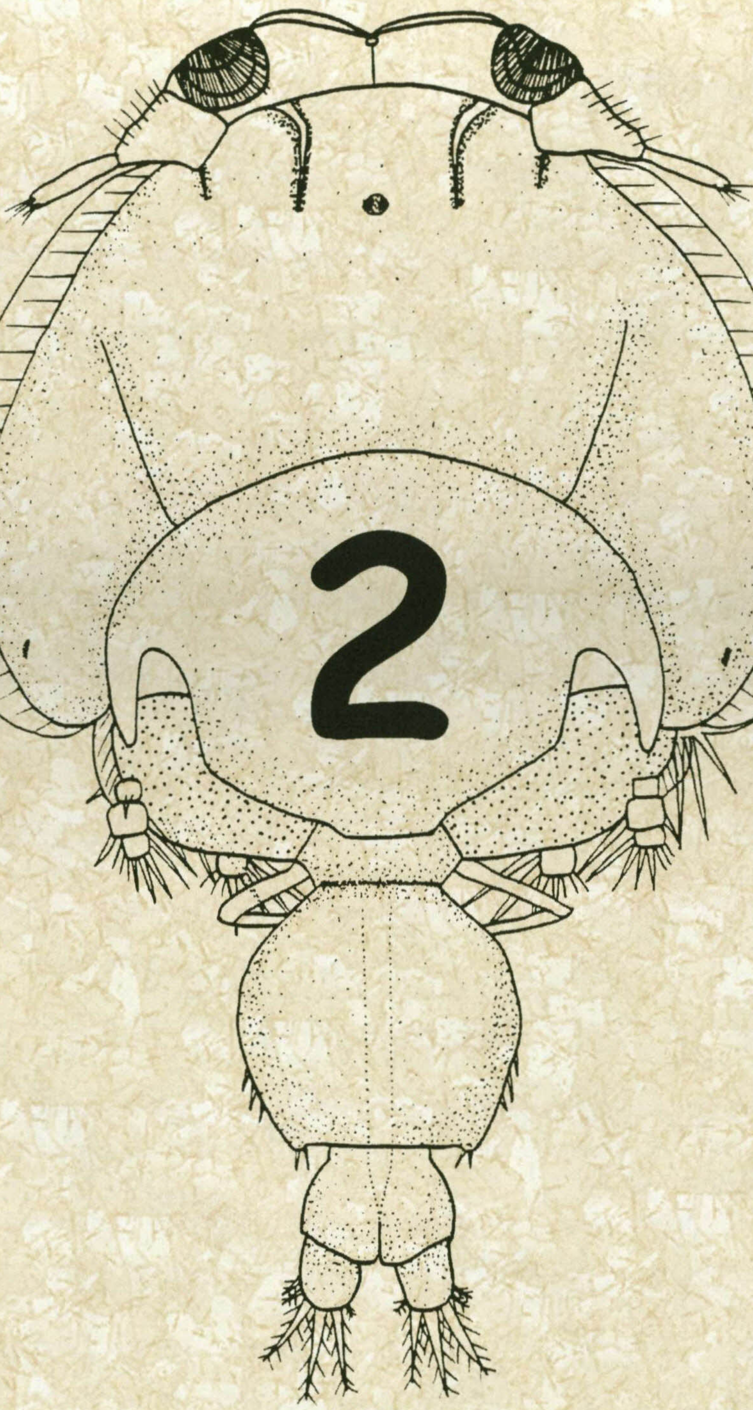
So far this program has led to the publication of our results in the form of **full length publications** (Basson & Van As 1992; Loubser, Van As & Basson 1995; Van As & Basson 1996; Van As, Basson & Van As 1998; Basson, Botha & Van As 1999; Smit, Van As & Basson 1999a; Smit & Davies, 1999; Van As, Van As & Basson 1999a); **congress proceedings** (Molatoli, Van As & Basson 1995; Van As, Van As & Basson 1995; Molatoli, Van As & Basson 1996; Smit, Van As & Basson 1996; Van As, Van As & Basson 1996a; Botes, Basson, & Van As 1997; Christison, Van As & Basson 1997; Grobler, Van As & Basson 1997; Van As, Basson & Van As 1997; Botes, Basson & Van As 1998; De Villiers, Van As & Van As 1998; Grobler, Van As & Basson 1998; Van As, Van As & Basson 1998; Smit, Van As & Basson 1998; Reed, Van As & Basson 1998; Botes, Basson & Van As 1999, Smit, Van As & Basson 1999b and Van As, Van As & Basson 1999b), as well as **extended abstracts** (Botha & Basson 1994; Loubser, Van As & Basson 1994; Van As & Basson 1994; Christison & Van As 1996; Molatoli & Basson 1996; Smit & Van As 1996; Van As, Van As & Basson 1996b).

This dissertation is based on the examination of data and material collected during fieldwork carried out at different localities during the last three years (1997-1999), especially at Lake St Lucia on the east coast, at De Hoop Nature Reserve and Jeffreys Bay on the south coast of South Africa. Material from Lake St Lucia include specimens that were collected during field trips in 1992, 1993 and 1994.

The present study was undertaken with the following specific objectives:

- to elucidate the morphology, ultrastructure and systematics of the different species of caligid copepods,
- to determine the diversity of caligid species along the South African coast,
- to investigate the basic life cycle of a caligid species, and
- to investigate the hypersymbionts associated with caligid species found in the Lake St Lucia system.

The dissertation layout is as follows: **Chapter 2** explains the material and methods used during field and laboratory work. The collection localities are described in detail as they form important ecological habitats for many a living organism. In **Chapter 3** the basic copepod morphology is first explained to give an overall understanding of the *Caligus* parasite morphology. **Chapter 4** deals with the species previously found along the South African coastline, followed by the comparative description of the species found in the present study. In **Chapter 5** the infestation statistics for the different fish host species are given. The basic life cycle of a *Caligus* species and the comparative description of chalimus IV of *Caligus acanthopagri* Lin, Ho & Chen, 1994, follow the statistical data. **Chapter 6** deals with hypersymbionts found on *Caligus* specimens. The ciliophorans are dealt with first, followed by the udonellids which are a very interesting hypersymbiont of caligids. The references, acknowledgements, abstract and appendix follow the hypersymbiont chapter.


2

Materials and Methods

Study Areas

The South African coastline and intertidal life are influenced by two major currents, i.e. the warm **Agulhas Current** along the east coast and the cold **Benguela** along the west coast. The Indian Ocean has a huge gyre of water circulating anticlockwise, driven by winds. This equatorial water mass splits when it reaches Madagascar, part moving around the island and down the coast of Mozambique, where it is known as the Mozambique current, while a second stream passes around the eastern side of Madagascar. The two currents unite again as they flow along the coast of Natal, forming an input into the Agulhas Current. This is the mightiest current bathing the South African coast, and brings warm water from the tropics to the east coast, with the result of a **warm subtropical east coast province**. As the Agulhas moves southwards its central core follows the edge of the continental shelf, where the relatively shallow coastal waters abruptly become deeper. The edge of the continental shelf swings away from the shore from Transkei southwards, deflecting the Agulhas current away from the coast. As a result, the **warm temperate south coast province**, from about Port St. Johns to Cape Point, has cooler coastal waters and a different set of animals and plants from that of the Natal and Mozambique coasts. Towards the south the Agulhas swings eastwards as the **Return Agulhas Current**, and unites with three smaller circuits known as the semi-basin, regional and Return Agulhas circulations (Branch & Branch 1995).

Under the influence of the currents described above, the southern African coastline is divided into four distinct **marine regions** as defined by Branch and Branch (1995):

West Coast: cold temperate waters, north of Walvis Bay to Cape Town;

South Coast: warm temperate waters, Cape Town to East London;

East Coast: subtropical waters, East London to north of Maputo and

East Coast: tropical waters, north of Maputo past Beira.

This study was, however, only conducted on the south and subtropical east coast. Coastal regions of the world can be divided into 16 marine zoogeographical provinces according to Wye (1991) of which the South African zoogeographical province extends from northern Namibia around the South African coast eastwards to southern Mozambique. In a global context the South African coast is regarded as a single zoogeographical marine province.

Lake St Lucia

As the meeting place of river and ocean, an estuary is a unique complex, driven by two major forces: **freshwater inflow** from the river's upstream reaches, and the **ebb and flow** of the ocean's tides, which together create a dynamic ecosystem. Estuarine salt marshes provide important nursery areas for almost 400 species of fish along a coast often lashed by violent storms. This essential refuge makes an important contribution to marine diversity: submerged grasses provide cover for juveniles during their vulnerable early life; adult fishes – marine migrants such as the grunter and stumpnose – search the sediment for invertebrates; garrick and elf, which are specialist predators, feed on the estuary's rich protein reserves. There are three groups of estuarine fishes, which may be classified according to their origin and salinity tolerance (Bruton & Cooper 1980). Firstly, the dominant group is the euryhaline marine fish which penetrate estuaries for distances that vary according to their salinity tolerances; they may be present as juveniles, for which the estuary acts as an essential nursery, or as adults seeking food; virtually all this group spawn in the sea. Secondly, there are a few species of euryhaline freshwater fish whose various salinity tolerances determine the degree to which they come into estuaries; and finally there is a small group of truly "estuarine" species which spend their whole life cycle in the estuary (Bruton & Cooper 1980).

Lake St Lucia (Figure 2.1, 2.2A), which receives the Mkuze, Hluhluwe, Nyalazi, Mzinene and Mpate rivers, forms the largest estuarine area in south-east Africa, occupying approximately 80% of the estuarine area of KwaZulu-Natal. It lies between latitudes 27°53'S and 28°25'S, is 300 km^2 in area and has a mean depth of only 1 meter. Lake St Lucia is subject to extreme long-term salinity fluctuations due to its shallow nature and irregular inflow of fresh water. The fresh water supply to the lake is derived from the rivers, from rainfall and from ground-water seepage along the eastern shores (Bruton & Cooper 1980).

Lake St Lucia supports a substantial subsistence fishing community and represents an important local source of income. The villagers harvest its resources with simple fishing baskets that are thrust to the bottom to trap the fish below. The practice has sustained these people for more than half a millennium. Gill nets are slowly replacing the ancient fishing methods, and thus more fish of different size are caught. Estuaries are always under threat because of various reasons. Siltation is the major threat, but urban sprawl in the catchment areas, dams, afforestation, alien invasive plants, agricultural run-off have all an adverse impact. UNESCO declared the St Lucia Lake system as a world heritage site in 1999, and conservation of this ecosystem must be upgraded before it is further degraded by human impact.

Jeffreys Bay and De Hoop Nature Reserve

The south coast of South Africa is famous for the rocky shores along the coastline. This unique ecological habitat is home to many invertebrates and vertebrates, especially intertidal fish species. Jeffreys Bay has a coastline consisting of sandy beaches as well as rocky shores (Figure 2.1). De Hoop Nature Reserve has a rocky shore coastline (Figure 2.1, 2.3A) and is famous for the many different invertebrate species found along this shoreline. As these areas have rocky shores, many intertidal pools are formed during the low tide. Many different fish species are trapped in these intertidal pools until the ebb tide release them to the open waters again. Many juvenile fish species (Figure 2.3B) are trapped in these pools, but adult fish species are also periodically entrapped in the intertidal pools.

Collection of fish hosts

The collection methods for the fish species varied according to their habitat preferences. Most of the fishes caught in Lake St Lucia were with the use of a series of gill nets (Figure 2.2B). These nets are 70 meters in length and consisted of graded mesh sizes. The minimum mesh size was 40 mm and the maximum 140 mm (40 mm, 70 mm, 90 mm, 100 mm, 110 mm, 120 mm & 140 mm). These nets were set at dusk, left overnight and lifted the following morning at sunrise. Using a fishing rod (Figure 2.2C) was particularly effective for collecting species like kingfish and garrick.

The collection of intertidal fish species was quite different than those used at Lake St Lucia. The use of gill nets in intertidal pools are non-effective, and you usually end up with torn nets and no fish at all. In deep intertidal pools, commonly found at the De Hoop Nature Reserve, cast nets (Figure 2.3C) and hand lines (Figure 2.3D) were used effectively during low tides. Great care was taken not to stress captured fish as the caligids tend to leave a stressed host that could result in inaccurate infestation data. As caligids were found on klipfish, each klipfish caught was placed in a plastic bag and sealed. After fish were examined, the water in the plastic bag was poured through a fine mesh to collect all the caligids that have left the host, and made it possible for more accurate infestation data. Fish were collected during a number of field excursions to De Hoop Nature Reserve (April 1997, 1998 & 1999), Jeffreys Bay (February 1997, 1998 & 1999) and Lake St Lucia (January, February 1996, 1997 & 1998).

Permits for collection and examination of fish were obtained prior to each survey from **Cape Nature Conservation** (Appendix 1, 2 & 3). Permits for collection and examination of fish at Lake St Lucia are in the possession of the Department of Zoology and Biology of the University of the North.

Examination of fish hosts

After collection, the fishes were taken to a field laboratory where they were examined (Figure 2.2D). Captured fish were placed in an aquarium filled with fresh sea water which was continuously aerated. The plastic bags in which the klipfish was held were each aerated separately. The collected fish were anaesthetised by using benzocaine (ethyl-4-aminobenzoate) and examined under a dissection microscope. Fish were identified using Smith and Heemstra (1986) and Branch, Griffiths, Branch and Beckley (1994). They were measured and examined for caligid copepods. Since the project forms part of a comprehensive program, a complete autopsy was carried out by other members of the study group in search of a variety of other parasites which included monogeneans, protozoans, myxosporideans, nematodes, acanthocephalans and trematodes, as well as parasitic crustaceans belonging to other families.

Caligids were carefully remove from the dead fish with the aid of a No. 270 soft hair brush. Collected specimens were fixed in 70% ethanol and supplied with a collection number. Hypersymbionts were simultaneously fixed with the caligids. Two different collection numbers were used for the east coast and the west coast. The collection number for the east coast is as follows: **field trip number / number of fish caught**. Specimen collection numbers from St Lucia are collective data numbers of the University of the North, as they collected most of the specimens from Lake St Lucia. For example 17 / 05 refers to the 17th fieldtrip and the fifth fish that was caught. The collection number for the south coast is as follows: **Year / Month / Day – collection number**. Data from Jeffreys Bay and De Hoop Nature Reserve were collected by the author and these specimen collection numbers represent only fish host collections, and was thus not part of the collections by the University of the North. All the specimens collected and studied in this dissertation are stored in the parasite collection of the Aquatic Parasitology Research Group of the University of the Free State.

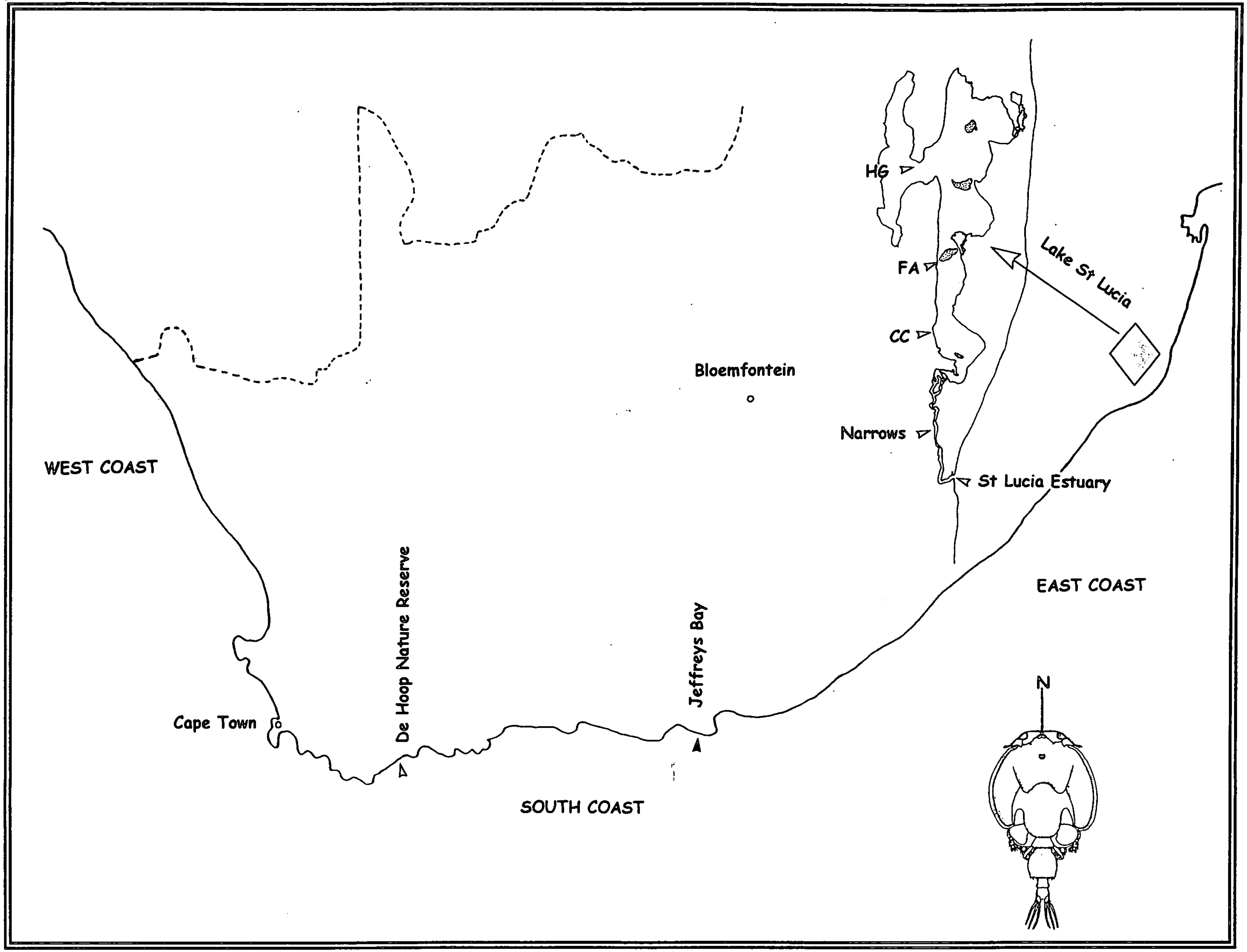
Figure 2.1

Map of southern Africa showing the collection localities of the De Hoop Nature Reserve, Jeffreys Bay and Lake St Lucia System (indicated by arrows) along the South African coastline.

HG= Hell`s Gate

FA= Fanies Island

CC= Charters Creek



HG
FA
CC
Lake St Lucia
Bloemfontein
Narrows
St Lucia Estuary
WEST COAST
EAST COAST
De Hoop Nature Reserve
Jeffreys Bay
Cape Town
SOUTH COAST
N

Figure 2.2

Photographs of the collection localities and collection methods used at Lake St Lucia on the east coast of South Africa.

A. View of Lake St Lucia

B. Setting out of gill nets by boat

C. Fishes caught with fishing rods

D. Examination of fish hosts at field laboratory

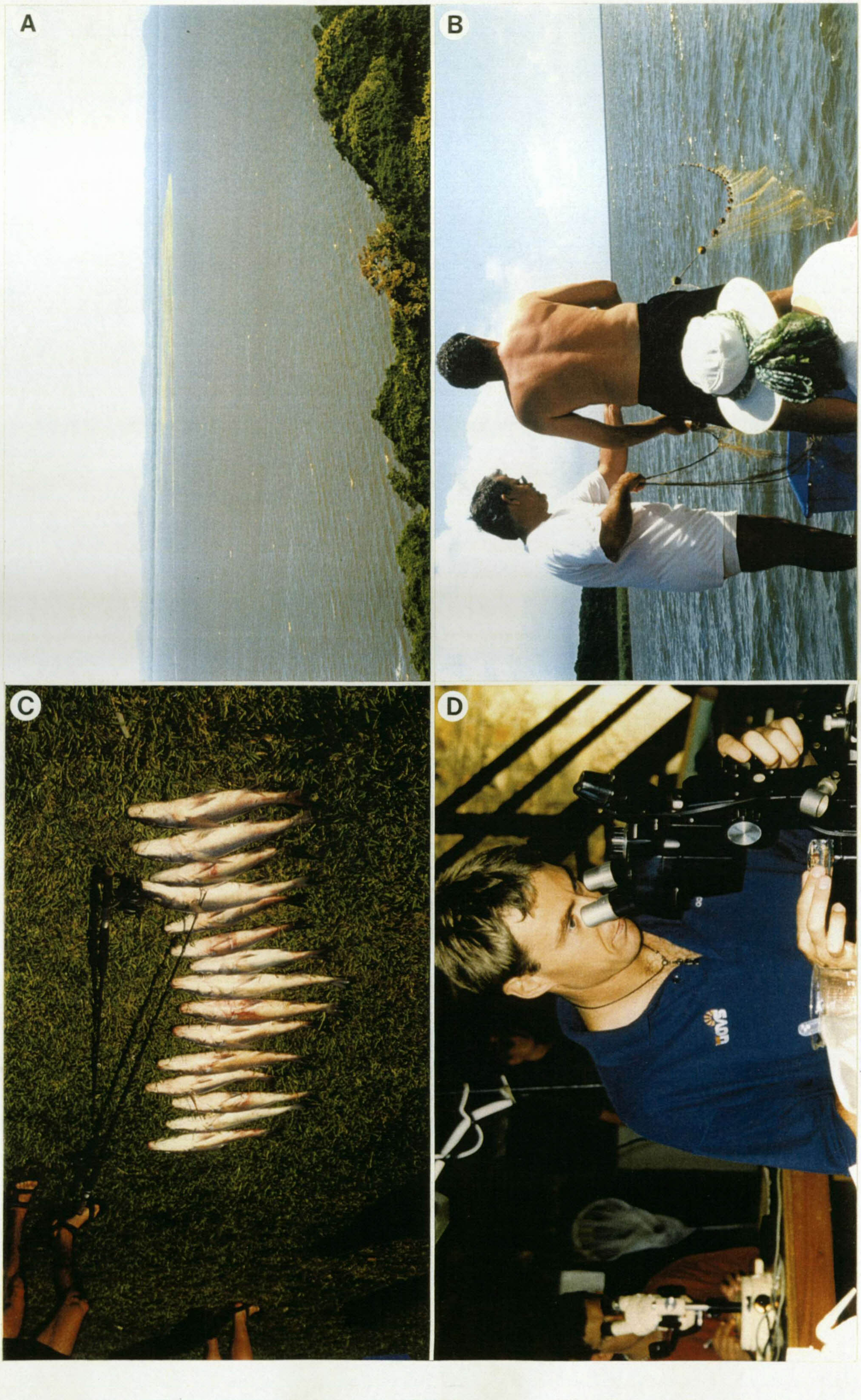

A
B
C
D

Figure 2.3

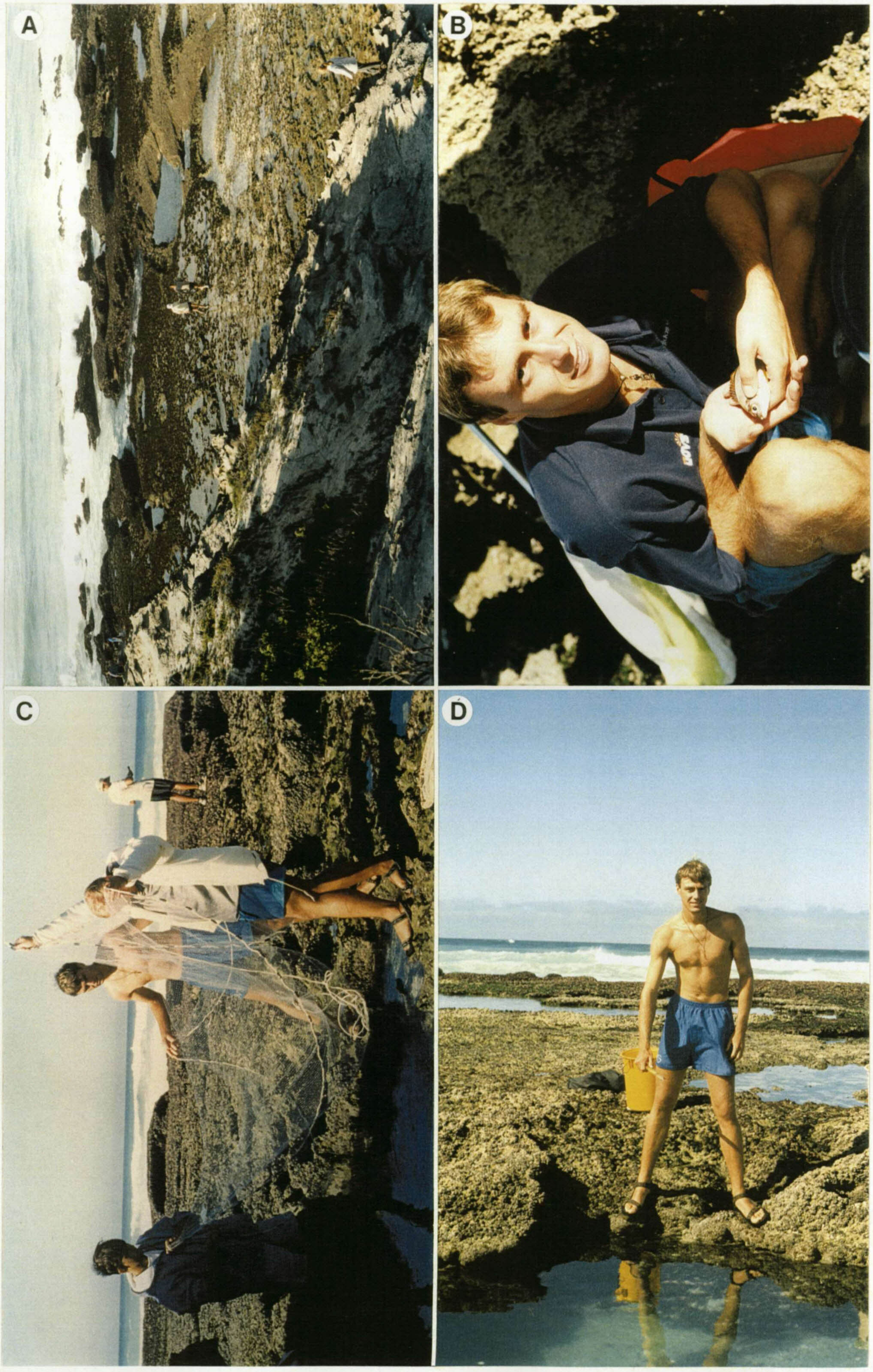
Photographs of the collection localities and collection methods used at De Hoop Nature Reserve and Jeffreys Bay on the south coast of South Africa.

A. Rocky shore line at De Hoop Nature Reserve

B. Juvenile fish caught in intertidal pools

C. Casting net used for collection of fish species in intertidal pools

D. Use of hand lines in deep intertidal pools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Preparation of material for scanning electron microscopy (SEM)

In the laboratory in Bloemfontein the fixed specimens were hydrated from 70% ethanol to fresh water. The caligid copepods were washed for one day in fresh water in order to get rid of salt crystals and debris. After washing, the specimens were again cleaned using the soft hair brush to remove any excess debris. Specimens were then placed in a phosphate buffer (Table 2.1) to remove any excess mucous and debris, without damaging the tegument. Clean specimens were dehydrated through a series of graded ethanol concentrations as follows:

fresh water
30% ethanol – 20 minutes
50% ethanol – 20 minutes
70% ethanol – 20 minutes
80% ethanol – 20 minutes
90% ethanol – 20 minutes
96% ethanol – 20 minutes
and 100% ethanol – 40 minutes, renewing each concentration every ten minutes.

Thereafter the specimens were cleaned for the final time using the soft hair brush. Specimens were critical point dried and mounted on conical stubs specially made by the Department of Instrumentation of the Faculty of Natural Sciences. The aim of this particular design was to enable a tilt of the SEM stage of almost 90°, thereby ensuring an even black background on the micrographs.

Specimens were mounted on the stubs using commercial brand Japan Gold Size (Winsor and Newton), a rapid-drying varnish normally used in gilding. The varnish gives a very smooth background if micrographs need to be taken with the conical stub in picture. Specimens were sputter coated with gold and studied with the aid of a JEOL WinSEM JSM 6400 scanning electron microscope at 10 kV with the stage tilted at 70° to 90°.

Micrographs were taken with the aid of 50 ASA Ilford Pan F films. All electron microscope preparations, operation of the SEM, as well as all darkroom work was done by the author.

Table 2.1 Recipe formula for phosphate buffer

PHOSPHATE BUFFER

Solution A

$Na_2HPO_4.12H_2O$	35.814 g/l
or Na_2HPO_4	14.19 g/l

Solution B

KH_2PO_4	13.610 g/l

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

Light microscopy

A technique described by Humes and Gooding (1964) for the examining of small crustaceans was used for the species comparative descriptions. Caligid specimens were placed in lactic acid for at least 24 hours. Lactic acid is a clearing agent for the preparation of temporary mounts of whole or dissected copepods. Fresh or ethanol fixed specimens became clear within a few minutes to some hours, depending upon their size and the duration of preservation. When first placed in the undiluted acid, the copepods may become somewhat contracted, but soon regain, and thereafter retain, their normal size and shape.

Lactic acid renders the cuticle more supple than it is in most preservatives and thus more favourable for dissection, since setae, etc., are less easily broken off and lost. The refractive index of lactic acid is particularly suitable for study of fine detail. A very small quantity of lignin pink is dissolved in the lactic acid, for fine structures are more easily seen when it is stained with lignin pink. The fine structure of setae is easily seen under the compound microscope, and even very small hair is easily seen with the aid of lignin pink.

In a wooden slide (of a soft, smooth-grained wood) measuring 75 X 25 mm (the dimensions of a standard microscope slide) and 1.5 mm in thickness, a centered hole 15 mm in diameter is bored (Figure 2.4). Using a metal stamp 22 mm in diameter, a depression is made on one surface of the slide (Figure 2.4), forming a shelf 3.5 mm wide around the hole. A cover glass of No. 1 thickness is glued with nail polish to hold the cover glass in place. With the slide upside down, the specimen is placed in a small drop of lactic acid on the exposed surface of the cover glass. The specimen may then be examined under the compound microscope by inverting the slide. Dissection of appendages was made with the aid of minute needles, and drawn with the aid of a drawing tube connected to the compound microscope.

One of the major advantages of this open-mount technique is that a single specimen can usually provide a full set of observations, since dissection can be stopped at any point and the results examined and/or drawn under the compound microscope, even with oil immersion lens. Another useful feature is that the caligids and their dissected parts suffer little or no compression, since they are hanging in a drop of fluid. Thus, more accurate views result.

Morphological measurements

The total lengths of all the caligids were obtained from microscope projection drawings. In both the females and males the total length was measured from the frontal border of the frontal plate to the posterior border of the caudal rami, excluding the setae on the caudal rami (Figure 2.5). In Chapter 4 the mean length of the specimen is given, followed by the minimum and maximum values of specimens measured.

Museum material

In order to do a redescription of caligid species from southern Africa, type material was obtained by courtesy of Ms. Michelle van der Merwe from the South African Museum. The only type species that the author could acquire was that of *Caligus engraulidis* Barnard, 1948. The SAM number of the type species is A 8520. Unfortunately the specimen in the holder was disintegrated and brought under the attention of Ms. van der Merwe. No comparison could be made with the material that was collected by Barnard (1948).

Infestation statistics

Infestation statistics for the different species collected along the South African coast are presented in Chapter 5. These include prevalence, intensity and mean intensity defined below according to Margolis, Esch, Holmes, Kuris and Schad (1982).

Prevalence: Number of individuals of a host species infested with a particular species divided by the number of host examined. Usually expressed as a percentage.

Intensity: Number of individuals of a particular parasite species on each infested host in a sample. Frequently expressed as a numerical range.

Mean intensity: Mean number of individuals of a particular parasite species per infested host species in a sample.

Studying of *Caligus* larval stages

A few developmental stages of *Caligus acanthopagri* Lin, Ho & Chen, 1994 were found attached to the hosts mentioned in Chapter 5. Most of the developmental stages examined were in bad shape and no comparative descriptions could be made. Only one chalimus III stage were thus prepared for SEM study. The comparative description of chalimus III differs from the species descriptions in Chapter 4, and is based only on SEM detail. All the morphological characters could thus not be drawn and the description of chalimus III will not be a complete larval description.

Studying of hypersymbionts

All the hypersymbionts were found attached to the caligids. None of the hypersymbionts were removed from their hosts, and they were prepared for scanning electron microscopy as described earlier in the chapter. No live material could be examined, as the author did not know about the hypersymbionts until it was seen on the SEM micrographs. As the SEM micrographs do not give any internal structural detail, comparative descriptions of the hypersymbionts are made with the use of the detail on the SEM micrographs.

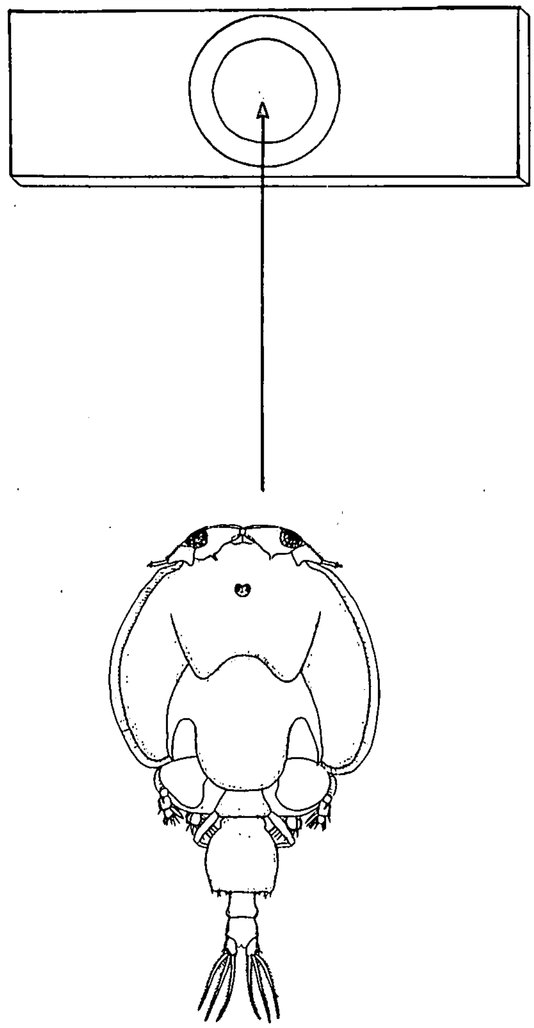


Figure 2.4 Diagram illustrating the wooden slide used for the dissection and drawing of appendages of caligid copepods.

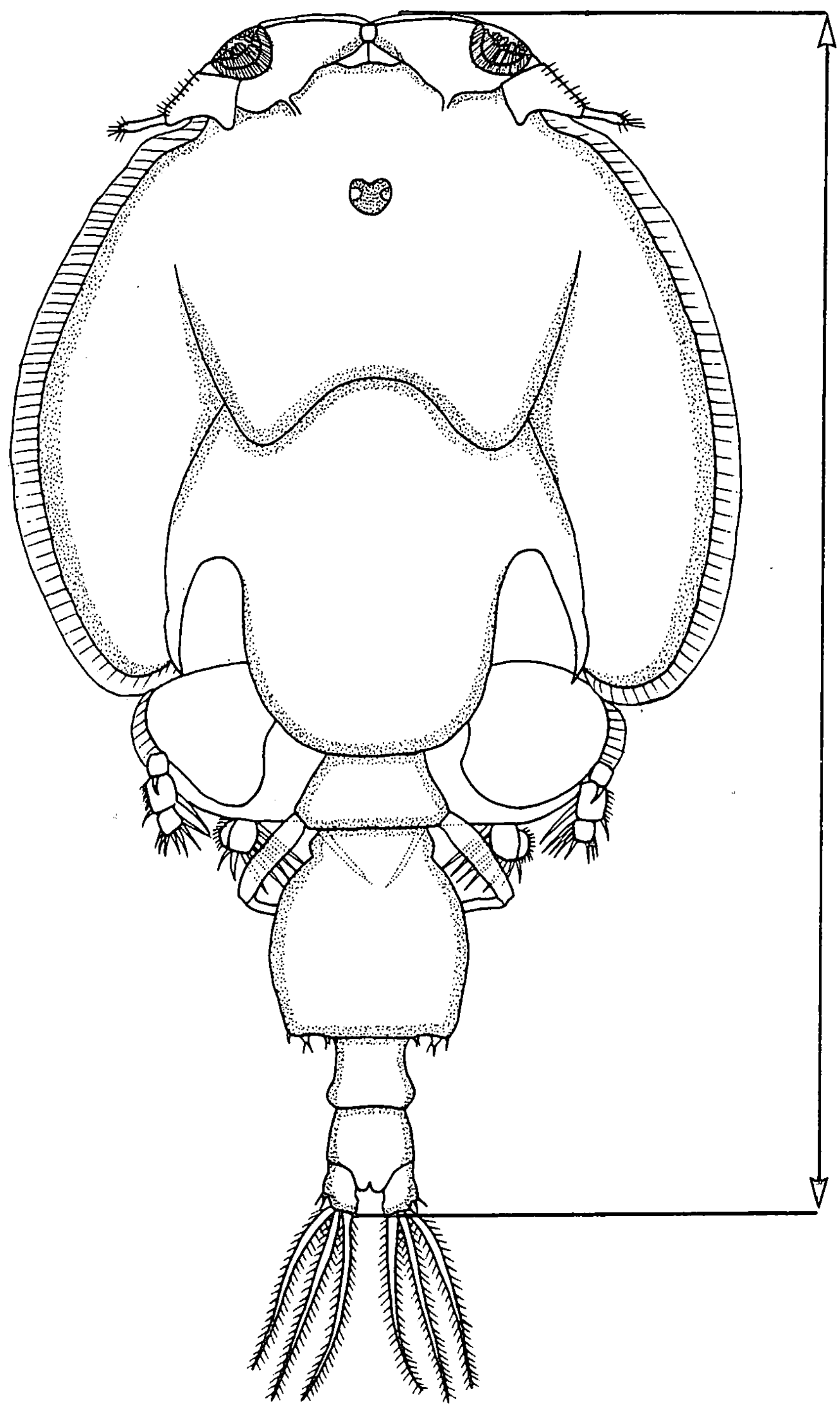
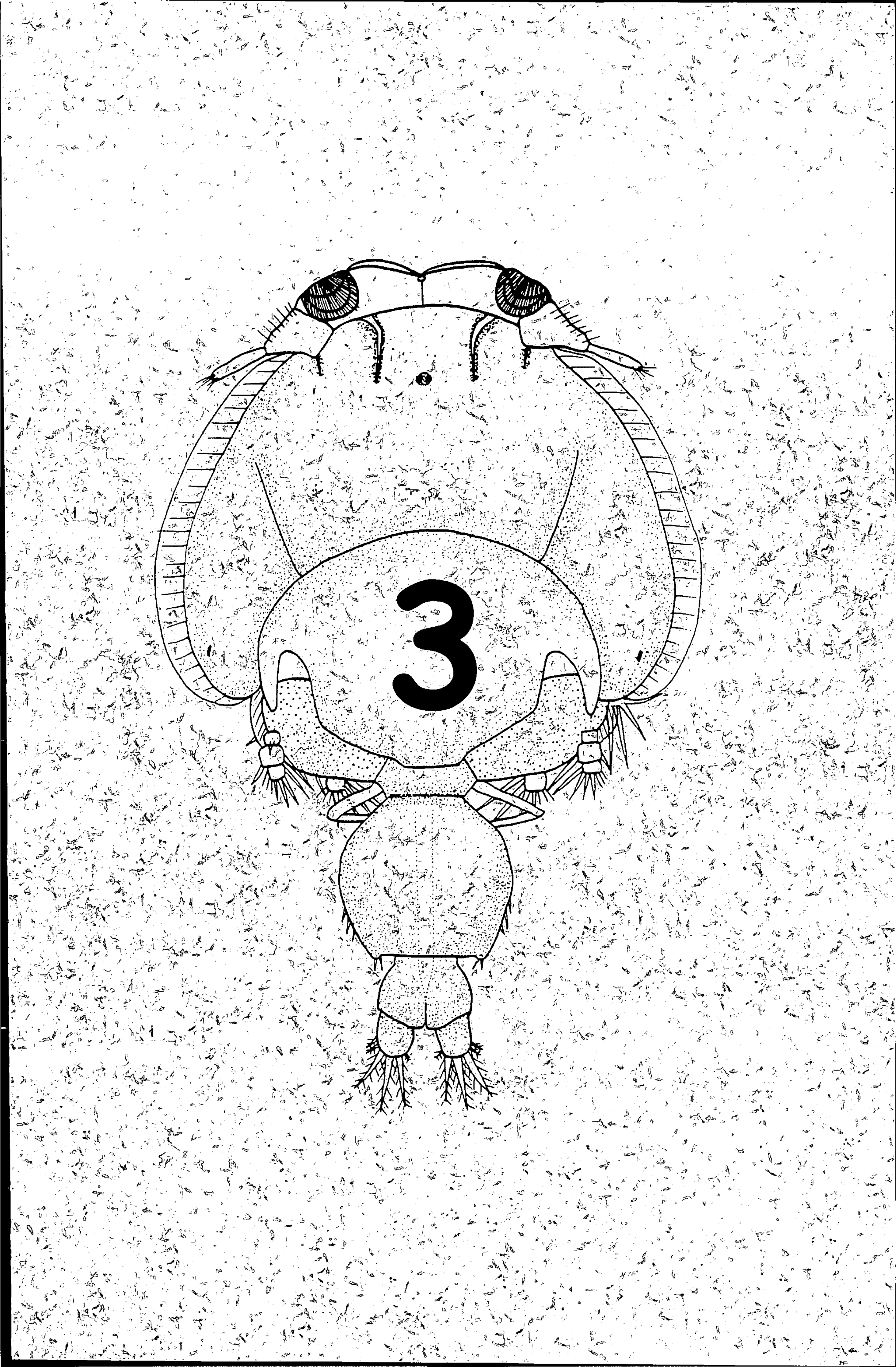


Figure 2.5 Diagram illustrating the morphological measurements (body length) used in the comparative descriptions of the caligid copepods.


3

The Genus *Caligus* Müller, 1785

Copepods are so diverse that it is difficult to select a typical representative to serve as an introduction to the group as a whole. Presenting the basic copepod appendages will give a more accurate impression of copepod morphology. There is no standard terminology that is in universal use for all copepods. Specialists working in the three major fields of copepod research (on the planktonic, the meiofauna, or the parasites) tend to have their own terminology, adapted to fit the particular taxa involved (Huys & Boxshall 1991). The basic copepod appendages described below are composites, showing the fundamental components of each.

The idea is to illustrate the basic plesiomorphic copepod morphology and the morphology of *Caligus curtus* Müller, 1785 and thus illustrate the transformation from a basic free-living copepod to a well-adapted parasitic copepod. To appreciate the extent of changes in the morphology of copepods by their adaptation to a life of dependence on other animals, one should become acquainted with a free-living copepod. An example of such a copepod is probably best represented among the cyclopoids, copepods that could be morphologically not too dissimilar from the presumptive ancestors of some present-day parasitic forms. The basic copepod morphology will be explained first, followed by the morphology of the type species *Caligus curtus*. The transformation of a plesiomorphic copepod to an apomorphic copepod will be explained by drawings of appendages of both the basic copepod and *Caligus curtus*. The history of *C. curtus* does not include a great deal of confusion and a full historical review of the species was given by Parker, Kabata, Margolis & Dean (1968). The male of *Caligus curtus* is illustrated in Figure 3.1 and the female is illustrated in Figure 3.2.

Antennule (First antenna)

The female and male antennule is illustrated in Figure 3.3A. The female antennule is uniramous and 28-segmented. The antennule of the male is similar to that of the female except that it is geniculate at a position corresponding to the articulation between segments 20 to 21 of the female (Huys & Boxshall 1991). In male copepods there are always some segmental fusions associated with the geniculation mechanism, for example segments 21 to 23 denotes a triple segment fusion, giving the male only 25 segments.

Antennule of *Caligus curtus* is two-segmented (Figure 3.3B). Proximal segment is much broader than the distal segment and carries 26 setae on the anterior margin. Distal segment is rod-shaped and carries 13 terminal setae and one aesthete. Most of the segments present in the free-living cyclopoids have fused together and only two segments remained in *C. curtus*. The setae are still present, but in different numbers and shape, as all setae are plumose (Parker *et al.* 1968).

Antenna (Second antenna)

The antenna (Figure 3.4A) is biramous, consisting of a coxa and basis, a ten-segmented exopod and a four-segmented endopod (Huys & Boxshall 1991). In the majority of copepods the fourth segment is completely incorporated into the third segment. The coxa bears a single medial seta and the basis bears two medial setae. Exopodal segments one to nine carries a seta on the inner margin, the tenth segment has three apical setae. This corresponds to a setal formula of 1,1,1,1,1,1,1,1,1,3 which is always given in sequence from proximal to distal. The first endopodal segment has two setae, the second segment nine, the third segment five and the fourth segment two. The tiny fourth segment is incompletely fused to the third segment in some calanoids and the setal formula is given as 2,9,5+2. In the majority of copepods the fourth segment is completely incorporated into the third segment and the setal formula is given as 2,9,7.

Antenna of *C. curtus* is three-segmented (Figure 3.4B). Proximal segment smallest with pointed posterolateral corner. Second segment largest and robust. Terminal segment a strongly curved hook, bearing one basal seta and one marginal seta. Antenna of the male is more robust, claw with two sharp, short tines diverging from base and with short, robust seta. One large and one small corrugated patch or adhesion pad are present on the second segment. The antenna bears no other setae as is present in the free-living cyclopoids (Parker *et al.* 1968).

Mandible

The mandible (Figure 3.5A) consists of a coxa bearing a large medially directed gnathobase, plus a biramous mandibular palp comprising the basis bearing a five-segmented exopod and two-segmented endopod. The coxal gnathobase bears teeth along its distomedial margin and two dorsal setae (Huys & Boxshall 1991). The basis bears four medial setae. Exopodal segments one to four bear a seta on the inner margin, the fifth segment has two setae. This corresponds to a setal formula of 1,1,1,1,2 which is given from proximal to distal. The first endopodal segment has six setae, the second segment has 11 setae, corresponding to a setal formula of 6,11.

Mandible of *C. curtus* is four-segmented (Figure 3.5B1). Twelve blunt, posteriorly curving teeth are present on the terminal segment (Figure 3.5B2). The mandible bears no other setae as is present in the free-living cyclopoids (Parker *et al.* 1968).

Maxillule (First maxilla)

The maxillule (Figure 3.6A) is biramous and has a three-segmented protopod consisting of praecoxa, coxa and basis (Huys & Boxshall 1991). The coxa bears a single elongate endite armed with six setae and a well-developed outer lobe, the epipodite, carrying nine setae. The basis bears two endites, the proximal is well developed and has four apical setae, the distal is largely incorporated into the segment and carries five setae. The basis also has an outer lobe, the exite, bearing two setae. The exopod is one-segmented and is armed with 11 marginal setae. The endopod is three-segmented, the first segment bears six setae, the second segment four and the third segment seven, corresponding to a setal formula of 6,4,7.

Maxillule of *C. curtus* is dentiferous (Figure 3.6B) with a broad base. The base is abruptly tapering to short, tender tip. Basal papillae are present and are represented by one long and two shorter setae. The maxillule bears no other setae as is present in the free-living cyclopoids (Parker *et al.* 1968).

Maxilla (Second maxilla)

The maxilla (Figure 3.7A) is uniramous and seven-segmented, consisting of a praecoxa, coxa, basis and four-segmented endopod (Huys & Boxshall 1991). The praecoxa has two endites, the proximal bearing ten setae and the distal three setae. The coxa has two endites, each with three setae. The setal formula of the praecoxal and coxal endites is given as 10,3,3,3. An outer seta is present on the coxa and probably represents the epipodite. The basis bears a single endite armed with four setae. The first endopodal segment bears four setae, the second three, the third two and the fourth four. This corresponds to a setal formula of 4,3,2,4.

Maxilla of *C. curtus* is two-segmented and brachiform (Figure 3.7B1). Lacertus is unarmed, brachium longer and more slender than lacertus, with well-developed flabellum. Brachium (Figure 3.7B2) terminates into two elements, the calamus and canna. The calamus is much longer than canna. The maxilla bears no other setae as is present in the free-living cyclopoids (Parker *et al.* 1968).

Maxilliped

The maxilliped (Figure 3.8A) is uniramous and nine-segmented, consisting of praecoxa, coxa, basis and six-segmented endopod (Huys & Boxshall 1991). The praecoxa has a single endite bearing one seta. The coxa has three endites, the proximal bearing two setae, the middle and distal four setae each. The corresponding setal formula for the praecoxal and coxal endites is 1,2,4,4. An outer seta is present on the coxa and probably represents the epipodite. The basis has three setae on its medial margin. The first endopodal segment bears two inner setae, the second and third segment each have four inner setae, the fourth has three setae on the inner margin with the fifth bearing three setae on the inner margin plus one seta on the outer margin. The sixth segment has five setae. The setal formula 2,4,4,3,3+1,5 give the endopodal setation pattern.

Maxilliped of female of *C. curtus* is three-segmented with long, slender corpus (Figure 3.8B1). Shaft robust and slightly curving. Claw curving and with barbel at base. Maxilliped of male (Figure 3.8B2) is much more robust than female. Corpus much broader, with two large pointed processes on medial margin (Parker *et al.* 1968). Shaft and claw as in female. The maxilliped bears no other setae as is present in the free-living cyclopoids.

Swimming legs

In the spine and seta formula for the swimming legs devised by Sewell (1949) spines are denoted by Roman numerals and setae by Arabic numerals. The element or elements on the outer margin of any segment are given first, separated by a hyphen from the inner margin element or elements. The armature on the terminal segment of each ramus has three components separated by commas and is given in the sequence: outer margin, distal margin, inner margin. The armature formulae of the segments within a ramus are separated by semicolons (Huys & Boxshall 1991).

Another aspect is the differentiation of a seta and spine. The best way to distinguish between a seta and spine is to use the definition by Watling (1989). A **seta** is an articulated cuticular extension of virtually any shape or size and may vary from very small (10-20μm) to very large (more than 1mm in length). It is robust and often with a very wide base. A seta does not always have an apical pore, nor does it always have an annulus (a faint ring circumscribing the shaft). A **spine** is a non-articulated cuticular extension that has a base that is generally not as wide as the structure is long. Regardless of its size and shape, a spine has no socket.

The basic copepod swimming leg (Figure 3.9A) consists of a well developed coxa and basis, with the latter bearing two three-segmented rami (Huys & Boxshall 1991). The coxa bears an inner seta. The basis bears an inner and an outer seta. The first exopodal segment carries one (leg 1) or two (legs 2 to 5) outer spines and an inner seta. The second segment carries one outer spine and one inner seta. The third exopodal segment is armed with three spines on the outer margin, a terminal spine and either four (legs 1 and 5) or five (legs 2 to 4) setae on the inner margin. The first endopodal segment has a single seta on the inner margin. The second has two inner setae in legs 1 to 4, only one seta in leg 5. The third endopodal segment has one setae (leg 1) or two setae (legs 2 to 5) on the outer margin, two on the distal margin and two (leg 5), three (legs 1 and 4) or four (legs 2 and 3) setae on the inner margin. This setation pattern corresponds to the following spine and seta formula:

	coxa	basis	exopod segment 1 2 3	endopod segment 1 2 3
leg 1	0 – 1	1 – I	I – 1; I – 1; III,I,4	0 – 1; 0 – 2; 1,2,3
leg 2	0 – 1	1 – 1	II – 1; I – 1; III,I,5	0 – 1; 0 – 2; 2,2,4
leg 3	0 – 1	1 – 1	II – 1; I – 1; III,I,5	0 – 1; 0 – 2; 2,2,4
leg 4	0 – 1	1 – 1	II – 1; I – 1; III,I,5	0 – 1; 0 – 2; 2,2,3
leg 5	0 – 1	1 – 1	II – 1; I – 1; III,I,4	0 – 1; 0 – 1; 2,2,2

Caligus curtus have four well-developed legs in both the female and male. Fifth legs (female and male) and sixth legs (male) are vestigial or rudimentary. **Leg 1** (Figure 3.9B) with vestigial endopod. Second segment of exopod with terminal setae 1-3 of about equal length, with rows of fine denticles along parts of one margin and some across tips. Seta 4 longer and more slender, unarmed. Three long pinnate setae on posterior margin of distal segment. **Leg 2** (Figure 3.10A) endopod with fringe of fine setules on all three segments on lateral margin. First segment with one seta, second segment with two setae and third segment with six setae. Exopod is three-segmented. First segment with outer spine and inner seta. Second segment with short outer spine and long inner seta. Third segment with three outer spines of different length, and five setae of different length. **Leg 3** (Figure 3.10B) endopod is two-segmented. First segment with one inner seta. Second segment with three setae of different length and three spines of different length. Exopod one-segmented with four setae of same size and three spines of different size. Adhesive pad on ventrolateral surface. **Leg 4** (Figure 3.11A) with robust sympod and two-segmented exopod. Distal segment of exopod with three setae, all with basal pectens. Seta 1 much longer than other two, with single row of denticles, seta 2 slightly longer than seta 3, both with two rows of serrated membranes. Seta of proximal segment similar to short setae of distal segment. Border between two segments of exopod often indistinct. **Leg 5** (male and female) vestigial, consisting of two small papillae surmounted by short pinnate setules, two and one respectively. **Leg 6** (male) almost completely reduced, on tip of inner posterolateral lobe (Parker *et al.* 1968).

Sternal furca (Figure 3.11B) with rectangular, long base and divergent tines. Tines are shorter than base, blunt and devoid of flanges (Parker *et al.* 1968).

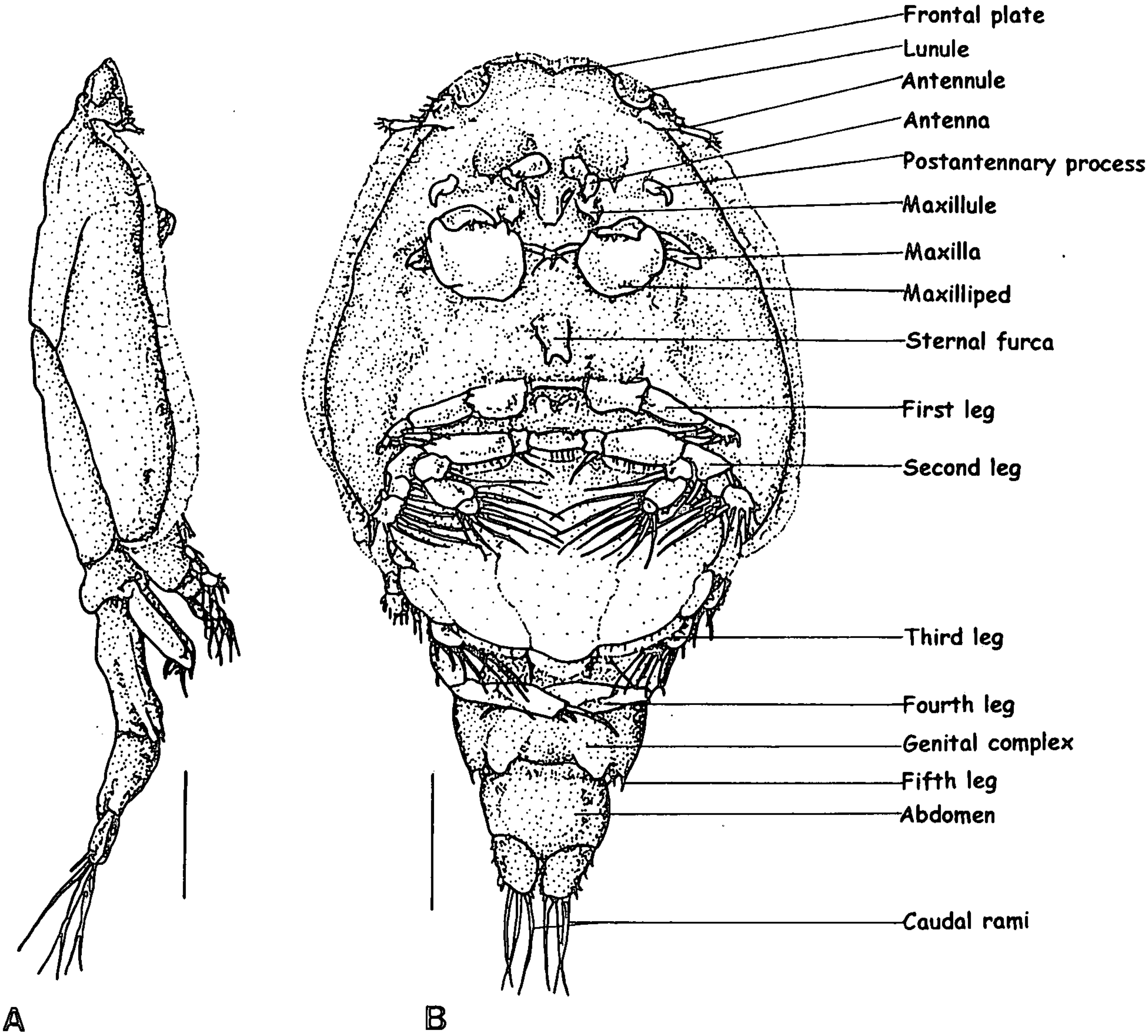


Figure 3.1 Diagram illustrating the morphological features of an adult *Caligus curtus* Müller, 1785 male, redrawn from Kabata (1979)

A – lateral, B – ventral

Scale-bar: A & B – 2mm

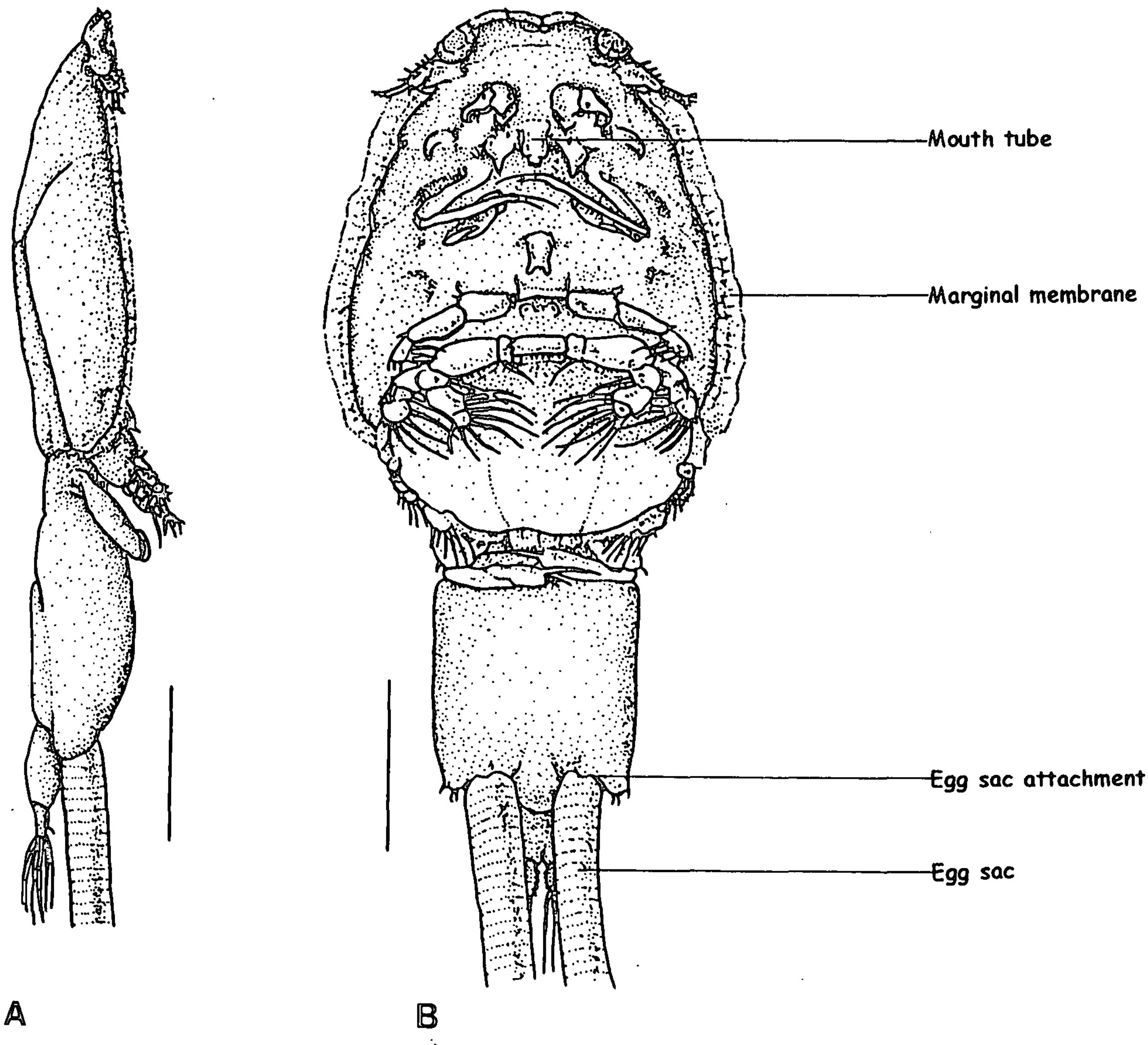


Figure 3.2 Diagram illustrating the morphological features of an adult *Caligus curtus* Müller, 1785 female, redrawn from Kabata (1979)

A – lateral, B – ventral

Scale-bar: A & B – 2mm

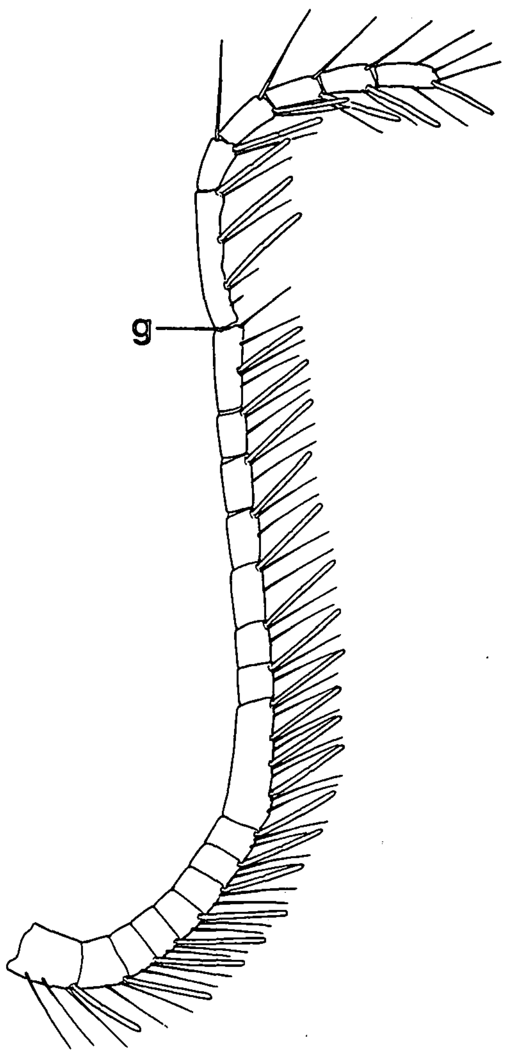
Figure 3.3

Diagram illustrating the differences between the basic copepod antennule and the antennule of *Caligus curtus* Müller, 1785

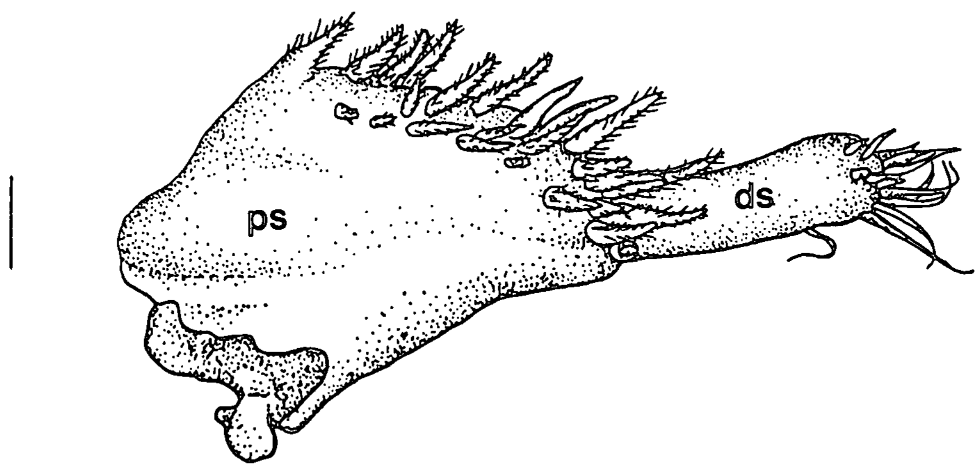
A. Basic copepod antennule, redrawn from Huys & Boxshall (1991)
g – geniculation

B. Antennule, redrawn from Kabata (1979)
ds – distal segment
ps – proximal segment

Scale-bar: 100μm



A



B

Figure 3.4

Diagram illustrating the differences between the basic copepod antenna and the antenna of *Caligus curtus* Müller, 1785

A. Basic copepod antenna, redrawn from Huys & Boxshall (1991)

c – coxa

b – basis

ex – exopod

en – endopod

B. Antenna, redrawn from Kabata (1979), showing the male (B1) and female (B2) antenna

ps – proximal segment

ms – middle segment

ts – terminal segment

Scale-bar: 100μm

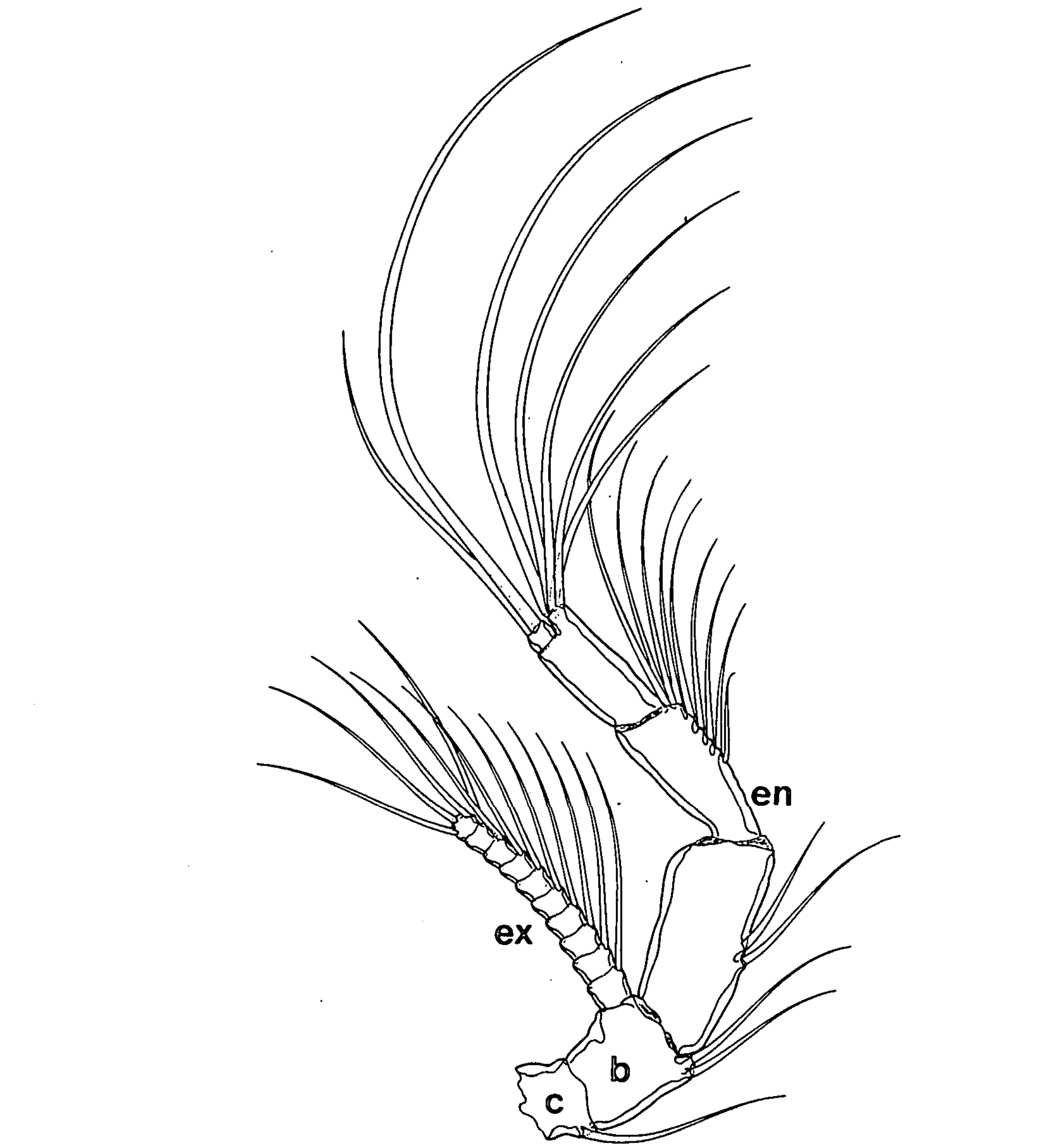

en
ex
b
c
A
ts
ms
ps
B1
B2

Figure 3.5

Diagram illustrating the differences between the basic copepod mandible and the mandible of *Caligus curtus* Müller, 1785

A. Basic copepod mandible, redrawn from Huys & Boxshall (1991)

g – gnathobase

c – coxa

b – basis

ex – exopod

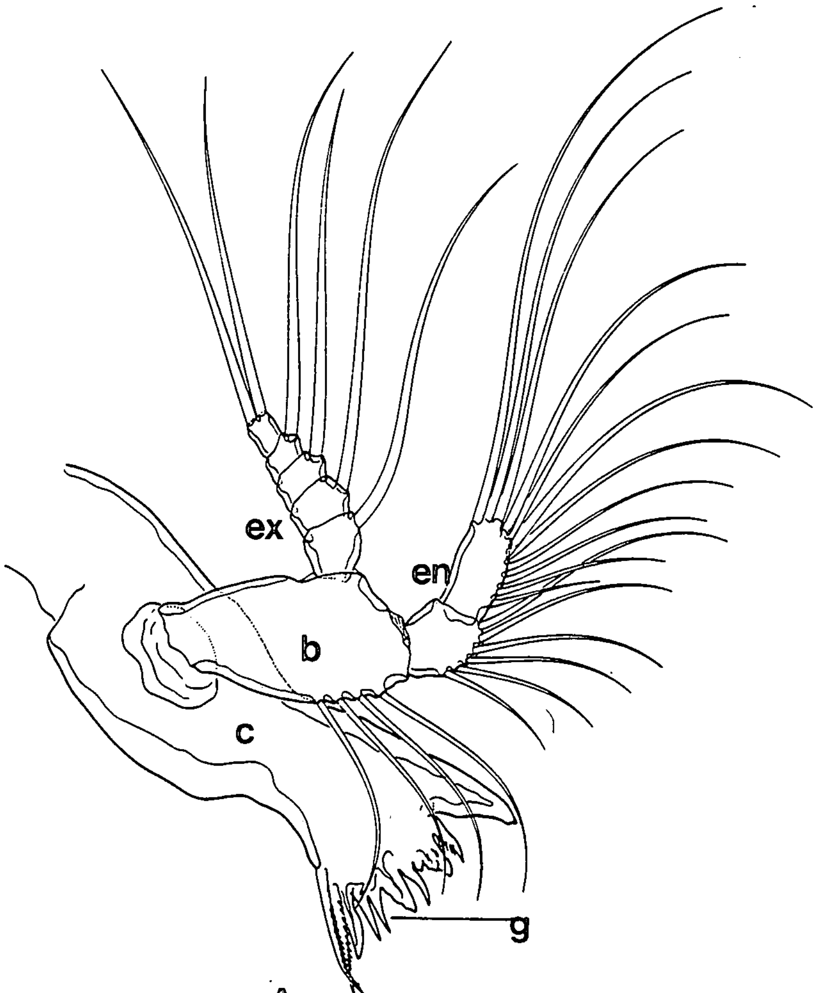
en – endopod

B. Mandible, redrawn from Kabata (1979), showing the mandible lateral (B1) and the blade-like tip (B2)

bl – blade-like tip

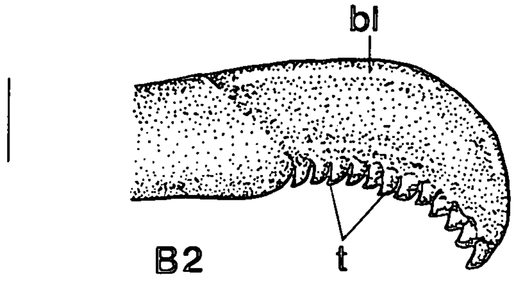
t – teeth

Scale-bar: 100µm



A

B1



B2

Figure 3.6

Diagram illustrating the differences between the basic copepod maxillule and the maxillule of *Caligus curtus* Müller, 1785

A. Basic copepod maxillule, redrawn from Huys & Boxshall (1991)

pc – praecoxa

c – coxa

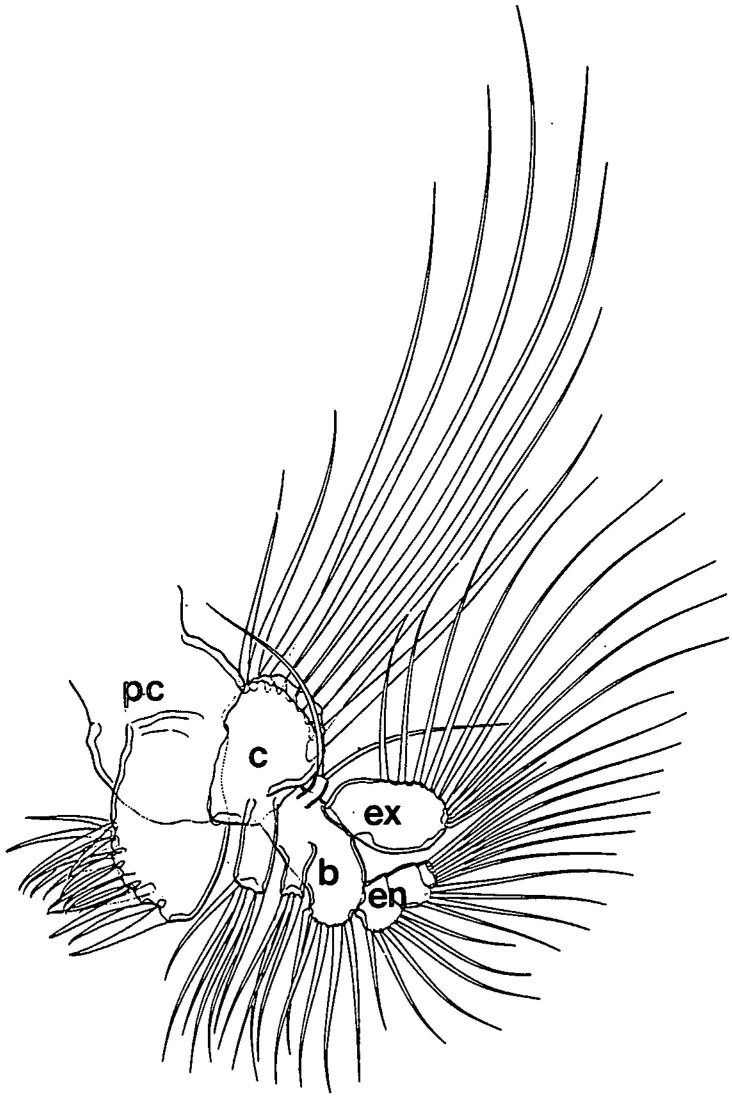
b – basis

ex – exopod

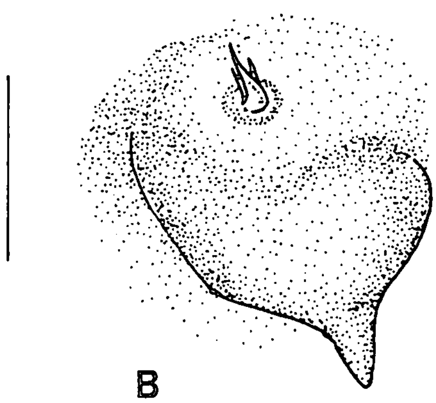
en – endopod

B. Maxillule, redrawn from Kabata (1979)

Scale-bar: 250µm



A



B

Figure 3.7

Diagram illustrating the differences between the basic copepod maxilla and the maxilla of *Caligus curtus* Müller, 1785

A. Basic copepod maxilla, redrawn from Huys & Boxshall (1991)

pc – praecoxa

c – coxa

b – basis

en – endopod

B. Maxilla, redrawn from Kabata (1979), showing the maxilla ventral (B1) and the brachium enlarged (B2)

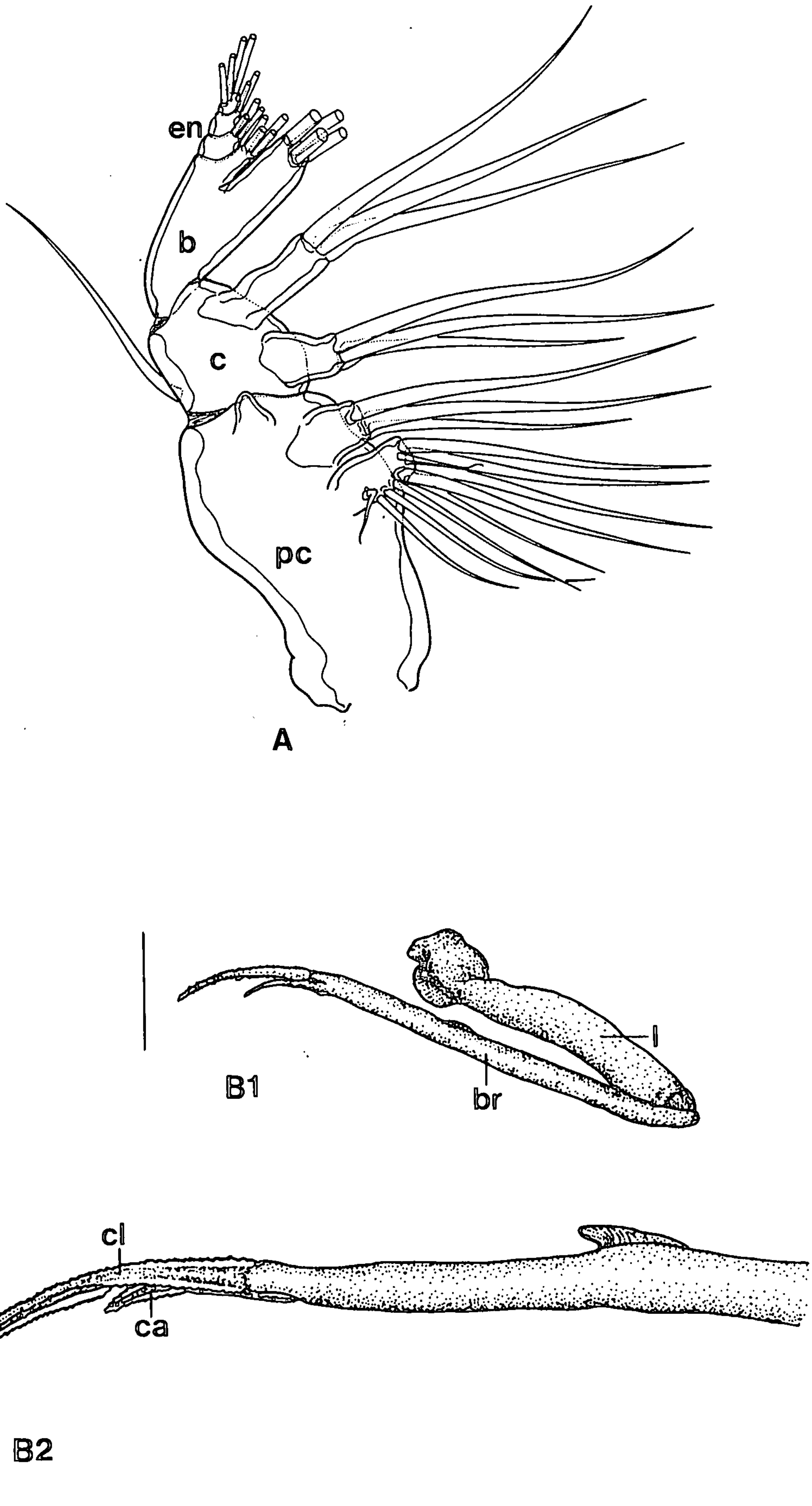
l – lacertus (proximal segment)

br – brachium (distal segment)

cl – calamus

ca – canna

Scale-bar: 250µm



en
b
c
pc
A
l
br
B1
cl
ca
B2

Figure 3.8

Diagram illustrating the differences between the basic copepod maxilliped and the maxilliped of *Caligus curtus* Müller, 1785

A. Basic copepod maxilliped, redrawn from Huys & Boxshall (1991)

pc – praecoxa

c – coxa

b – basis

en – endopod

B. Maxilliped, redrawn from Kabata (1979), showing the female (B1) and adult male (B2) maxilliped

co – corpus

sh – shaft

cw – claw

m – myxa

Scale-bar: 500µm

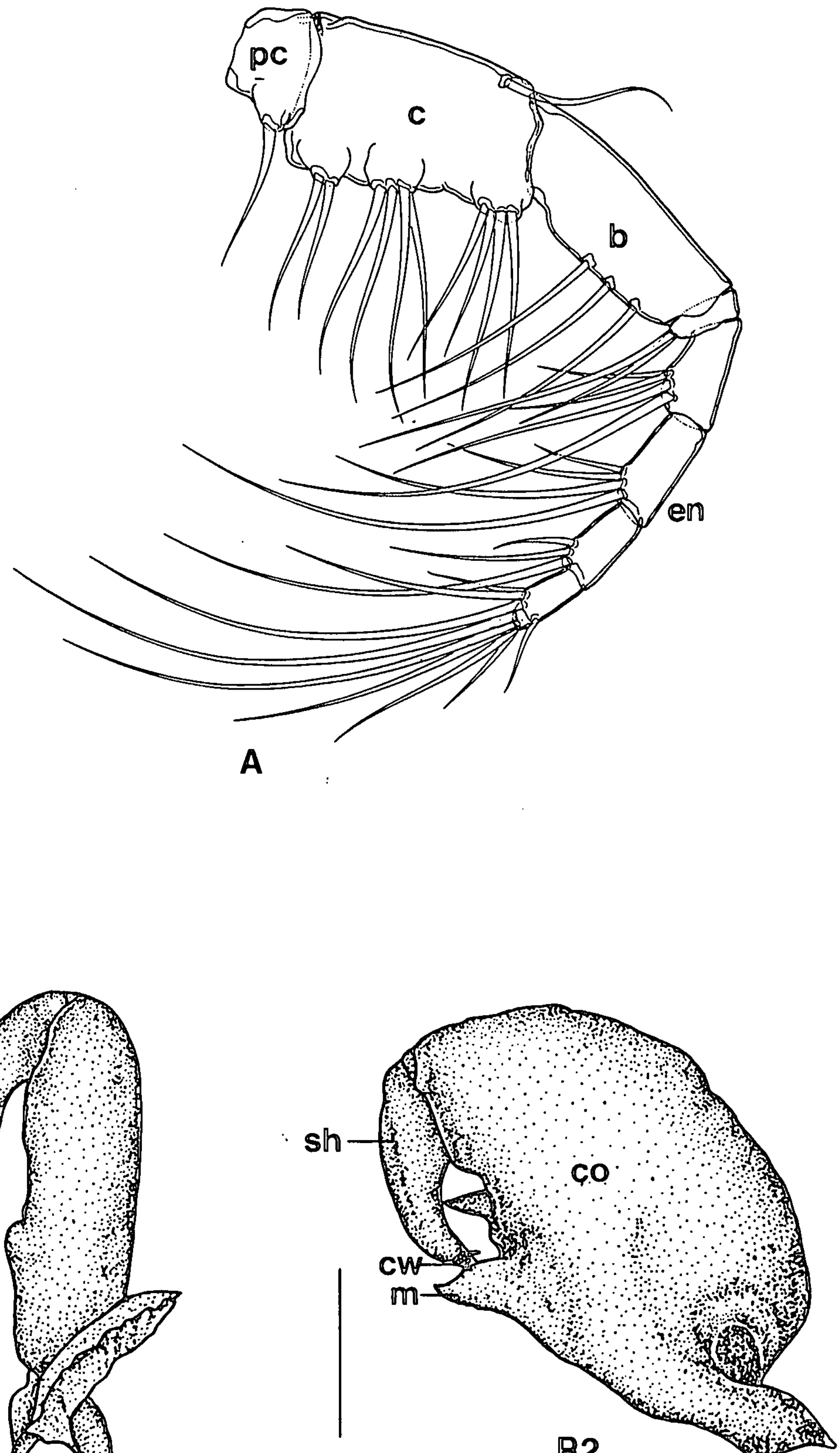

pc
c
b
en
A
sh
co
cw
m
B1
B2

Figure 3.9

Diagram illustrating the differences between the basic copepod swimming leg and the first leg of *Caligus curtus* Müller, 1785

A. Basic copepod swimming leg, redrawn from Huys & Boxshall (1991)

c – coxa

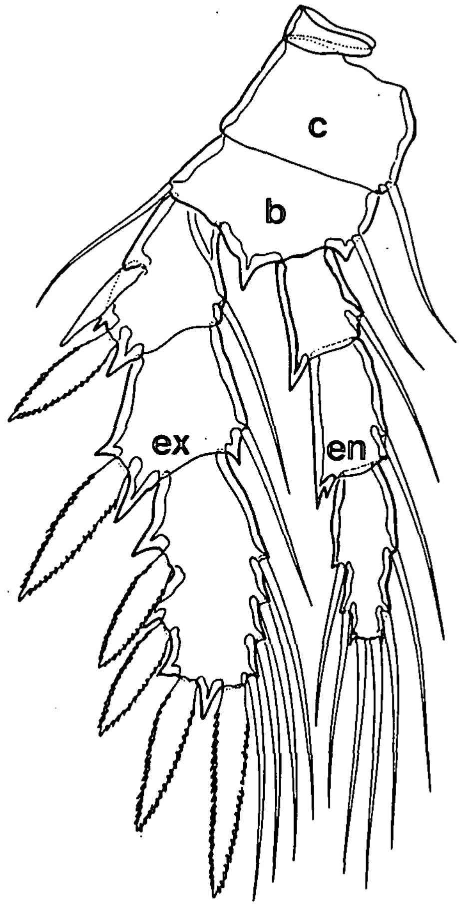
b – basis

ex – exopod

en – endopod

B. First leg, redrawn from Kabata (1979)

Scale-bar: 250µm



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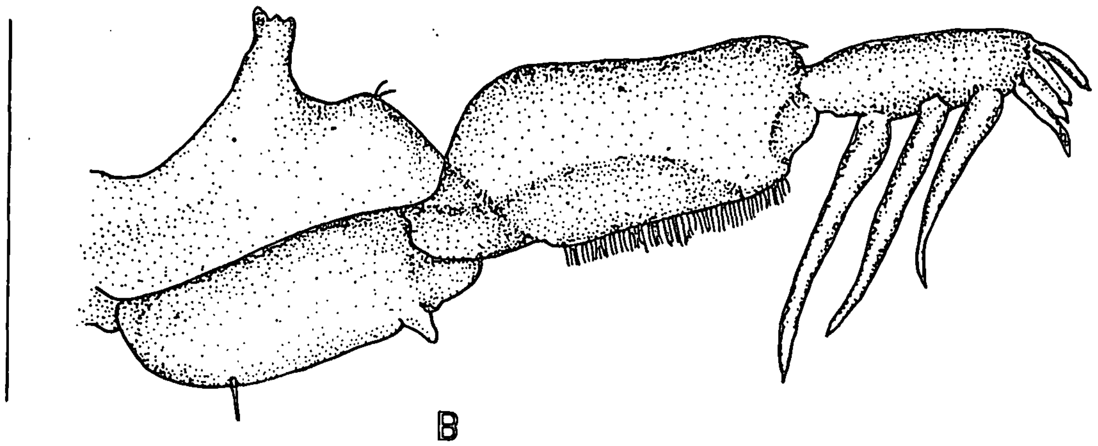


B

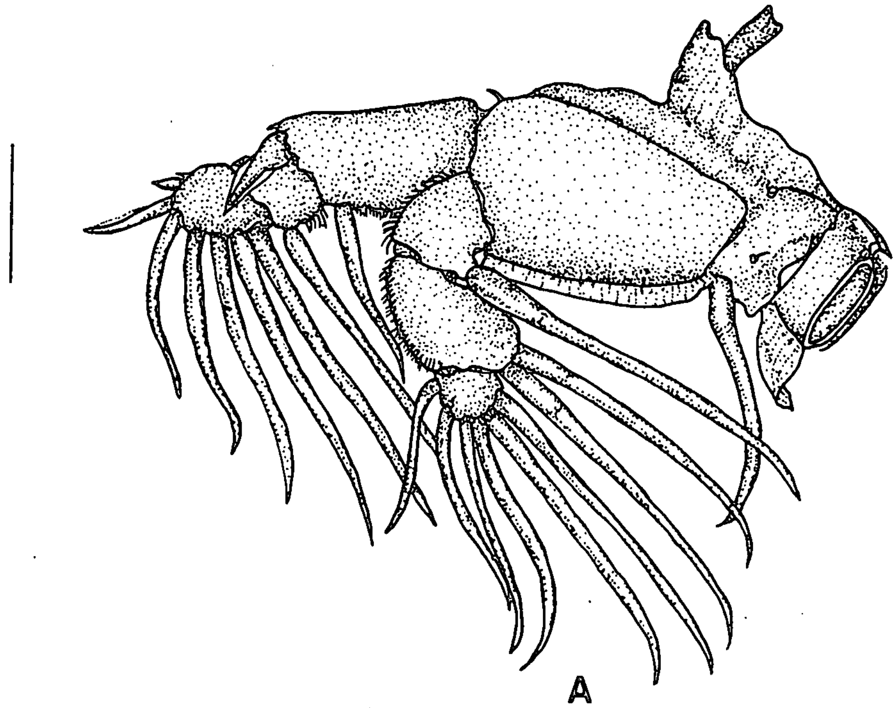
Figure 3.10

Diagram illustrating the second and third leg of *Caligus curtus* Müller, 1785, redrawn from Kabata (1979)

A. Second leg

B. Third leg

Scale-bar: 500µm



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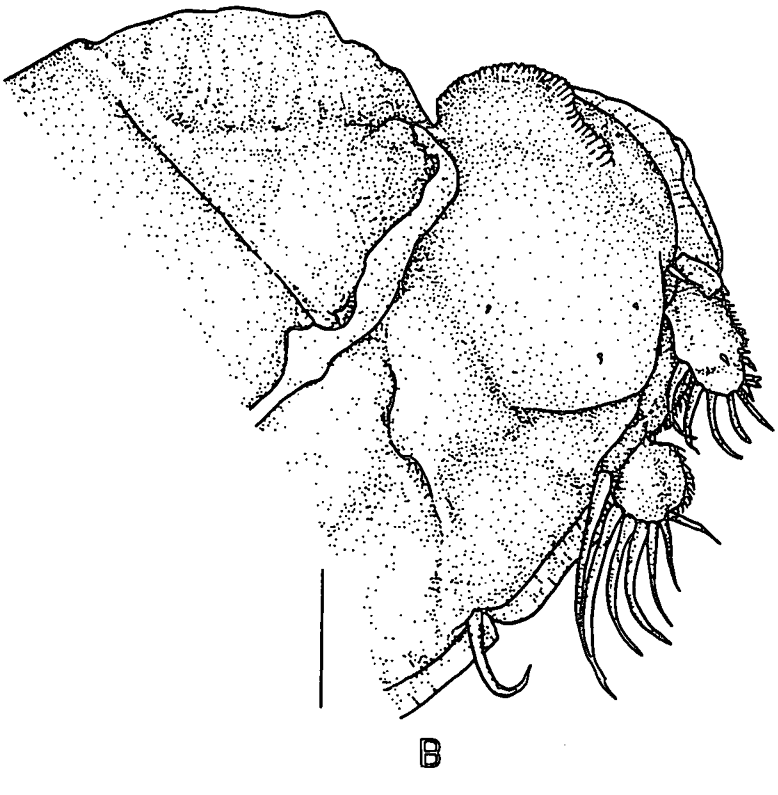

B

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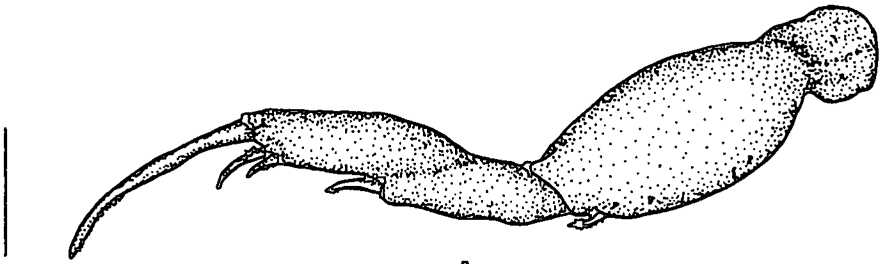
Figure 3.11

Diagram illustrating the fourth leg and the sternal furca of *Caligus curtus* Müller, 1785, redrawn from Kabata (1979)

A. Fourth leg

B. Sternal furca

Scale-bar: 500µm



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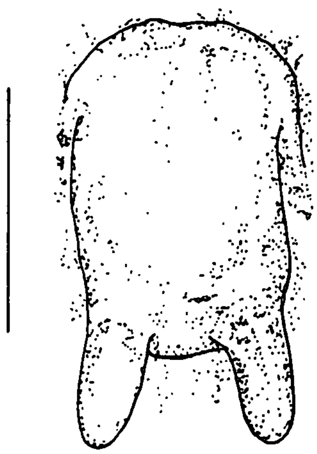


B

General Morphology of the Genus *Caligus* Müller, 1785

The genus *Caligus* is one of the most successful genera of parasitic copepods and consists of more than 200 species, distributed throughout the oceans and seas of the world. A synopsis of the genus was published by Margolis, Kabata & Parker in 1975. In chapter 4 of this thesis I have given a synopsis of the South African species of *Caligus*, with new records of species found in South African coastal waters as well as new host records. *Caligus* parasitises innumerable species of fishes, some species have very broad ranges of hosts, others are known from a single host species. It appears that the genus *Caligus* is better represented in tropical and subtropical waters than in the higher latitudes (Kabata 1979).

Classification of the genus *Caligus* Müller, 1785

Empire	Eukaryota
Kingdom	Animalia
Phylum	Arthropoda
Subphylum	Mandibulata
Infraphylum	Crustacea Pennant, 1777
Class	Maxillopoda Dahl, 1956
Subclass	Copepoda Milne Edwards, 1840
Infraclass	Neocopepoda Boxshall, 1991
Superorder	Podoplea Giesbrecht, 1882
Order	Siphonostomatoida Thorell, 1859
Family	Caligidae Burmeister, 1835
Subfamily	Caliginae Dana, 1852
Genus	*Caligus* Müller, 1785

All caligid parasites are of similar shape. The most characteristic feature of representatives of the family Caligidae is the structure of the cephalothorax. This tagma functions like a sucker-like attachment organ, with anterior and lateral margins sealed by frontal plates and marginal membranes respectively. The posterior rim of the sucker is created by the third pair of legs, the sympods of which form, together with the interpodal bars, a broad lamina, effectively cutting off the concave interior of the sucker from the outside (Kabata 1992). The convex dorsal shield is applied to the fish in the manner of an inverted saucer. The caligid body consists of four tagmata, in addition to the cephalothorax, also the fourth leg-bearing segment, genital complex and abdomen. The structure of *Caligus* can thus be used as a typical example of the family Caligidae.

Cephalothorax

The cephalothorax incorporates the thoracic segments up to and including the third leg-bearing segment (Kabata 1992). It is a roundish or oval structure, covered by a slightly convex dorsal shield, its rims overhanging most of the appendages, and applied to the surface of the fish in the manner of an inverted saucer. The third pair of legs form an uniterrupted wall sealing off the posterior end of the cavity formed by the cephalothorax and is a hallmark of representatives of the Caligidae. The cephalothorax covers most of the appendages. The only appendages that are not covered by the cephalothorax are the fourth and fifth legs, and the sixth legs in the males.

Lunules

Located ventrally on the plates at the frontal margin of the cephalothorax, these two semicircular structures function as sensory organs. Many authors have mistakenly identified the lunules as suckers, but the lunules are used in conjunction with the antennules as sensory organs. The lunules develop from the anterior margin from part of the marginal membrane. The cups of the lunules are of different depths, in some species they are very shallow, with incomplete margins (Kabata 1979). The lunules are characteristic of all *Caligus* parasites.

Antennule

The antennule is the first cephalic appendage and of copepods living parasitically on fishes it is more insignificant in size. It has become flat and its base fits neatly under the frontal plate. The sensory function of the antennule was demonstrated by Scott

(1901), who found these appendages very richly innervated, each seta receiving a separate branch of the antennular nerve. This author saw the tips of the antennule in *Caligus* repeatedly raised and lowered while the copepod was in motion, and it appeared to palpate the substrate (Kabata 1979).

Antenna

The antenna is the second cephalic appendage and caligid copepods use their piercing antennae to anchor them on the host, in addition to the suction of the inverted saucer-shaped shield. The piercing antennae pull the copepod firmly down onto the host, and create thus a very low-profile shape. To produce suction, the saucer-like cephalothorax must be pressed down, and the downward pressure on the bases of the antenna translates itself into displacement of the elbow-like joint of the appendage and locks in the claws that are inserted into the tissues of the fish. To loosen this grip the suction must be released and the joint unflexed. The copepod is then ready to move (Kabata 1979). Water resistance is minimized by this downward pressure and allow the caligid copepods to cling to their hosts' surfaces without the danger of being swept away by a current of water.

Mouthparts

Copepods parasitic on fishes can be divided into two groups by the type of their mouths, the poecilostomes and the siphonostomes. The poecilostome mouth is, in effect, a transverse slit and the anterior side of the slit is overhung by the labrum. The mouth of the Cyclopoida is similar to that of the Poecilostomatoida. *Caligus* species have cone-shaped, sucking mouthparts and is formed by partial fusion of the labrum and labium, and is characterised as a siphonostome mouth. This siphonostome mouth is a tube or syphon, built around and above the oesophageal opening and separating it from the buccal rim by a distance equal to the length of the lips (Kabata 1979). The lateral margins of the lips remain separate from each other for a short distance at the base, creating a small triangular opening through which the mandibles enter the buccal cone. The tip of the labium carries a structure known as the strigil, and is armed with about 100 fine sharp teeth. A rhythmic fluctuation in the pressure pushing the tip of the labium into the skin would cause the two halves of the strigil to move away from each other, pivoting on a common base, each divergent move being followed by a convergent one. As can be supposed from their structure, the teeth of the strigil would execute sawing movements, particularly effective during their inward stroke. The resulting accumulation of debris can be picked up from the surface by the movement of the mandibles, the mandibular teeth acting as conveyors moving the fish tissue into the buccal cavity (Kabata 1979).

Mandible

The adults of the caligiform siphonostomes are fairly uniform in the structure of the mandible which forms the third cephalic appendage. A series of either uniform or varied teeth is usually borne on the blade-like tip. In representatives of the Caligidae the mandible consists of four parts which may or may not correspond to segments (Kabata 1979). In other families mandibular segmentation is often obscure or absent.

Maxillule

Forming the fourth cephalic appendage, Lewis (1969) concluded that in "Caligoidea" the true maxillule is the structure which consists at least of a spine and a setiform node or papilla lateral to the mouth cone. Judging from the size and structure of the maxillule in the parasitic Crustacea, the maxillule is no longer directly involved in feeding, and certainly not in the manipulation of food (Kabata 1979). It is not opposable with the other member of the pair and has limited opportunity of contact with the particles of food being ingested. Its setous armature might have a sensory function and therefore be construed as a kind of "taster", searching for food debris, but it is just speculation from Kabata (1979).

Maxilla

The maxilla is the fifth and last cephalic appendage. Kabata (1979) referred to the maxilla as brachiform, in recognition of the superficial resemblance it bears to that of a human arm. The proximal, more robust part of the appendage is described as lacertus, or upper arm. The lacertus articulates with the brachium, or lower arm. The distal end of the brachium is connected with a third flexible and armed rod, the calamus. A similar, shorter rod, the canna, arises from the brachium on the outer side of the calamus. The brachiform maxilla is most frequently used to manipulate the frontal filament during the developmental stages of most siphonostomes (Kabata

1979). In adult Caligidae, the maxilla also assists in movements over the surface of the fish.

Maxilliped

A striking feature in male *Caligus* species is the broad and robust maxilliped. In the siphonostome copepods the maxilliped is a subchelate appendage (Kabata 1979). The corpus, or main body, is a robust structure and unsegmented. The corpus has near its mid-length the myxa, a low swelling that is often armed with a patch of denticles and/or a short spiniform seta or spine. The corpus articulates with the subchela. The subchela consists of the shaft and claw. The maxilliped functions as a prehensile limb and is probably also associated with feeding. The male uses the maxilliped to grasp the female during mating and might use it also to manipulate and transfer the spermatophores. The female maxilliped is never used in any activity associated with reproduction.

Swimming legs

Fusion of the third leg-bearing segment with the cephalothorax, as in *Caligus*, brings with it extensive modification of the series of swimming legs. The endopod of the first leg is retained as a mere vestige. The second leg shows no changes, but the third leg has been profoundly modified. Expansion of the sympods of this pair, accompanied by a great increase in the width of the interpodal bar results in the development of a broad apron, which extends right across the posterior margin of the dorsal shield. Both rami are reduced and the space between them filled by an oval cuticular flap, the velum. Made watertight along the anterior and lateral margins by a hyaline strip of marginal membrane, the shield is now an inverted saucer-like structure perfectly suited to act as a sucker. The first two pairs work together as locomotory appendages, propelling the copepod along the surface of the fish or through the water (Kabata & Hewitt 1971). The fourth leg remains outside the cephalothoracic shield and is functionally divorced from the preceding legs. It loses its endopod and its exopod is greatly modified. The fifth pair of legs is located on the ventral side of the posterolateral corner of the genital complex and is vestigial. The sixth leg is present normally only in the males and is also vestigial, comprising only three or four setae.

Cuticular spines

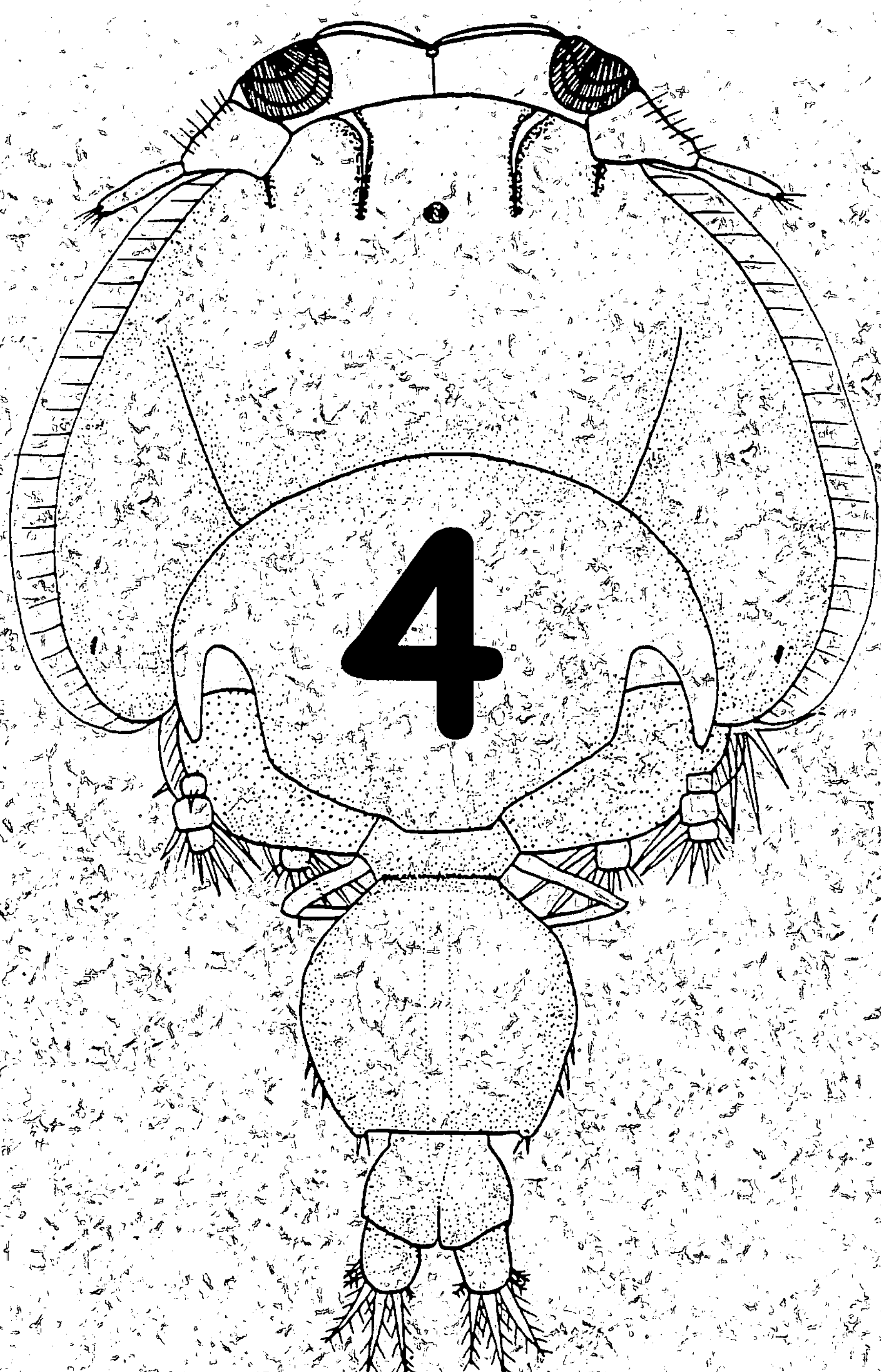
Cuticular spines are the most common structures present in parasitic copepods that are attributable to the influence of parasitism. Two well-known cuticular spines in *Caligus* parasites are the **postantennary process** and the **sternal furca**.

Postantennary process

Probably the best known and certainly the most controversial cuticular spine is the one known as the postantennary process (Kabata 1979). In the caligids the postantennary process is a simple, somewhat hooked sclerite with an inflated base, and is always associated with some sensory setae.

Sternal furca

Situated on the ventral surface in the interval between the maxillipeds and the first pair of legs, the sternal furca is a more or less rectangular box of cuticle with an open dorsal wall. By the appropriate action of two pairs of antagonistic muscles attached to the dorsal outgrowths the box can be tilted and the two posterior processes placed at different angles in relation to the surface of the body. The function of the sternal furca is not known, but it is said to act as a brake, when the copepod is in danger of slipping backwards over the host, or to assist in raising the arch of the cephalic shield to reduce pressure underneath and augment the force of its suction (Kabata 1979).


4

South African Species of the Genus *Caligus* Müller, 1785

Synopsis of *Caligus* species found along the South African coastline

The genus *Caligus* comprises approximately 315 nominal species (Margolis, Kabata & Parker 1975), of which only 39 have been recorded off the coast of Africa. Most of the information on this genus from the continent is limited to very old and often incomplete taxonomic descriptions, such as those of Basset-Smith (1898), Brady (1910), Capart (1941), Heegaard (1955), Nunes-Ruivo (1962) and others. The most recent information was given by Kensley and Grindley (1973) in a summary of the parasitic Copepoda of the fishes of southern Africa.

Oldewage and Van As (1989) gave an overview of *Caligus* parasites found in African coastal waters. These authors stated that 22 of the 39 species recorded from the African coast have been found on hosts around South Africa. This part of the continent has been researched more extensively due to the work of Basset-Smith (1898), Barnard (1948, 1955a, 1957), Kensley (1970) and Kensley and Grindley (1973). Dojiri (1989) reported 19 species, including one new species description, of *Caligus* from marine fishes of South Africa, which included two species that Oldewage and Van As did not mention in their overview.

The following 25 species of *Caligus* were described from fishes along the South African coast. A synopsis of host – and distribution records of the genus *Caligus* in South African coastal waters is listed below. **Host** and **locality** indicate the first collection of the specific *Caligus* species in South Africa, and the material examined under **remarks** include the males and females collected originally along the South African coast.

Synopsis of host and distribution records of *Caligus* parasites in South African coastal waters.

Caligus aesopus Wilson, 1940

Host: *Seriola lalandei*
Locality: False Bay
Other hosts & localities: *Seriola peruana*, Juan Fernandez. *Seriola grandis*, New Zealand.
Reference: Kensley & Grindley (1973)

Remarks

Material from False Bay included ten ovigerous females, 25 females, four males. Total length females 4.2-5.0 mm, males 3.9 mm. The four-segmented fourth thoracic leg, the shape of the genital segment, with its angular posterior corners, and the single segmented abdomen distinguish this species.

Caligus affinis Heller, 1866

Host: *Pomatomus saltatrix*
Locality: Durban
Other hosts & localities: *Sphyraena* sp., Congo River Mouth. *Umbrina cirrhosa*, Adriatic and Mediterranean.
Reference: Kensley & Grindley (1973)

Remarks

Material from Durban included one ovigerous female, one female, one male. Total length females 4.2-4.4 mm, male 3.0 mm. The present material agrees well with the descriptions of *Caligus affinis*, and falls within the size range given for females (3.30-5.45mm) by Brian (1934). The only difference appears to be the shape of the genital segment in the female, which in the Mediterranean and West African specimens seems to be slightly broader than in the present material.

Caligus africanus Oldewage & Van As, 1989

Host: *Arothron hispidus*
Locality: Cebe, Transkei
Other hosts & localities: No other records known to date.
Reference: Oldewage & Van As (1989)

Remarks

Oldewage & Van As (1989) stated that *Caligus africanus* has sensory setae on the base of the marginal membrane. These setae have a mechanosensory function and are used only when a host has been located.

Caligus arii **Basset-Smith, 1898**
Hosts: *Arius acutirostris*, *Arius caelatus* **Locality:** South Africa **Other hosts & localities:** *Ariodes dussumieri*, Zambezi River Mouth. *Arius acutirostris*, *Ariodes dussumieri*, *Pseudarius jatius*, Sri Lanka & India. **Reference:** Basset-Smith (1898)
Remarks The specimens recorded from South Africa by Barnard (1955a) differ from the specimens from Sri Lanka and India in the absence of the second abdominal segment. The fourth leg is three-segmented. Kirtisinghe (1964) considered these specimens as belonging to *Caligus dakari* van Beneden. This view appears to be correct but Kirtisinghe (1964) did not provide details about his specimens. Length female 6.0 mm.

Caligus assymmetricus **Pillai, 1965**
Hosts: *Scomberomorus commerson*, *Katsuwonus pelamis* **Locality:** Sodwana Bay **Other hosts & localities:** *Euthynnus affinis, E. yaito, E. alleteratus, Grammatorcycnus bilineatus, Sarda orientalis.* India (Kerala), Hawaii, Queensland, Marshall Islands. **Reference:** Oldewage & Van As (1989)
Remarks Original description from Kerala waters (India). Collected in Queensland and Hawaii. The male differs from the female in its distinctly two-jointed abdomen and the modified antenna and postantennary process. Second segment of the antenna has an inner distal adhesion pad and a short third segment. The postantennary process is a stout claw. Length female 3.5 mm.

Caligus biseriodentatus **She, 1957**
Hosts: *Scomberomorus commerson*, *Sarda sarda* **Locality:** Port Elizabeth **Other hosts & localities:** No other records known to date. **Reference:** Oldewage & Van As (1989)
Remarks None

Caligus bonito **Wilson, 1905**
Hosts & Localities: *Katsuwonus pelamis*, Sodwana Bay. *Sarda sarda*, False Bay, South Africa. **Other hosts & localities:** *Pelamys sarda* & *Cybium* sp., Mauritania. *Katsuwonus pelamis*, Baia forta, Angola. *Gymnosarda pelamis, G. allterata, Pomatomus saltatrix, Scomberomorus maculatus, S. cavella, Lutianus novemfasciatus, L. griseus, Mugil cephalus, Oligoplites saurus, Euthynnus pelamis, E. lineatus, E. affinis, E. alleteratus, Cratinus agassizi, Sarda orientalis, S. velox, S. chilensis, Thunnus thynnus.* Woods Hole, Genova, Florida, Japan, Mexico, Panama, Brazil, Louisiana, Texas, Black Sea, California, India, Hawaii, South Pacific, Queensland. **Reference:** Barnard (1955b), Oldewage & Van As (1989)
Remarks
Caligus bonito is a cosmopolitan species and differences in specimens collected are all minor. Length female 3.0 mm, male 2.0 mm.

Caligus brevicaudatus **Scott, 1901**
Host: No record **Locality:** No record **Other hosts & localities:** *Eutrigla gurnardus, Trigla capensis, T. lucerna.* Irish Sea, Barents Sea, Gulf of Naples. **Reference:** Barnard (1955b)
Remarks
Caligus brevicaudatus is a very rare species, although the range of the species is quite extensive.

Caligus confusus **Pillai, 1961**
Host: *Caranx djedaba* **Locality:** Durban **Other hosts & localities:** *Elagatis* sp., Panang, Galapagos. *Caranx* sp., Celebes, south India. *Caranx sansun, C. hippos, C. melampygus, Coryphaena hippurus, Seriola* sp. Sri Lanka, India (Kerala), Panama, Japan, Costa Rica, Marshall Islands. **Reference:** Kensley & Grindley (1973)
Remarks
Material from Durban included one ovigerous female, two females, from gill chamber of *Caranx djedaba*. Total length females 4.0 mm. Specimens described by Pillai (1961), total length female 2.9 mm, male 1.8 mm. The difference in size has no significance since such variations are common among parasitic copepods.

Caligus coryphaenae Steenstrup & Lütken, 1861

Hosts & Localities: *Katsuwonus pelamis*, Sodwana Bay. *Squalus acanthias*, Algoa Bay. *Thunnus obesus*, Cape Point. *Euthynnus pelamis*, Cape Point.

Other hosts & localities: Plankton monsters, Gulf of Guinea. *Corypaena hippurus, C. pelagica, Parathunnus obesus, P. sibi, Euthynnus alleteratus, E. yaito, R. lineatus, E. affinis, Sarda orientalis, Squalus acanthias, Neothunnus albacora, N. macropterus, Seriola dorsalis, Rachycentron canadus, Caranx hippos, C. melampygus, Isurus glaucus, Thunnus thynnus, Acanthocybium solandri, Echeneis* sp., *Sphaeroides inermis, Grammatorcycnus bilineatus, Elegatis bipinnulatus* This species occurs in basically all tropical and subtropical waters of all oceans including the Mediterranean.

Reference: Barnard (1955a), Kensley & Grindley (1973) and Oldewage & Van As (1989)

Remarks

Material from Cape Point included six ovigerous females from *Thynnus obesus*, one ovigerous female, three males, from *Euthynnus pelamis*. Total length females 7.2-8.5 mm, males 5.4 mm. Salmon pink colour when alive, genital segment and abdomen yellowish. Three important characters are given for distinguishing this species by Kensley and Grindley (1973). These are the sternal furca arms which are apically pointed and divergent, the basal hook of the exopod of the third thoracic leg, which is straight or outcurved, and the ultimate claw of the fourth thoracic leg which is obviously longer than the penultimate one. Pillai (1985) gave the following characteristics for this species: It has a well chitinised body. The distal segment of the antennule carries exceptionally long setae which are plumose, a character which is unusual in caligids. The armature of the distal segment of the first leg is very characteristic and distinguishes this species from most species of *Caligus*. The five-jointed abdomen is unique.

Caligus elongatus Nordmann, 1832

Host: No host recorded

Locality: Fishes caught from a Cape-line ship, but not necessarily from South African waters.

Other hosts & localities: Very broad host range with over 80 host species recorded. Recorded from most regions of the world's oceans.

Reference: Barnard (1955a)

Remarks

The length of its synonymy, accrued during more than a century of research publications, reflects also the ubiquity of *Caligus elongatus* and the extraordinary range of its known hosts. Throughout most of its recorded history, it has been confused with *Caligus rapax* Edwards, 1840, as the result of misidentification by Baird (1850). The confusion was not unravelled until Parker (1969) published his excellent account of the species.

***Caligus engraulidis* Barnard, 1948**
Host: *Stelophorus holodon* **Locality:** Zwartkops River, Algoa Bay **Other hosts & localities:** No other records known to date. **Reference:** Barnard (1948)
Remarks
Fourth leg with one long and one short spine on apex of third joint, both serrated on both margins.

***Caligus hottentotus* Barnard, 1957**
Host: *Pachymetopon blochi* **Locality:** Table Bay **Other hosts & localities:** No other records known to date. **Reference:** Barnard (1957)
Remarks
None

***Caligus infestans* Heller, 1865**
Host: No host record **Locality:** Sodwana Bay **Other hosts & localities:** *Cybium commersoni, C. sphyrenae, C. maculatum, Euthynnus alleteretus, Scomberomorus commersoni.* Java, Aden, Madagascar, Sri Lanka, Queensland. **Reference:** Oldewage & Van As (1989)
Remarks
Pillai (1985) redescribed this species from a single female specimen in the British Museum. The shape of the genital segment, sternal furca and the fourth leg distinguish this species.

***Caligus labracis* Scott, 1902**
Host: *Clinus superciliosus* **Locality:** Table Bay **Other hosts & localities:** *Labrus bergylta, L. mixtus.* British waters. **Reference:** Barnard (1955b)
Remarks
Caligus labracis is a very distinctive species, identifiable without difficulty. Its characteristic features (spatulate tines of sternal furca, basal tine of postantennary process, exopod of fourth leg) assure its immediate recognition even on cursory examination. *Caligus labracis* is known almost exclusively around the British Isles. A surprising record from outside the British Isles region is that of Barnard (1955a) from the South African waters, where it was found on *Clinus superciliosus.* This record calls for confirmation.

Caligus lalandei Barnard, 1948
Host: *Seriola lalandei* **Locality:** Kalk Bay **Other hosts & localities:** No other record known. **Reference:** Barnard (1948)
Remarks
Material from Barnard (1948) included four females and one male. Total length female 10.5 mm, male 16 mm. Noteworthy on account of the length of the caudal rami in both sexes, but especially the male.

Caligus lunatus Wilson, 1928
Host: *Seriola lalandi* **Locality:** False Bay **Other hosts & localities:** No other records known to date. **Reference:** Barnard (1955b)
Remarks
None

Caligus mauritanicus Brian, 1924
Hosts: *Pomatomus saltatrix, Caranx angolensis, Corvina cameronensis, Dentex filosus, Dentex* sp., *Plectorhynchus mediterraneus, Pagrus pagrus.* **Locality:** False Bay **Other hosts & localities:** *Argyrosomus regius, Cynoglossus* sp., West Coast of Africa. *Diagramma mediterraneum, Arius heudeloti, Pagrus* sp., *Corvina nigra, Caranx* sp., Mauritania Congo estuary. *Pomatomus saltatrix*, Mauritania. *Polydactylus quadrifilis, Trachurus trachurus, Trigla lyra, Ombrina* sp., Angola. **Reference:** Barnard (1955b)
Remarks
None

Caligus mortis Kensley, 1970
Hosts: *Clinus superciliosus* **Locality:** Saldanha Bay, South Africa **Other hosts & localities:** *Chorisochismus dentex, Parablennius cornutus, Clinus superciliosus*, Torra Bay, Möwe Bay & Swakopmund, Namibia. **Reference:** Kensley & Grindley (1973)
Remarks
Material from intertidal fish from Torra Bay, Möwe Bay, Swakopmund, Namibia, as well as Saldanha Bay, South Africa, included ten ovigerous females collected from the above mentioned hosts.

Caligus pelamydis **Krøyer, 1836**
Hosts & Localities: *Trigla capensis, Thyrsites atun,* False Bay & Table Bay. Simons Bay (no host record). **Other hosts & localities:** *Pelamys sarda, Gymnosarda pelamys.* Danish and British seas, Mediterranean, east coast of North America, New Zealand, Hawaii, California, Adriatic Sea, Black Sea. **Reference:** Brady (1910), Barnard (1955a)
Remarks
Fourth leg four-jointed. First abdominal segment four times the length of second abdominal segment. Yellowish-white. *Caligus pelamydis* is a very widespread species, with records in almost every ocean.

Caligus penrithi **Kensley & Grindley, 1973**
Hosts: *Cheilodactylus pixii, Cheilodactylus fasciatus* **Locality:** Algoa Bay **Other hosts & localities:** *Cheilodactylus fasciatus,* Möwe Bay, Namibia. **Reference:** Kensley & Grindley (1973)
Remarks
Material collected from *Cheilodactylus fasciatus* from Möwe Bay, Namibia included five ovigerous females, one female and eight males. Total length females 4.5 mm, egg sacs 2.5 mm, males 3.0 mm. Of the species of *Caligus* having the carapace less than half the total length, and a two-segmented abdomen about equal in length to the genital segment, *Caligus penrithi* most closely resembles *Caligus robustus* Basset-Smith. The elongate nature of the genital segment and abdomen of the latter species are very different, however, from *Caligus penrithi,* with its roughly quadrate genital segment and conical abdomen. There is some resemblance to *Caligus djedabae* Rangnekar, particularly in the shape of the carapace and genital segment of the female. The abdomen, however, consists of a single segment, albeit conical, and is relatively shorter than in *Caligus penrithi.* Other differences include the shape of the sternal furca and the fourth thoracic legs of the female.

Caligus productus **Dana, 1852**
Hosts: *Katsuwonus pelamis, Scomberomorus commerson, Thunnus albacares* **Locality:** Sodwana Bay **Other hosts & localities:** *Thunnus albacares,* Angola Bay. *Thunnus pelamys, Coryphaena hippurus, Naucrates ductor, Neothunnus albacora, Scomberomorus cavalla, S. maculatus, S. sierra, Sarda sarda, Elops saurus, Pogonias cromis, Auxis thazard, Seriola dorsalis, Paralabrax clahratus, P. maculatofasciatus, Verrunculus polylepos, Katsuwonus vagans, Sphyraena argentea, Calamus brachyomus, Euthynnus pelamis, E. affinis, Chrysophrys aurata.* Widely distributed in tropical and subtropical waters of all oceans. **Reference:** Oldewage & Van As (1989)
Remarks
Although *Caligus productus* is a common and widespread species, many authors in the past had difficulties in identifying it correctly, due to inadequacies of the early descriptions.

Caligus saucius Dojiri, 1989
Host: *Cirripectes castaneus* **Locality:** Kwazulu Reef **Other hosts & localities:** No other records known to date. **Reference:** Dojiri (1989)
Remarks
None

Caligus tetrodontis Barnard, 1948
Hosts & Localities: *Torquigener hypselogeneion*, Port Elizabeth. *Amblyrhynchotes honckenii*, Knysna. **Other hosts & localities:** No other records known to date. **Reference:** Barnard (1948), Oldewage & Van As (1989)
Remarks
Material collected from Barnard (1948) included two ovigerous females, two juvenile females, and four males. Total length 4-5 mm.

Caligus zei Norman & Scott, 1906
Host: *Thyrsites atun* **Locality:** False Bay **Other hosts & localities:** *Zeus faber*, British waters. **Reference:** Barnard (1955b)
Remarks
Caligus zei is not common. The record from Barnard (1955b) was a surprising one. No description or figures were given. Barnard (1955b) suggested that his identification was rather tentative and required corroboration.

In the present study five different species *Caligus* were found on different hosts around the South African coastline. Comparative descriptions of four species will be presented below, as well as new host records. Only one specimen of *Caligus epinepheli* Yamaguti, 1936 was collected form the blacktail, *Diplodus sargus capensis* Smith, 1844, at De Hoop Nature Reserve. No comparative description will be made of this specific species, as more material is needed to do a comparative description for this species. The *Caligus* species found on the east coast of South Africa in Lake St Lucia will be presented first, followed by the species found on the south coast of South Africa at Jeffreys Bay and De Hoop Nature Reserve.

Caligus acanthopagri Lin, Ho & Chen, 1994

Figures 4.1 – 4.14

Hosts: Riverbream *Acanthopagrus berda* (Forsskål, 1775) and Cape stumpnose *Rhabdosargus holubi* (Steindachner, 1881).

Localities: Hell`s Gate and Fanies Island in Lake St Lucia.

Reference material: 14 / 64 – 66; 15 / 029; 16 / 017; 16 / 022; 16 / 023; 16 / 030; 16 / 047; 16 / 078; 97 / 01 / 21 – 01-03; 97 / 01 / 21 –0 8; 97 / 01 / 21 – 10; 97 / 01 / 21 – 11

Material examined: A total of 480 adult specimens were collected from the body surface of the two hosts mentioned. A few developmental stages were also collected and include nauplius larvae and chalimus stages. A total of 241 adult specimens were collected from a single *Rhabdosargus holubi* host (total length of 330 mm) from Fanies Island.

Description of adult female: Body with typical appearance of *Caligus* (Figure 4.1, 4.2). Total length of female 4.61mm (4.22 – 4.73; n=20). Cephalothorax suborbicular, 1.1 times as long as wide. Frontal plates narrow; lunules small (Figure 4.3A, 4.11A). Posterior sinuses medium to deep; lateral zones not reaching fourth pediger (fourth leg-bearing segment). Tip of antennule not reaching lateral limit of dorsal shield. Fourth pediger prominently wider than long; distinctly separated from genital complex. Genital complex slightly wider than long; posterolateral corners forming gently rounded lobes. Abdomen short; one-segmented; slightly longer than wide. Boundary between genital complex and abdomen distinct. Caudal rami about as long as wide with strongly slanted anterior margin. Posterior margin of each ramus armed with two outer, one small medial and three large terminal setae. Egg sacs about two-thirds of total body length; containing 35 to 60 eggs.

Antennule: Two-segmented (Figure 4.3B, 4.11B). Proximal segment trapezoid, much broader than distal segment, with 14 large, stout, marginal setae, with 14 short, plumose ventral setae and two short, plumose dorsal setae (Figure 4.3C). Distal segment rod-shaped, much longer than wide; armed with 12 terminal setae, one aesthete and one subterminal seta on posterior margin.

Antenna: Three-segmented (Figure 4.3D, 4.11C). Proximal segment smallest with pointed posteromedial corner. Second segment largest, robust. Terminal segment a strongly curved hook, bearing one basal seta and one marginal seta.

Postantennary process: Hook-like (Figure 4.3E, 4.11D), with two basal papillae each bearing three long setules and one similar papilla located nearby on sternum.

Mouth tube: Longer than wide (Figure 4.3F, 4.11E & F). Distal margin of labium and labrum fringed with hyaline membrane. Labrum with submarginal row of denticles. Mandible (Figure 4.3G) with 12 teeth on mediodistal margin.

Maxillule: Dentiform (Figure 4.4A, 4.12A), sharply hook-like with papilla bearing three setae.

Maxilla: Two-segmented, brachiform (Figure 4.4B, 4.12B). Lacertus unarmed. Brachium slender with flabellum on medial margin bearing hyaline membrane. Calamus serrated on both margins (Figure 4.12C). Canna serrated on both margins, shorter than calamus (Figure 4.12D).

Maxilliped: Three-segmented (Figure 4.4C). Proximal segment stout, unarmed. Second and terminal segments fused, forming strong claw with subterminal, medial seta.

Sternal furca: Base longer than wide (Figure 4.4D, 4.12E), with parallel and bluntly pointed tines. Tines just more than half the length of base.

Leg 1: Biramous (Figure 4.5A, 4.12F). Protopod with one inner and one outer short, plumose seta. Exopod two-segmented; first segment with lateral distal spine and medial row of setules; second segment with four terminal elements which appear differently; first spine simple and longer than spines 2 or 3; spines 2 and 3 with spiniform secondary process, equaling half the length of spines; seta 4 four times as long as spine 1, robust, tapering and unarmed; three plumose, long setae on posterior margin of same segment. Endopod rudimentary, unarmed.

Leg 2: Large plumose seta on coxa and one setule near intercoxal plate; basis with one small, naked lateral seta, one long medial setule and a striated membrane along medial margin (Figure 4.5B, 4.13A). Exopod three-segmented; first segment with one slightly curved outer spine and one plumose inner seta; second segment with one outer spine and one long, plumose inner seta; third segment with three external spines constructed unequally and five long, plumose setae. Endopod three-segmented; first segment with one long, plumose inner seta; second segment with two long, plumose inner setae; third segment with six long, plumose terminal setae. Second and third segment with prominent ventrolateral patch of spinules.

Leg 3: Adhesive pad on ventrolateral surface, striated marginal membranes and two medial naked setae (Figure 4.6A, 4.13B). Exopod three-segmented; first segment with large spine bearing an outer membrane; second segment with one outer spine and one long, plumose inner seta; third segment with three spines of different length and four long, plumose setae. Second and third segment with rows of setules on lateral margins. Endopod two-segmented; first segment expanded laterally into velum on outer margin and bearing one long, plumose seta on medial margin; second segment with six long, plumose setae and outer row of setules.

Leg 4: Outer seta on protopod short and plumose. Long and slender exopod (Figure 4.6B, 4.13C & D); bases of three outer spines on exopod covered by hyaline membrane; mediodistal corner of exopod protruded into two processes bearing hyaline membrane. Endopod missing.

Leg 5: Represented by three short, plumose setae on posterolateral corner of genital complex.

Armature on rami of legs 1-4:

Leg 1	Exp 1-0; III, 1, 3	Enp (rudimentary)
Leg 2	Exp I-1; I-1; I, II, 5	Enp 0-1; 0-2; 6
Leg 3	Exp I-0; 1-1; 3, 4	Enp 0-1; 6
Leg 4	Exp I-0; I, III	Enp (absent)

Description of adult male: Total length of male 5.05mm (4.29 – 5.28; n=20). Adult male distinctly larger than female (Figure 4.7, 4.8, 4.14A & B). Cephalothorax suborbicular, less than 1.1 times as long as wide. Fourth pediger wider than long. Genital complex with rudimentary leg 5 (Figure 4.13E) and leg 6 (Figure 4.13F) on posterolateral margin. Leg 5 represented by three outer setae; leg 6 represented by two inner setae. Abdomen two-segmented; wider than long, with laterally protruded distal margin. Anal segment slightly wider than long. Caudal rami armed as in female; different in size. Urosome (Figure 4.9)

Antenna: Three-segmented (Figure 4.10A, 4.14C). Proximal segment unarmed. Second segment large; robust; armed distally with two corrugated patches. Terminal segment smallest.

Maxilliped: Three-segmented. Corpus bearing four unequal ridges on medial surface (Figure 4.10B, 4.14D).

Sternal furca: Base longer than in female.

Remarks: With the aid of the scanning electron microscope small detail and obscure structures are made visible. Not many strange structures were found associated with *Caligus acanthopagri*. Bacteria and fungi were found on these copepods, but will be discussed in chapter 6. An extension of the antennule on the dorsal side in the male of *C. acanthopagri* is showed in Figure 4.14E. Lin, Ho & Chen (1994) did not mention anything about this extension, but in the drawing of the species description it is evident that their specimen did have the extension of the antennule. It is probably used as a supplementary sensory organ. The eyes of *C. acanthopagri* are showed in Figure 4.14F. MacKinnon (1993) demonstrated the sensitivity of the eyes of copepodid larvae of *C. elongatus* to light. The larvae migrate upwards in the water column in daytime, but in the dark no migration took place. The small triangular eye contains structures that are photosensitive to pick up even the lowest densities of light (MacKinnon 1993).

The most characteristic features of *C. acanthopagri* are the possession of a short abdomen, an accessory process on the middle two of the terminal four elements on the exopod of leg 1, and a slender, two-segmented exopod bearing an armature of I; IV on leg 4. *Caligus acanthopagri* bears closest resemblance to *C. latigenitalis* that was first recorded by Shiino (1954) from the body surface of *Acanthopagrus schlegeli* in Japan. The only discernible morphological difference between these two closely allied species is the fine structure on the distal end of the exopod of leg 4. In *C. acanthopagri* the distal end of the exopod of leg 4 is equipped with two corner processes with two hyaline membranes, but in *C. latigenitalis* there are two short, but heavy, digital processes. *Caligus acanthopagri* displays an unusual feature for copepods in having the male distinctly larger than the female. This species was first collected in 1983 from black sea bream at the Tainan Branch of the Taiwan Fisheries Research Institute. This same species was found on *Acathopagrus berda* and *Rhabdosargus holubi* in the Lake St Lucia system during surveys in 1996 and 1997, and is also a new record along the South African coastline.

Figure 4.1

Microscope projection drawing of *Caligus acanthopagri* Lin, Ho and Chen, 1994 female (dorsal) occurring on the fish host *Acanthopagrus berda* (Forsskål, 1775), collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

Scale-bar: 1mm

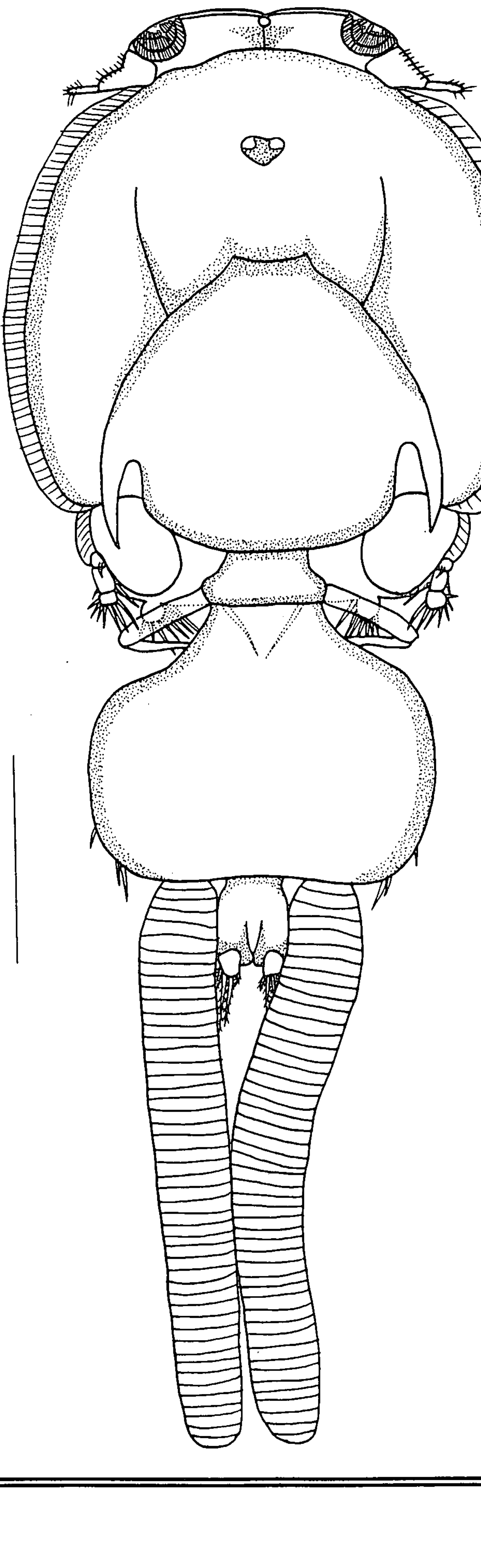


Figure 4.2

Microscope projection drawing of *Caligus acanthopagri* Lin, Ho and Chen, 1994 female (ventral) occurring on the fish host *Acanthopagrus berda* (Forsskål, 1775), collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

Scale-bar: 1mm

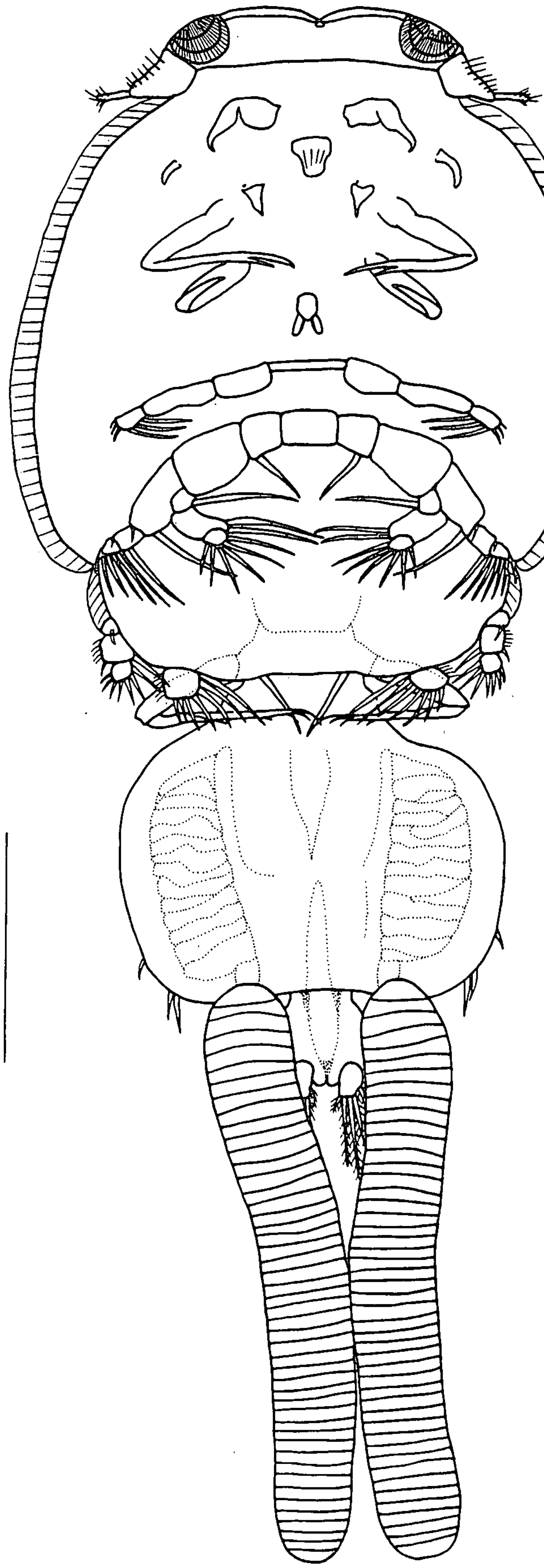


Figure 4.3

Microscope projection drawing of *Caligus acanthopagri* Lin, Ho and Chen, 1994 female occurring on the fish host *Acanthopagrus berda* (Forsskål, 1775), collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Frontal plate and lunule

B. Ventral view of antennule

C. Dorsal view of antennule

D. Antenna

E. Postantennary process

F. Mouth tube

G. Mandible

Scale-bar: G - 10µm. C, D, E & F - 100µm. A & B - 200µm

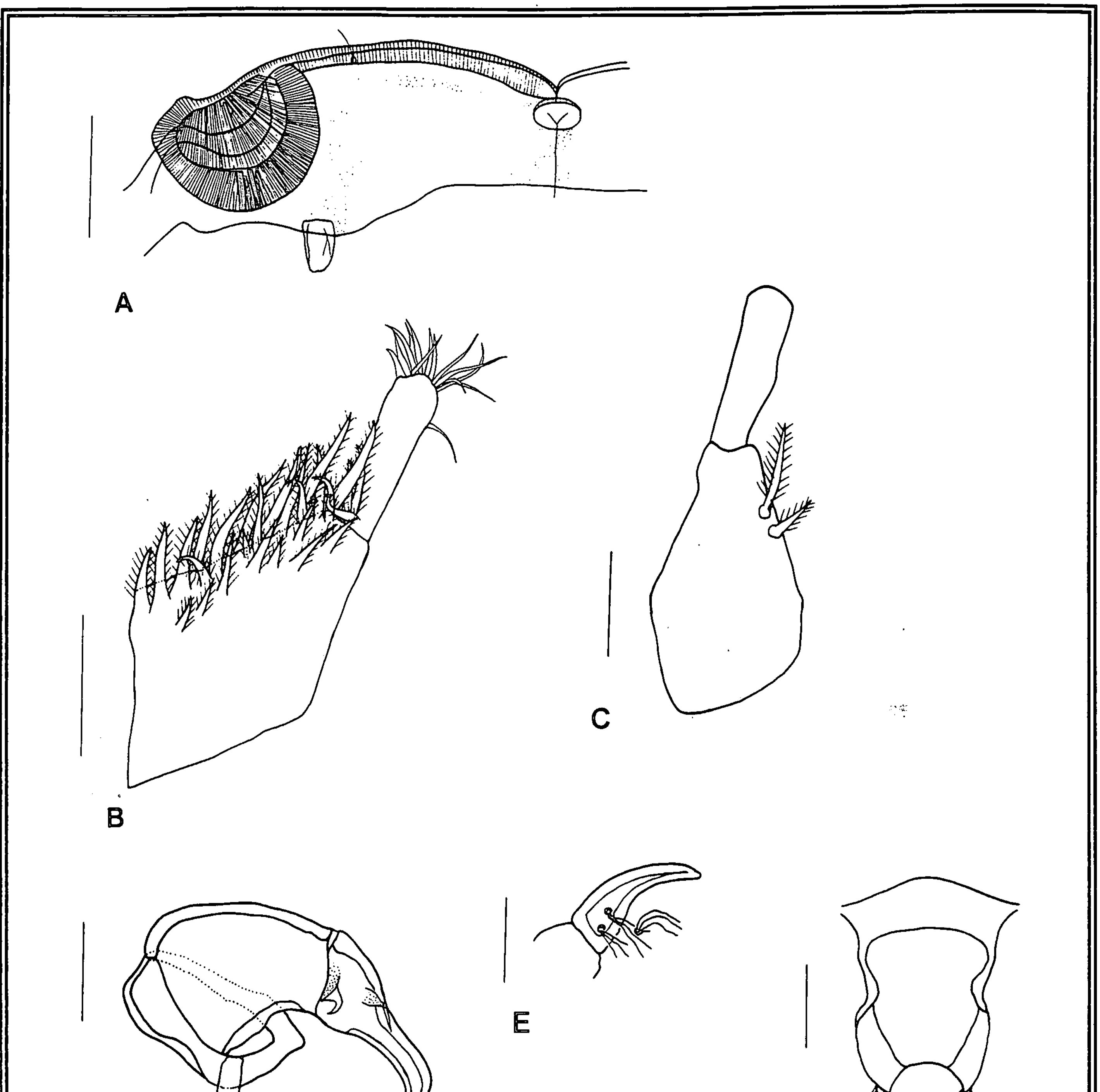

A
B
C
D
E
F
G

Figure 4.4

Microscope projection drawing of *Caligus acanthopagri* Lin, Ho and Chen, 1994 female occurring on the fish host *Acanthopagrus berda* (Forsskål, 1775), collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Maxillule

B. Maxilla

C. Maxilliped

D. Sternal furca

Scale-bar: A & D - 100μm. B & C - 200μm

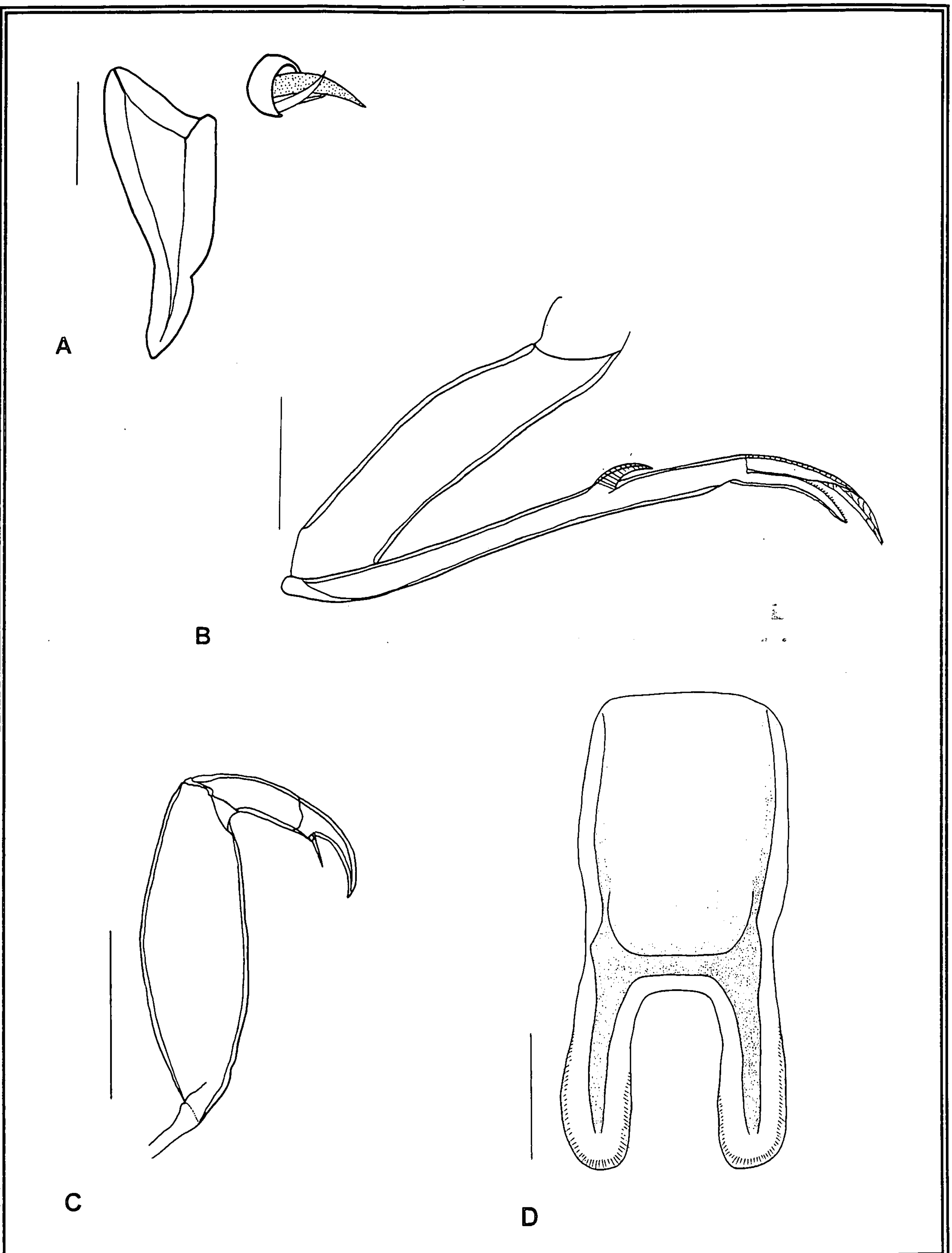

A
B
C
D

Figure 4.5

Microscope projection drawing of *Caligus acanthopagri* Lin, Ho and Chen, 1994 female occurring on the fish host *Acanthopagrus berda* (Forsskål, 1775), collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Leg 1

B. Leg 2

Scale-bar: A & B - 300µm

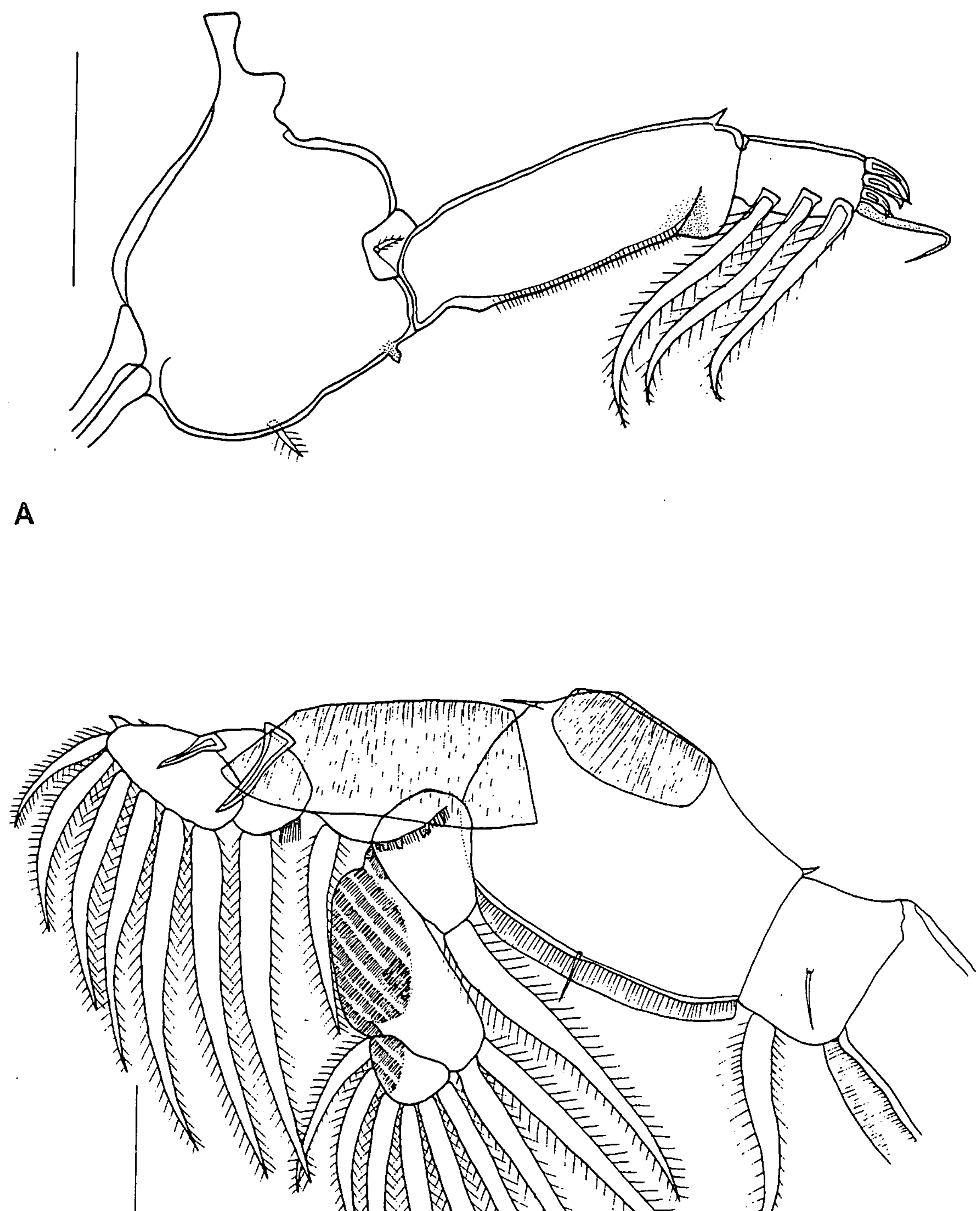

A
B

Figure 4.6

Microscope projection drawing of *Caligus acanthopagri* Lin, Ho and Chen, 1994 female occurring on the fish host *Acanthopagrus berda* (Forsskål, 1775), collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Leg 3

B. Leg 4

Scale-bar: A & B - 300μm

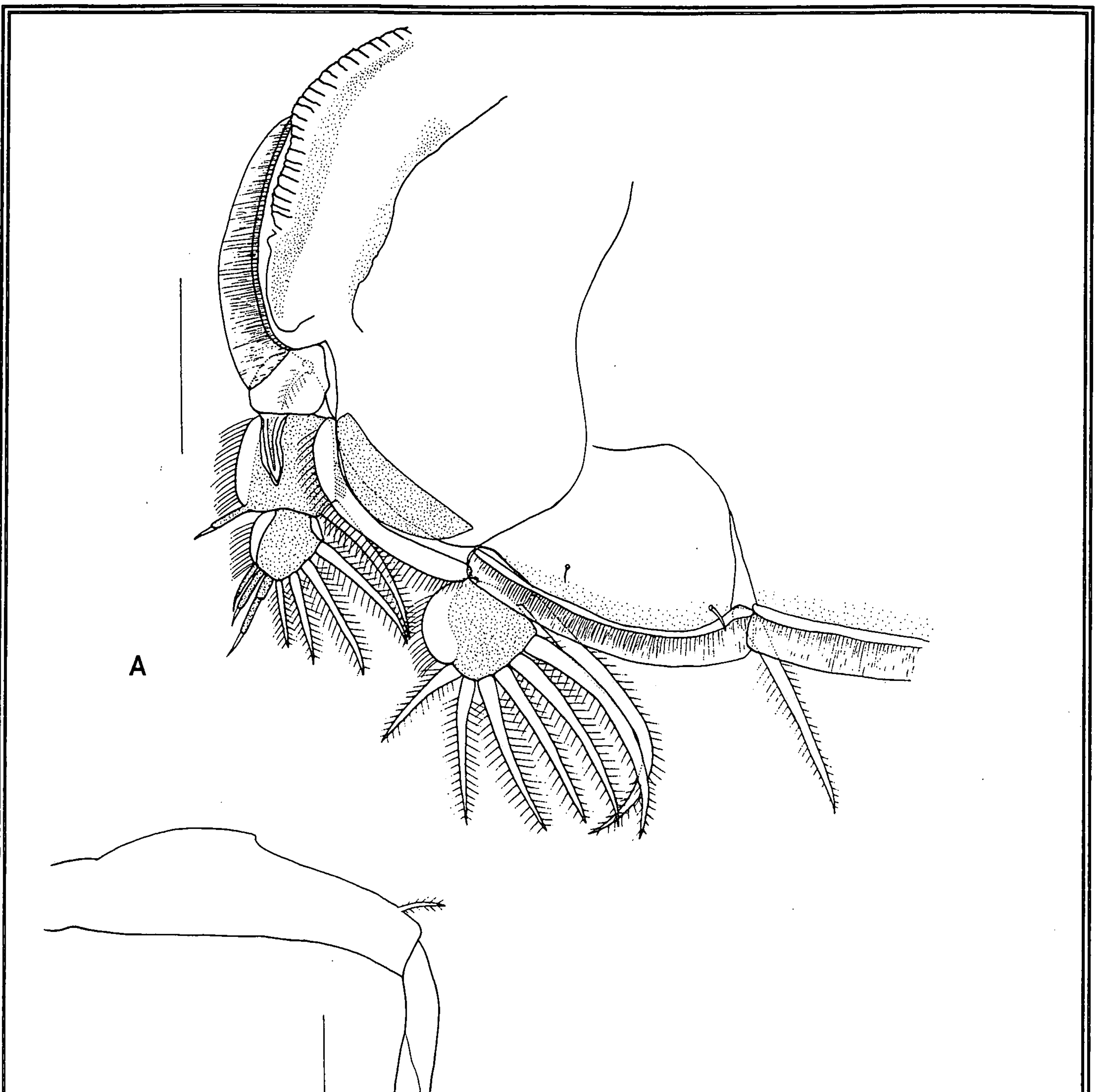

A
B

Figure 4.7

Microscope projection drawing of *Caligus acanthopagri* Lin, Ho and Chen, 1994 male (dorsal) occurring on the fish host *Acanthopagrus berda* (Forsskål, 1775), collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

Scale-bar: 1mm

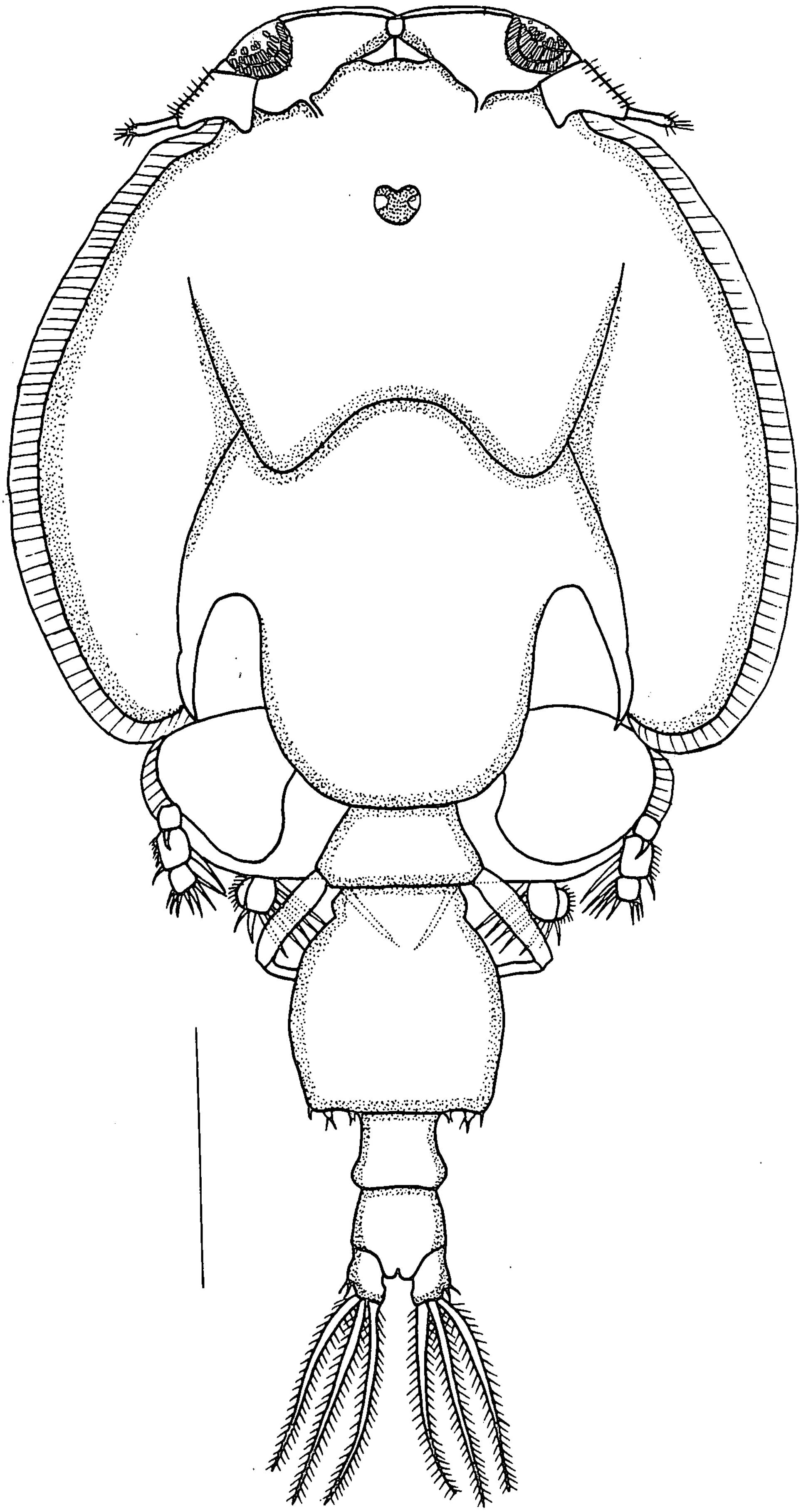


Figure 4.8

Microscope projection drawing of *Caligus acanthopagri* Lin, Ho and Chen, 1994 male (ventral) occurring on the fish host *Acanthopagrus berda* (Forsskål, 1775), collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

Scale-bar: 1mm

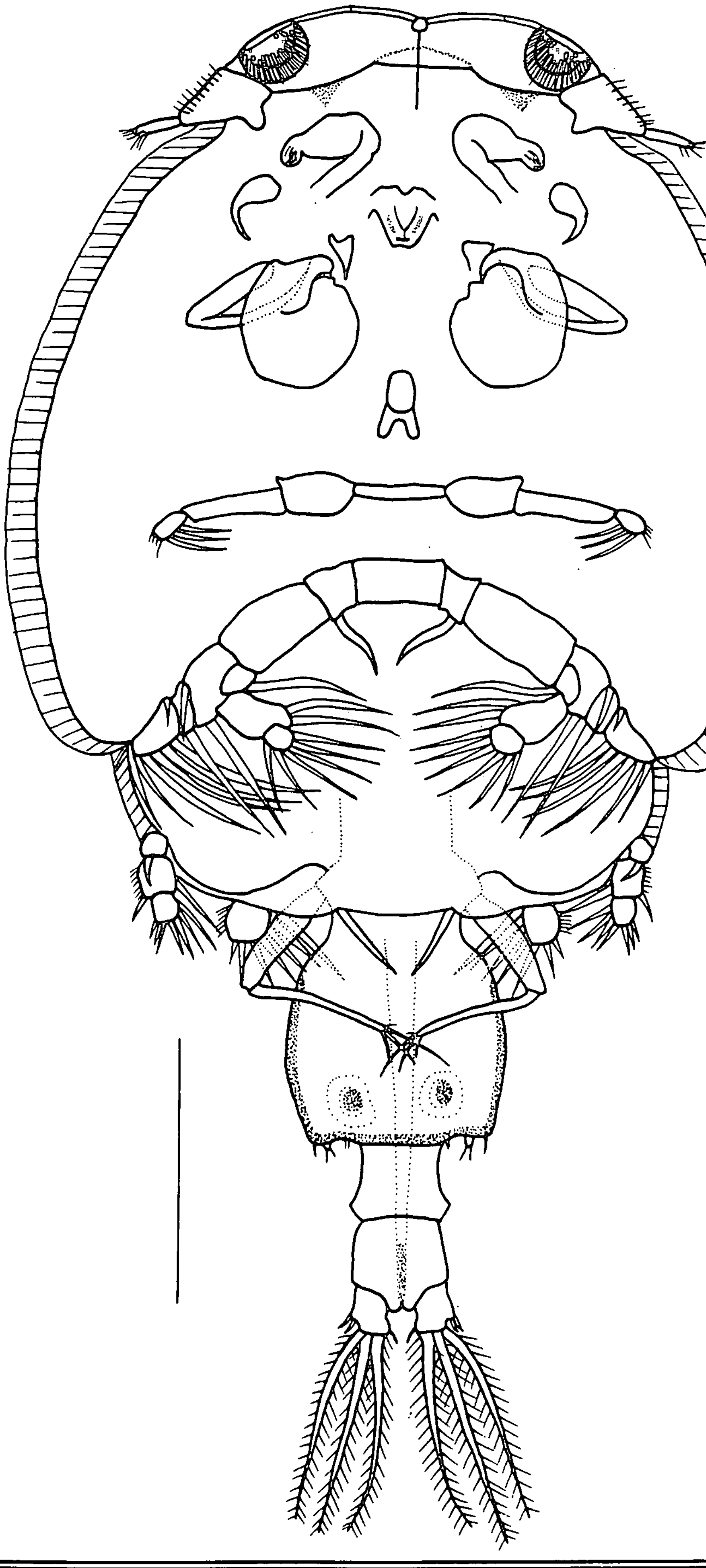


Figure 4.9

Microscope projection drawing of the urosome of *Caligus acanthopagri* Lin, Ho and Chen, 1994 male occurring on the fish host *Acanthopagrus berda* (Forsskål, 1775), collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

Scale-bar: 500μm

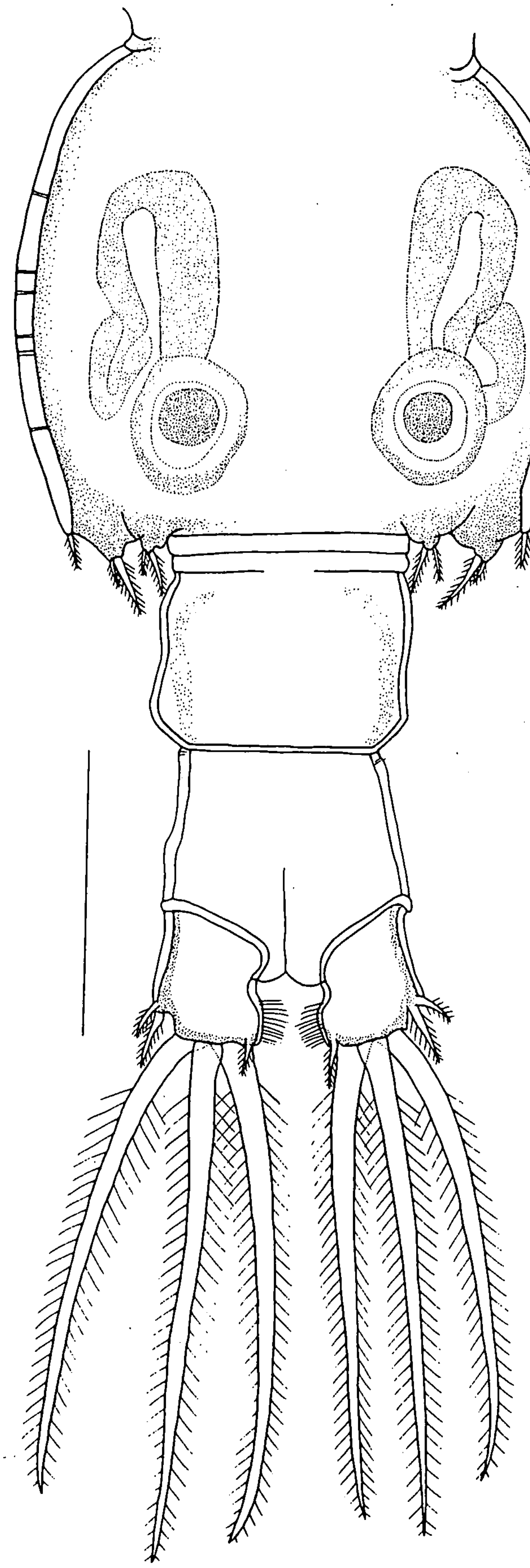


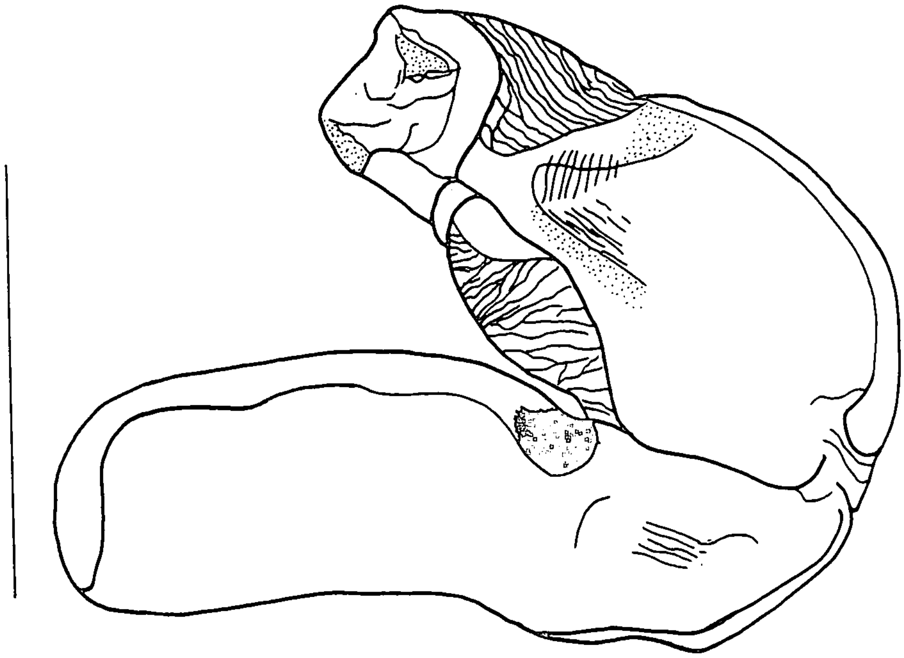
Figure 4.10

Microscope projection drawing of *Caligus acanthopagri* Lin, Ho and Chen, 1994 male occurring on the fish host *Acanthopagrus berda* (Forsskål, 1775), collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

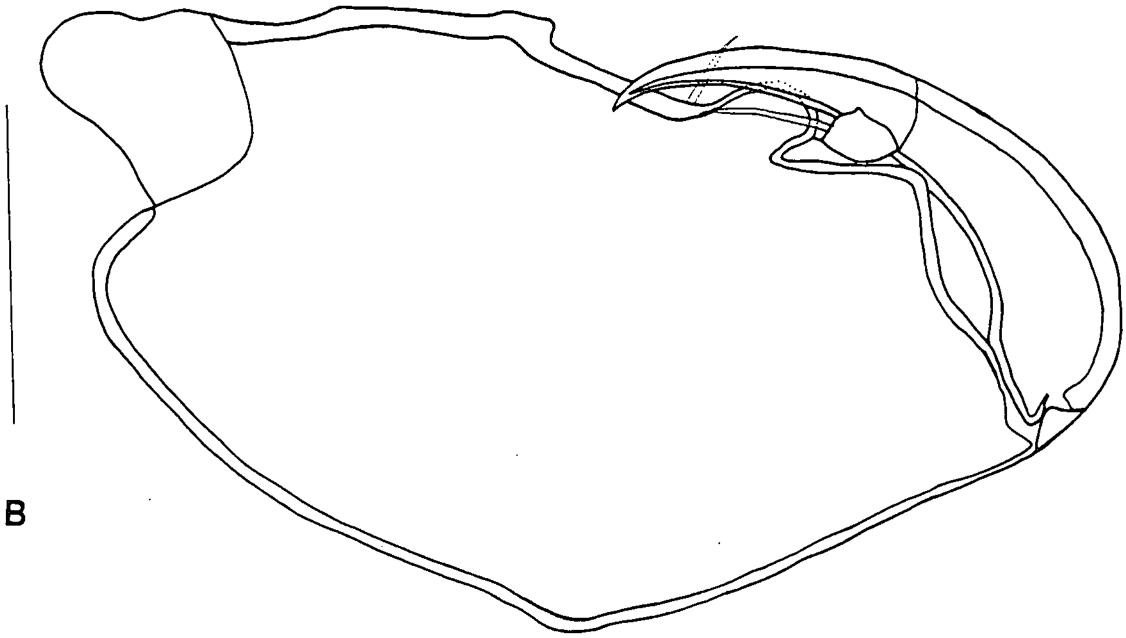
A. Antenna

B. Maxilliped

Scale-bar: A & B - 300μm



A



B

Figure 4.11

Scanning electron micrographs of *Caligus acanthopagri* Lin, Ho and Chen, 1994 female occurring on the fish host *Acanthopagrus berda* (Forsskål, 1775), collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Lunule

B. Antennule

C. Antenna

D. Postantennary process

E. Oral region, showing the antennae, mouth tube and maxillules

F. Mouth tube

Scale-bar: A & D - 10µm. B, C, E & F - 100µm

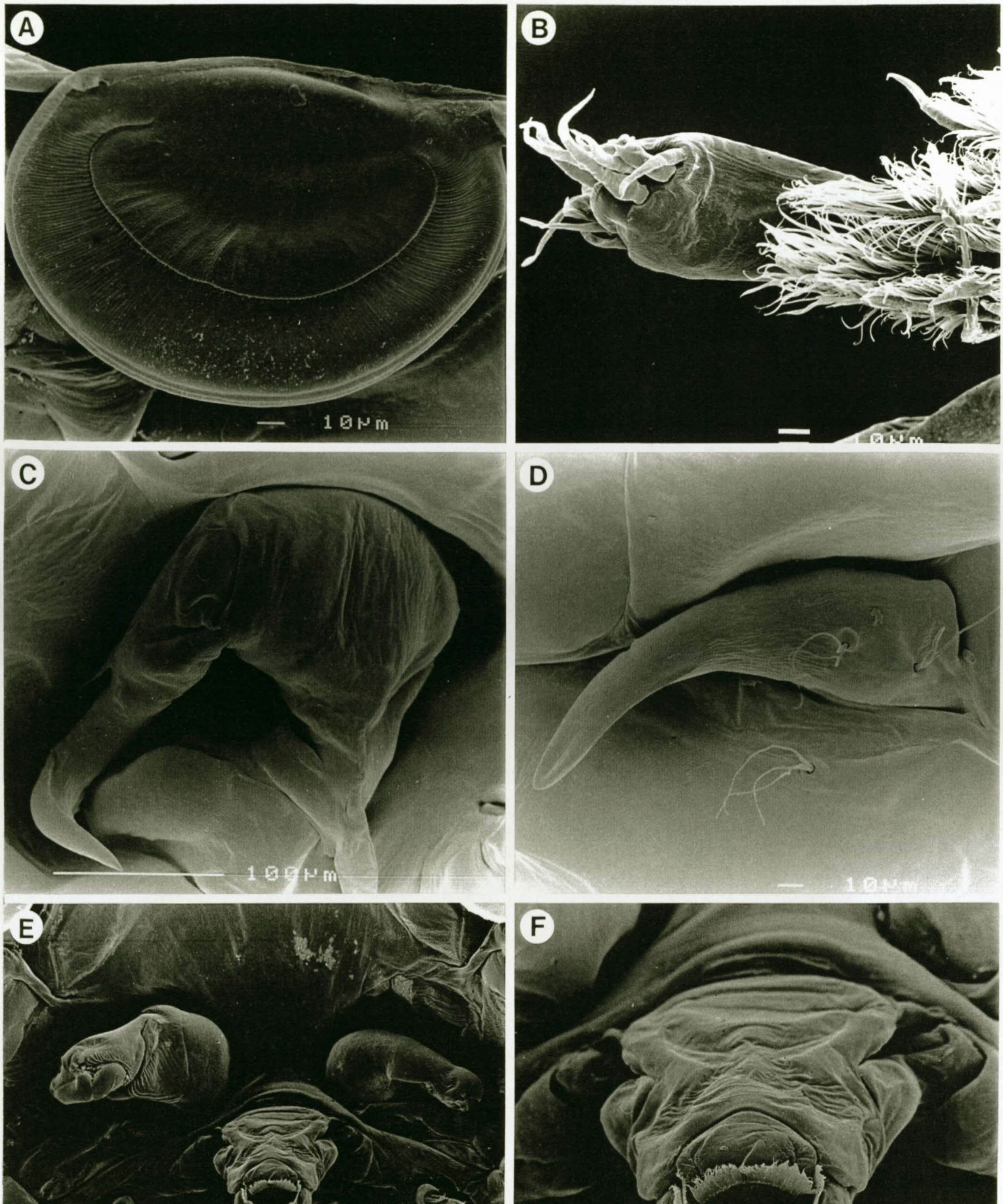

A
10µm
B
C
100µm
D
10µm
E
100µm
F
100µm

Figure 4.12

Scanning electron micrographs of *Caligus acanthopagri* Lin, Ho and Chen, 1994 female occurring on the fish host *Acanthopagrus berda* (Forsskål, 1775), collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Maxillule

B. Maxilla

C. Tip of calamus

D. Tip of canna

E. Sternal furca

F. Leg 1

Scale-bar: D - 1µm. A & C - 10µm. B, E & F - 100µm

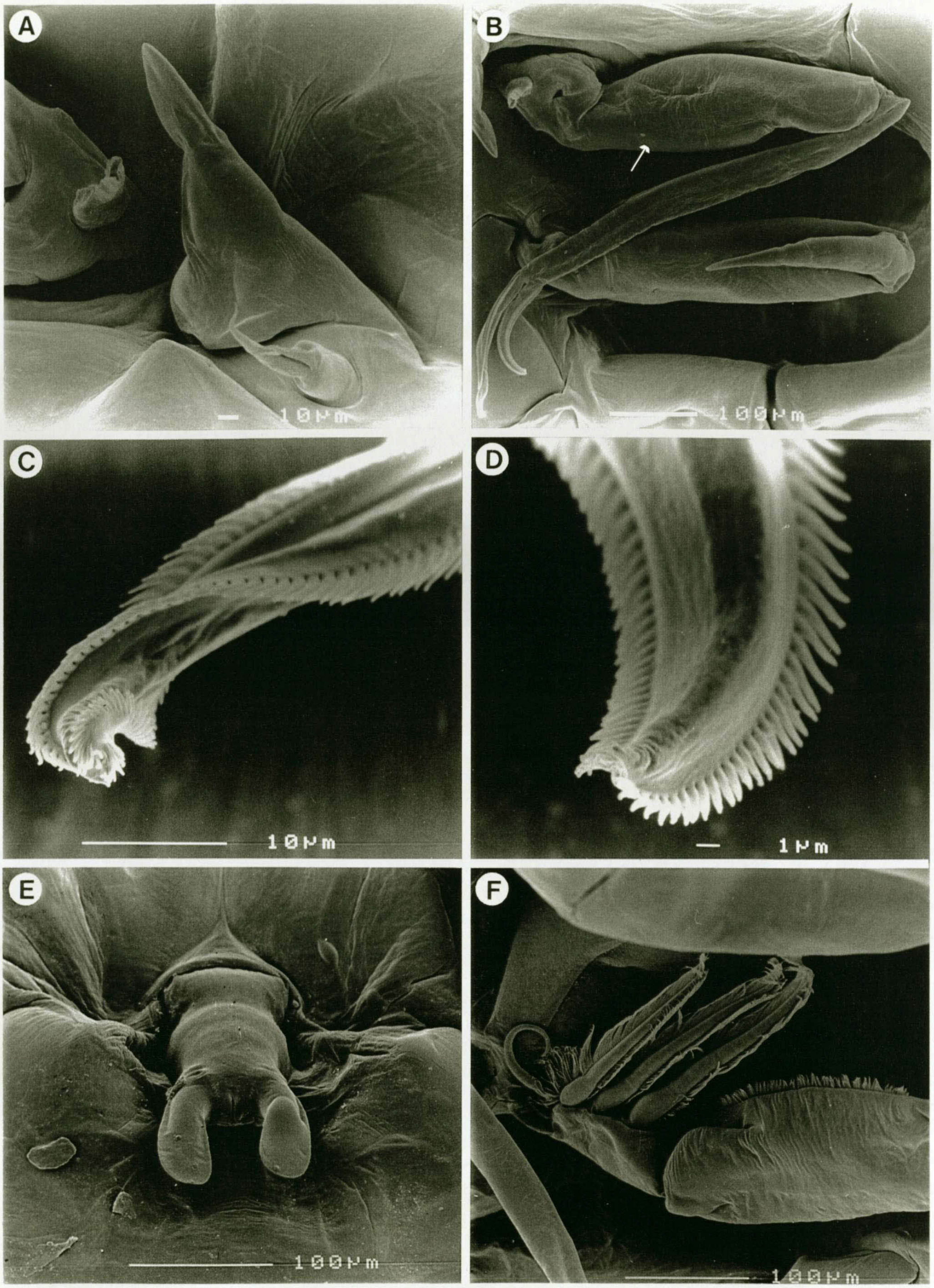

A
10µm
B
100µm
C
10µm
D
1µm
E
100µm
F
100µm

Figure 4.13

Scanning electron micrographs of *Caligus acanthopagri* Lin, Ho and Chen, 1994 female (A - D) and male (E & F) occurring on the fish host *Acanthopagrus berda* (Forsskål, 1775), collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Leg 2

B. Leg 3

C. Outer spine of first segment of leg 4

D. Terminal spines on leg 4 exopod

E. Leg 5

F. Leg 6

Scale-bar: C, D, E & F - 10µm. A & B - 100µm

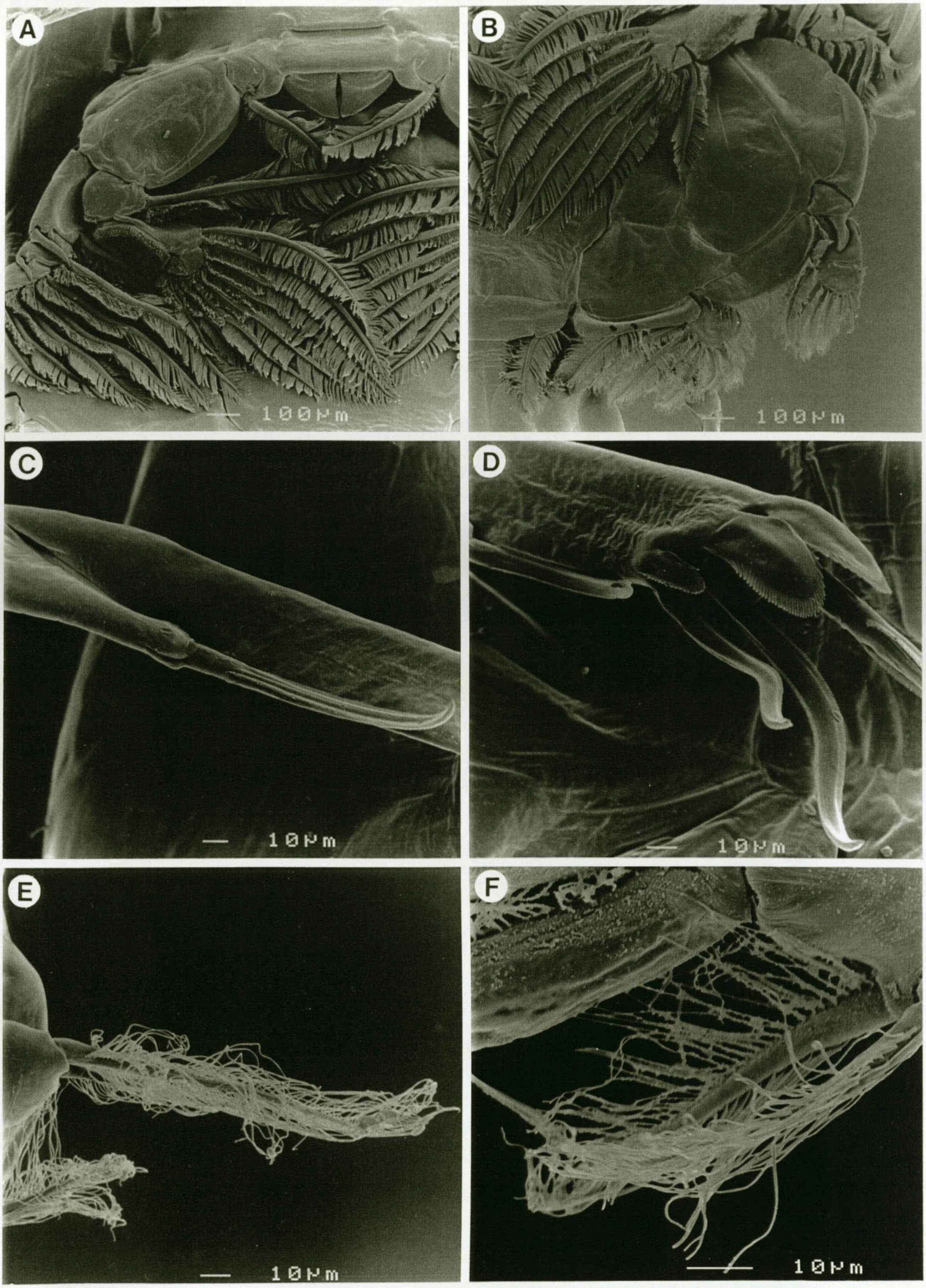

A
100µm
B
100µm
C
10µm
D
10µm
E
10µm
F
10µm

Figure 4.14

Scanning electron micrographs of *Caligus acanthopagri* Lin, Ho and Chen, 1994 male occurring on the fish host *Acanthopagrus berda* (Forsskål, 1775), collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Dorsal view

B. Ventral view

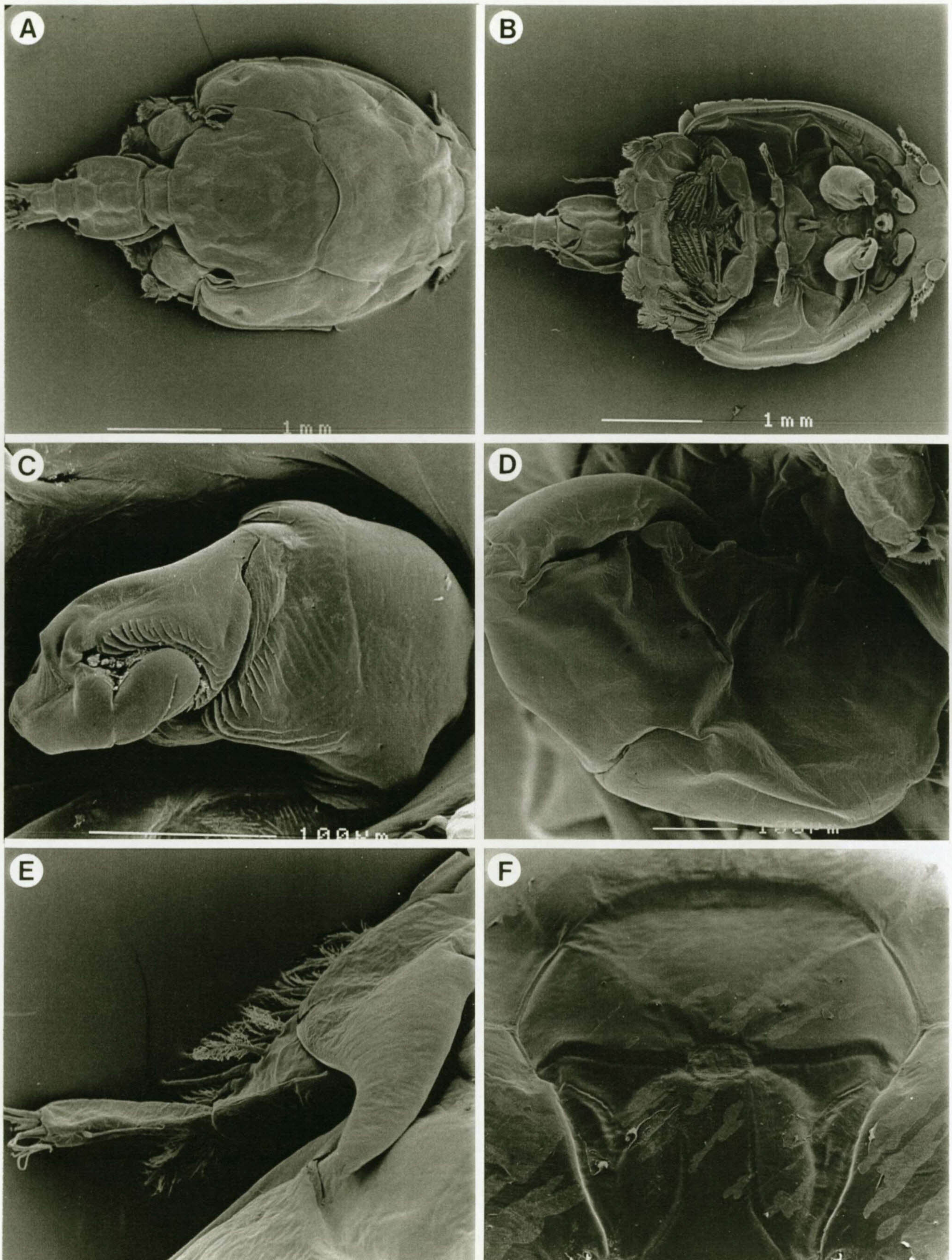
C. Antenna

D. Maxilliped

E. Extension of antennule

F. Eyes

Scale-bar: A & B - 1mm. C, D, E & F - 100µm


A
B
1 mm
1 mm
C
D
100 μm
E
F
100 μm
100 μm

Caligus confusus Pillai, 1961

Figures 4.15 – 4.28

Hosts: Bigeye kingfish *Caranx sexfasciatus* Quoy & Gaimard, 1825 and Cape stumpnose *Rhabdosargus holubi* (Steindachner, 1881).

Localities: Fanies Island and Charters Creek in Lake St Lucia.

Reference material: 6 / 046; 8 / 044; 8 / 046; 10 / 12; 10 / 13.

Material examined: 13 females and eight males were collected from the gill rakers of *Caranx sexfasciatus*. Two females and one male were collected from the gills of *Rhabdosargus holubi*.

Description of adult female: Body with typical appearance of *Caligus* (Figure 4.15, 4.16, 4.24A). Total length of female 5.03mm (4.79 – 5.24; n=5). Cephalothorax suborbicular, large, 1.1 times as wide as long. Frontal plates narrow (Figure 4.24B); lunules moderately large (Figure 4.24C). Posterior sinuses deep; lateral zones not reaching fourth pediger. Tip of antennule fairly long, not reaching lateral limit of dorsal shield. Fourth pediger wider than long; distinctly separated from genital complex; rounded lobes overlapping base of legs. Genital complex swollen; anterior neck narrow; postero-laterally produced into well rounded lobes. Abdomen short; one-segmented; suborbicular. Boundary between genital complex and abdomen distinct. Caudal rami very small (Figure 4.24D). Posterior margin of each ramus armed with one outer, one small medial and three longer terminal setae. Females without egg sacs.

Antennule: Two-segmented (Figure 4.17A). Proximal segment trapezoid, much broader than distal segment, with 14 large, stout, marginal setae, with 13 short, plumose ventral setae and two short, plumose dorsal setae (Figure 4.17B). Distal segment rod-shaped, slender, much longer than wide; armed with 13 terminal setae and one subterminal seta on posterior margin.

Antenna: Three segmented (Figure 4.17C, 4.24E). Proximal segment and second segment of equal size. Second segment robust, bearing one posterolateral seta. Terminal segment a strongly curved hook, bearing one basal seta and one marginal seta.

Postantennary process: Moderately large (Figure 4.17D, 4.24F). Irregular, bearing basal accessory process. Claw flattened with two basal papillae each bearing three long setules and one similar papilla located nearby on sternum bearing four long setules.

Mouth tube: Longer than wide with two spiniform processes inside mouth opening on dorsal side (Figure 4.25A & B).

Maxillule: Dentiform (Figure 4.18A, 4.25C). Proximal inner hump broad, followed by conical process. Claw flattened, apically rounded. Papilla at base bearing three setae.

Maxilla: Two-segmented, brachiform (Figure 4.18B). Lacertus unarmed. Brachium slender with flabellum on medial margin bearing hyaline membrane (Figure 4.25D). Calamus serrated on both margins. Canna serrated on both margins, shorter than calamus.

Maxilliped: Three-segmented (Figure 4.18C, 4.25E). Proximal segment stout, unarmed. Second and terminal segments fused, forming strong claw with subterminal, medial seta.

Sternal furca: Squarish base (Figure 4.18D, 4.25F). Tines parallel, inner borders diverging; tines about the length of base.

Leg 1: Biramous (Figure 4.19A). Protopod with one inner and one outer short, plumose seta. Exopod two-segmented; first segment with lateral distal spine and medial row of setules; second segment with four terminal elements which appear differently; first spine simple and longer than spines 2 or 3; spines 2 and 3 with spiniform secondary process (Figure 4.26A), equaling half the length of spines; spine 4 equal in length of spine 2 and 3, robust, tapering and unarmed; three plumose, long setae on posterior margin of same segment, different in size. Endopod rudimentary, unarmed.

Leg 2: Large plumose seta on coxa and one setule near intercoxal plate (Figure 4.19B); basis with one small, naked lateral seta, one long medial setule and a striated membrane along medial margin. Exopod three-segmented; first segment with one outer spine and one plumose inner seta; second segment with one outer spine and one long, plumose inner seta; third segment with three external spines constructed unequally, bearing serrated wings, and five long, plumose setae; first outer spine serrated on both margins; second outer spine with hyaline membrane on outer margin and serrated on inner margin; third outer spine with striated membrane along outer margin and setae on inner margin. First and second segments with rows of hairs on inner margin. Endopod three-segmented; first segment with one long, plumose inner seta and prominent crest of spines on outer margin; second segment with one long, plumose inner setae and a row of hairs on outer margin; third segment with six long, plumose terminal setae and a row of hairs on outer margin.

Leg 3: Adhesive pad on ventrolateral surface and striated marginal membranes (Figure 4.20A). Row of denticles above exopod. Circlet of strong teeth above endopod (Figure 4.26B); apically bifid projecting rib inner to teeth (Figure 4.26C). Exopod three-segmented; first segment with large basal claw, strongly curved; second segment with one outer spine and one plumose inner seta; third segment with three spines of different length and four plumose setae of equal length. Second and third segment with rows of setules on lateral margins. Endopod two-segmented; first segment expanded laterally into velum on outer margin and bearing one long, plumose seta on medial margin; second segment with five long, plumose setae.

Leg 4: Four-segmented (Figure 4.20B, 4.26D). Two outer setae on protopod short and plumose. Exopod three-segmented; first segment with two outer setules and one spine; second segment with one spine; third segment with three terminal spines of different length. Bases of five spines on exopod covered by pectinated membrane. Endopod missing.

Leg 5: One short seta on posterolateral corner of genital complex (Figure 4.26E).

Leg 6: Three short setae on posterolateral corner of genital complex (Figure 4.26F).

Armature on rami of legs 1-4:

Leg 1	Exp 1-0; III, 1, 3	Enp (rudimentary)
Leg 2	Exp I-1; I-1; I, II, 5	Enp 0-1; 0-1; 6
Leg 3	Exp I-0; 1-1; 3, 4	Enp 0-1; 5
Leg 4	Exp I-0; I-0, III	Enp (absent)

Description of adult male: Total length of male 2.51mm (2.39 – 2.68; n=5). Adult male distinctly smaller than female (Figure 4.21, 4.22, 4.27A & B). Cephalothorax large, suborbicular, less than 1.1 times as wide as long. Fourth pediger wider than long. Genital complex carry rudimentary leg 5 (Figure 4.27C) and leg 6 (Figure 4.27D) on posterolateral margin. Leg 5 represented by four setae; leg 6 represented by three setae. Abdomen one-segmented; wider than long (Figure 4.27E). Caudal rami larger than in female (Figure 4.27F), armed as in female.

Antenna: Three-segmented (Figure 4.23A, 4.28A). Proximal segment armed with corrugated patch. Second segment large; robust; armed distally with two corrugated patches. Terminal segment long with two subterminal, medial setae.

Maxillule: Hump absent (Figure 4.23B, 4.28B). Median ventral corrugated patch. Corrugated patch and papilla bearing three setae on sternum.

Maxilliped: Corpus bearing two unequal ridges on medial surface (Figure 4.23C, 4.28C).

Remarks: The strong teeth and bifid projecting rib (Figure 4.26B) that are used for accessory adhesion is characteristic of this species. These structures are found also on *Caligus constrictus* Heller, 1968, but the teeth patch is much longer than in *C. confusus*. Patterns on the dorsal shield of the male of *C. confusus* were also observed (Figure 4.28D, E & F). No such patterns were observed in any other *Caligus* species studied, and it may be just of ornamental importance. These patterns were observed only in the male, which is remarkably smaller than the female. The female bears a fifth leg as well as a sixth leg, which are both rudimentary.

Caligus confusus was described by Pillai in 1961 from *Caranx* species. Kensley and Grindley (1973) collected *C. confusus* specimens from the gill chambers of *Caranx djedaba* from Durban. These specimens were much larger than those described by Pillai (1961), but difference in size has no significance since such variations are common among parasitic copepods. The females in this study are even larger than those collected by Kensley and Grindley (1973). *Caligus confusus* has been found on many different *Caranx* species, but no mention was made of the host *Caranx sexfasciatus*. These caligids were found in the gill chambers of both *Caranx sexfasciatus* and *Rhabdosargus holubi* in the Lake St Lucia system during surveys in 1996 and 1997, and is also new host records for the South African coastline.

Figure 4.15

Microscope projection drawing of *Caligus confusus* Pillai, 1961 female (dorsal) occurring on the fish host *Caranx sexfasciatus* Quoy and Gaimard, 1825, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

Scale-bar: 1mm

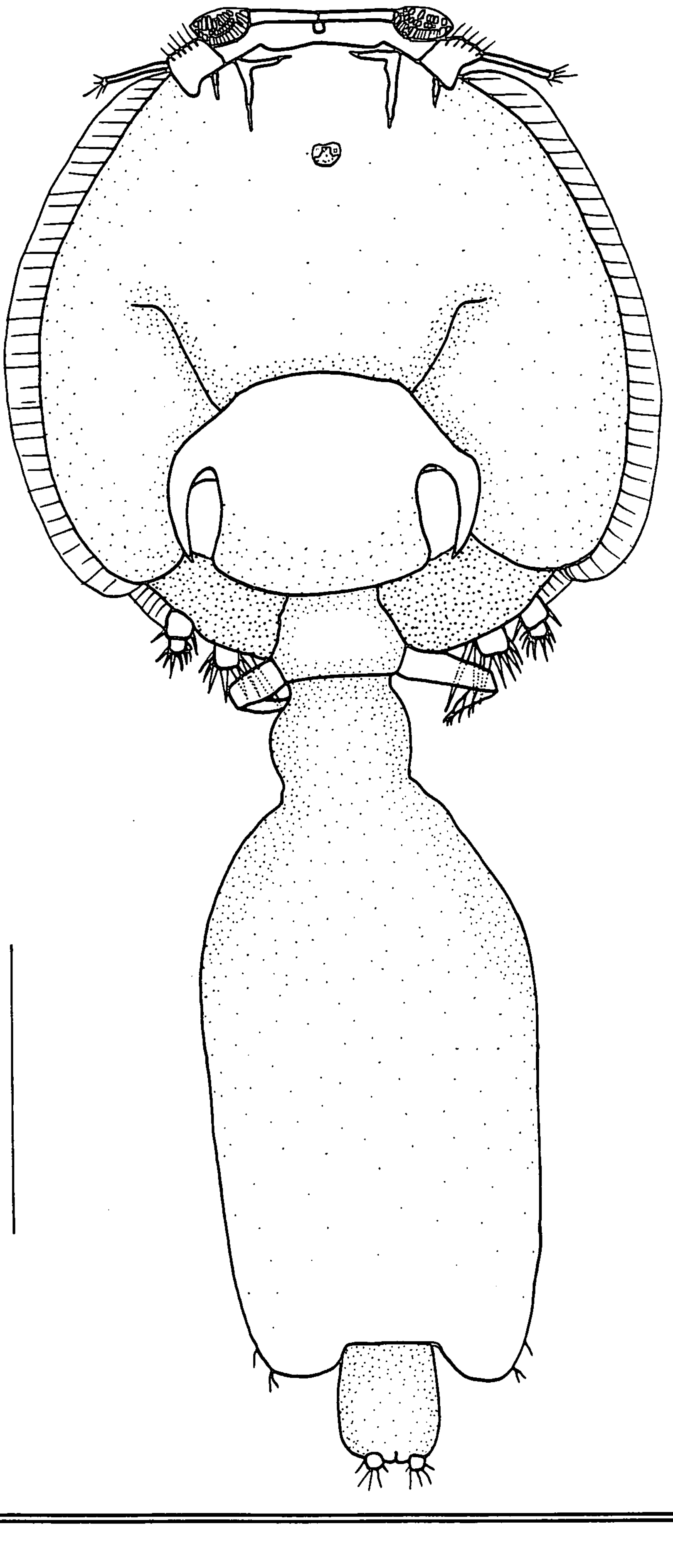


Figure 4.16

Microscope projection drawing of *Caligus confusus* Pillai, 1961 female (ventral) occurring on the fish host *Caranx sexfasciatus* Quoy and Gaimard, 1825, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

Scale-bar: 1mm

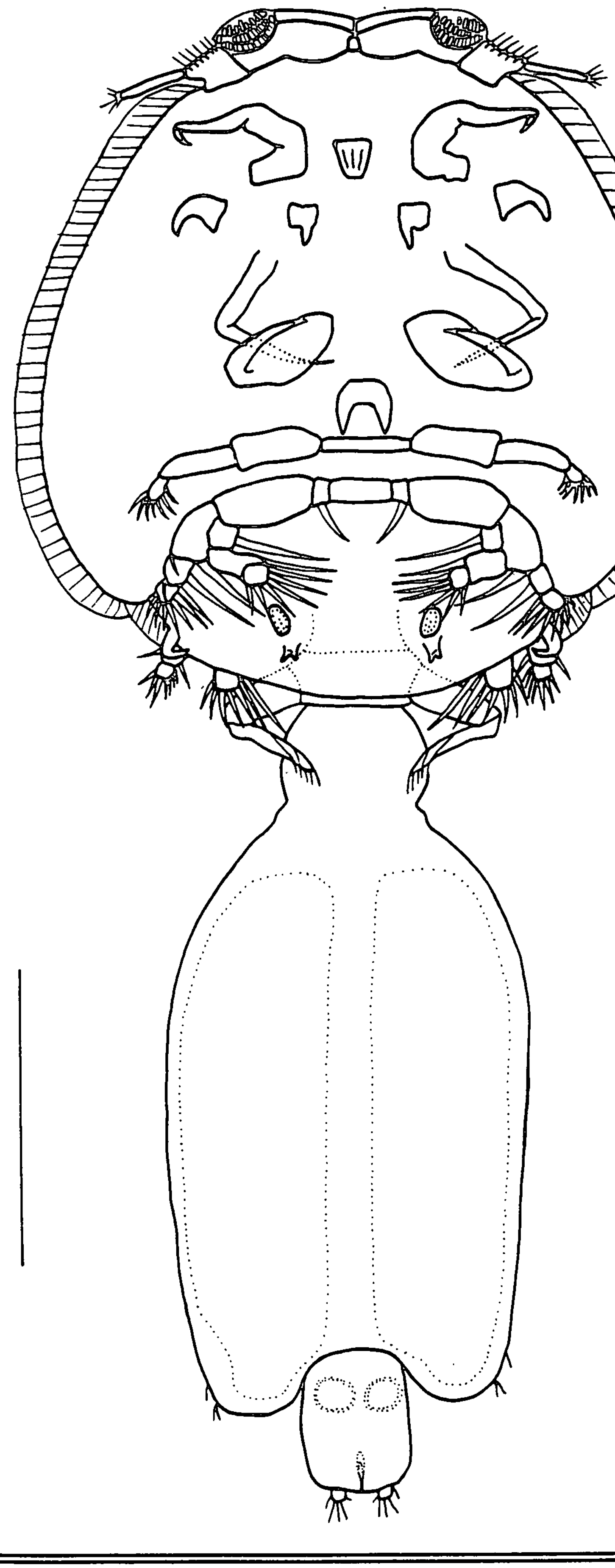


Figure 4.17

Microscope projection drawing of *Caligus confusus* Pillai, 1961 female occurring on the fish host *Caranx sexfasciatus* Quoy and Gaimard, 1825, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Ventral view of antennule

B. Dorsal view of antennule

C. Antenna

D. Postantennary process

Scale-bar: A, B & C - 100µm. D - 10µm

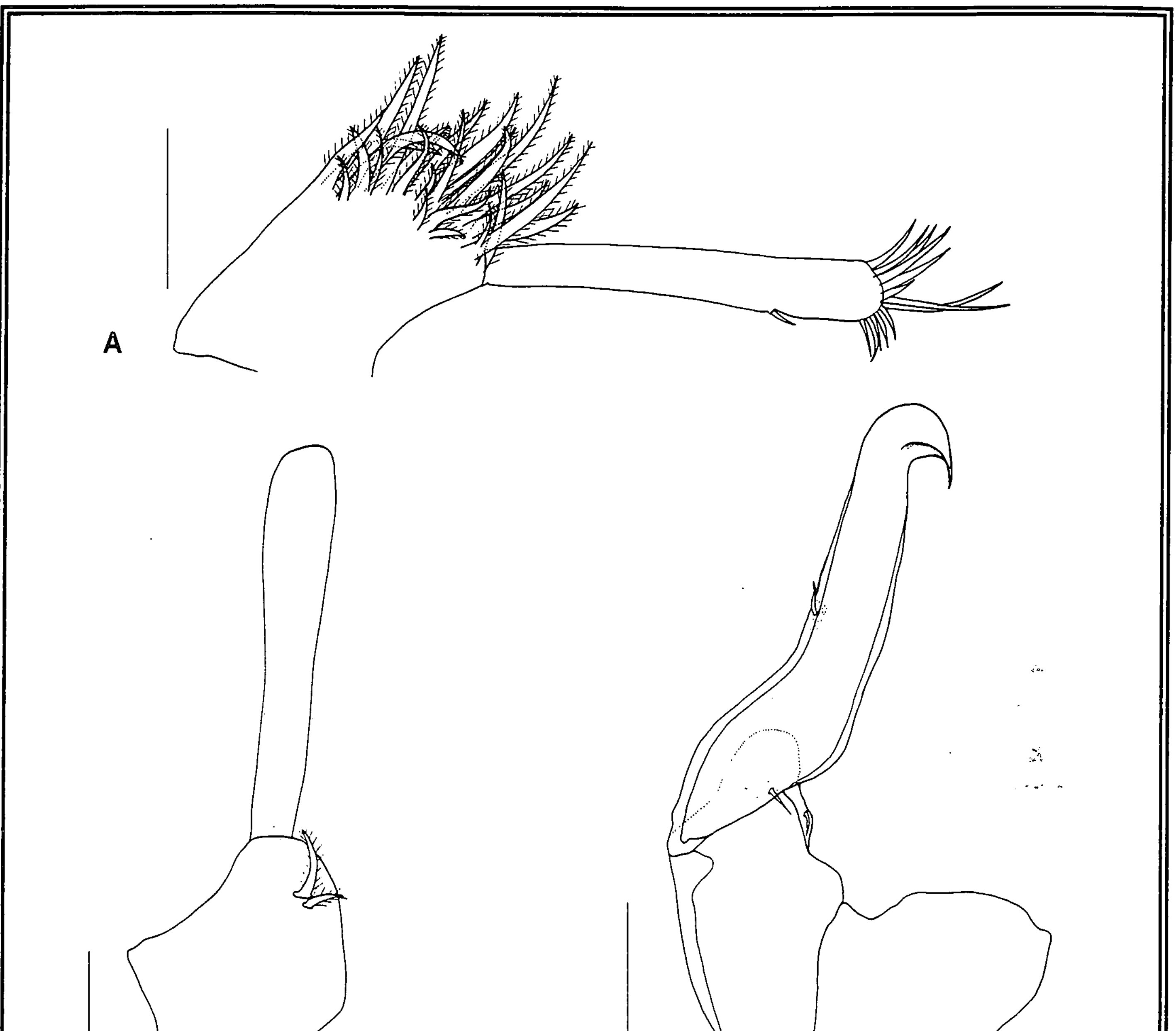

A
B
C
D

Figure 4.18

Microscope projection drawing of *Caligus confusus* Pillai, 1961 female occurring on the fish host *Caranx sexfasciatus* Quoy and Gaimard, 1825, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Maxillule

B. Maxilla

C. Maxilliped

D. Sternal furca

Scale-bar: B, C & D - 100µm. A - 10µm

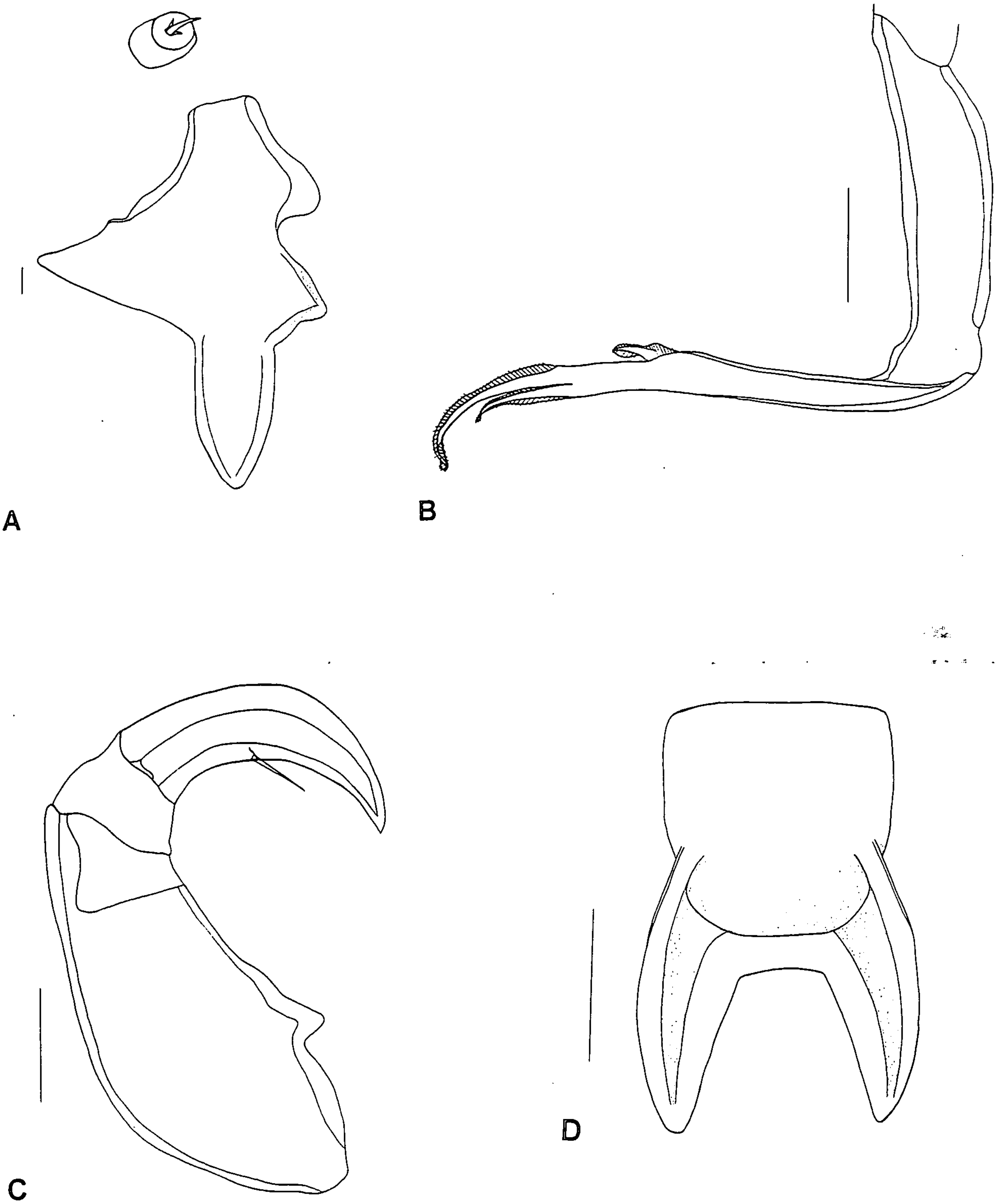

A
B
C
D

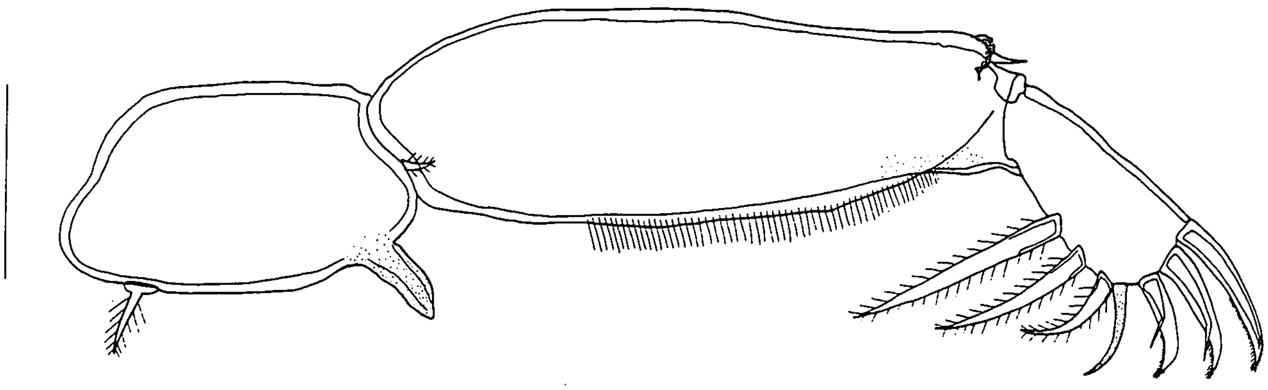
Figure 4.19

Microscope projection drawing of *Caligus confusus* Pillai, 1961 female occurring on the fish host *Caranx sexfasciatus* Quoy and Gaimard, 1825, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

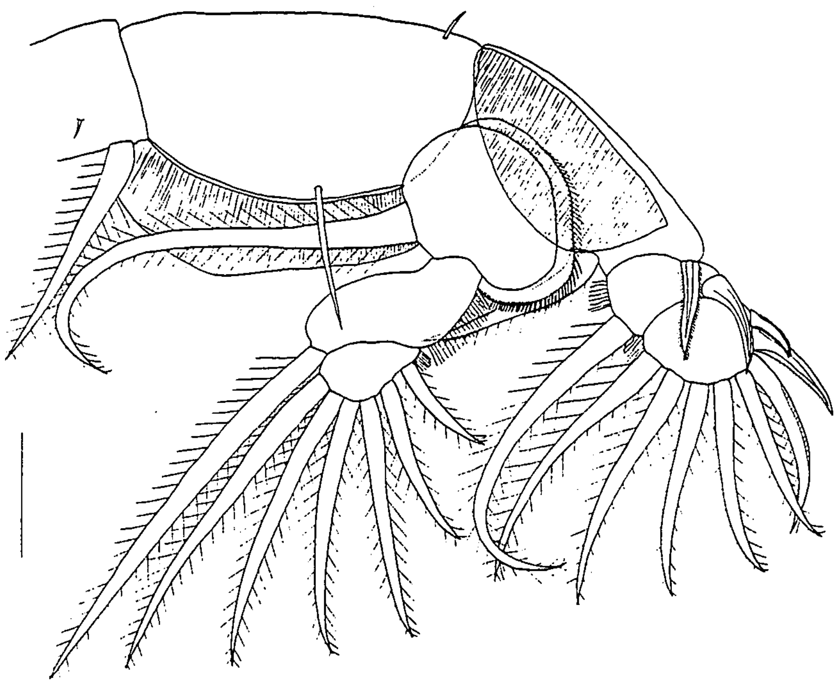
A. Leg 1

B. Leg 2

Scale-bar: A & B - 100μm



A



B

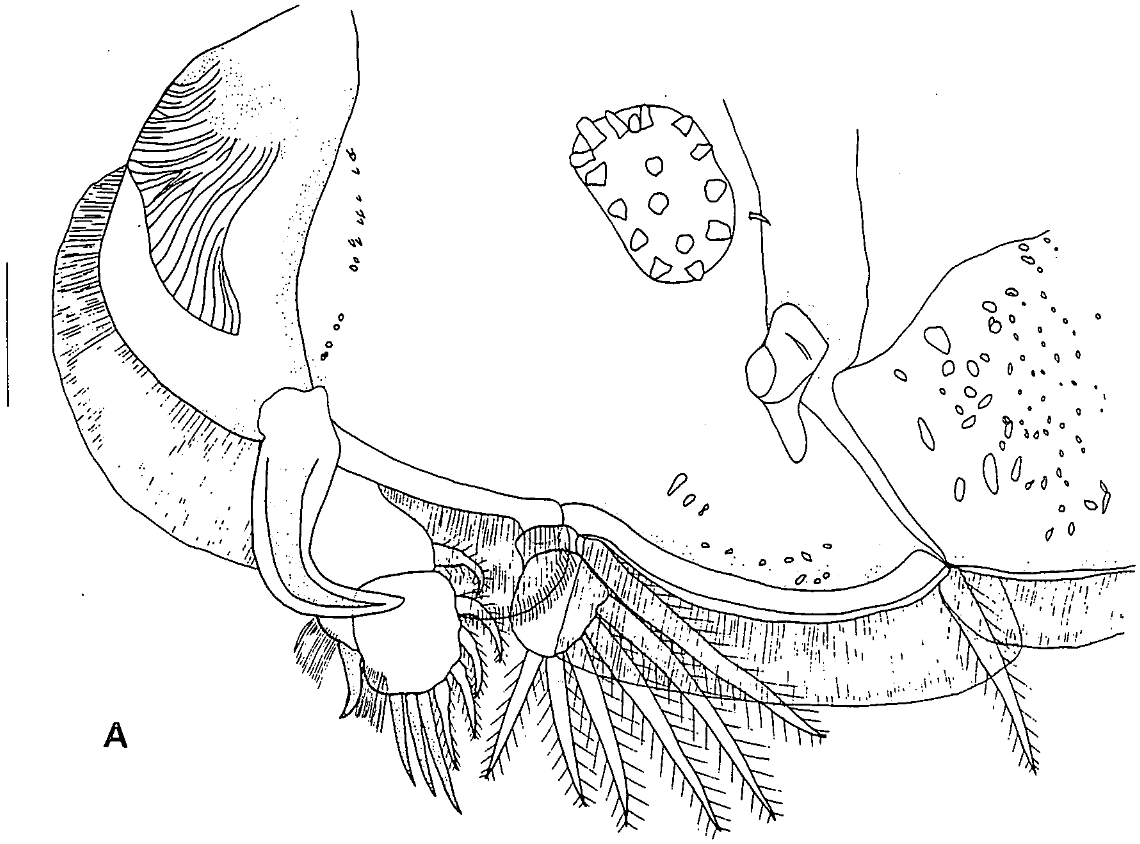
Figure 4.20

Microscope projection drawing of *Caligus confusus* Pillai, 1961 female occurring on the fish host *Caranx sexfasciatus* Quoy and Gaimard, 1825, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

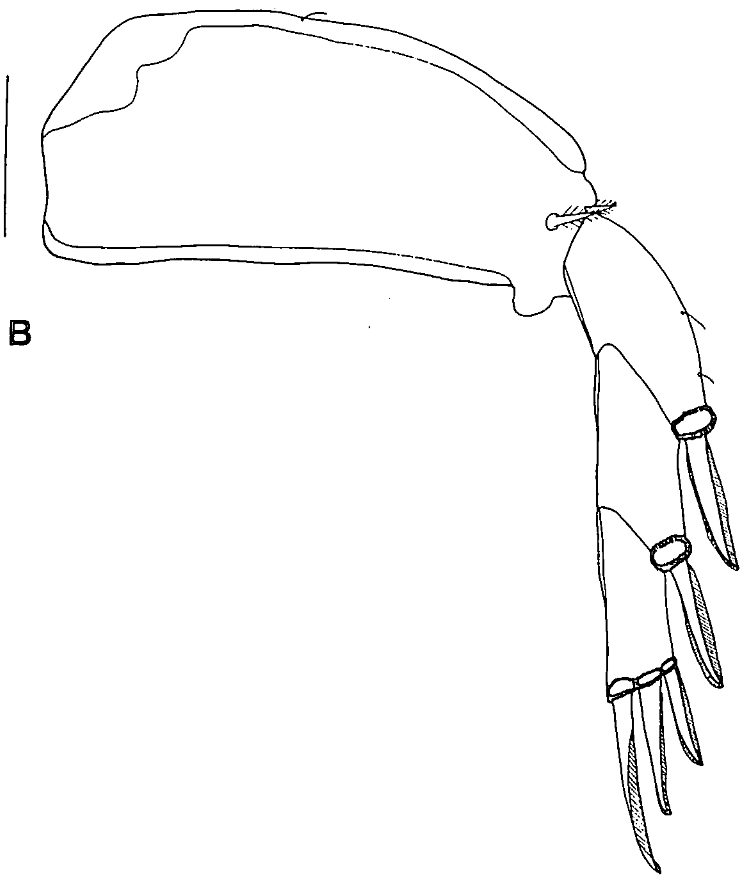
A. Leg 3

B. Leg 4

Scale-bar: A & B - 100μm



A



B

Figure 4.21

Microscope projection drawing of *Caligus confusus* Pillai, 1961 male (dorsal) occurring on the fish host *Caranx sexfasciatus* Quoy and Gaimard, 1825, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa

Scale-bar: 1mm

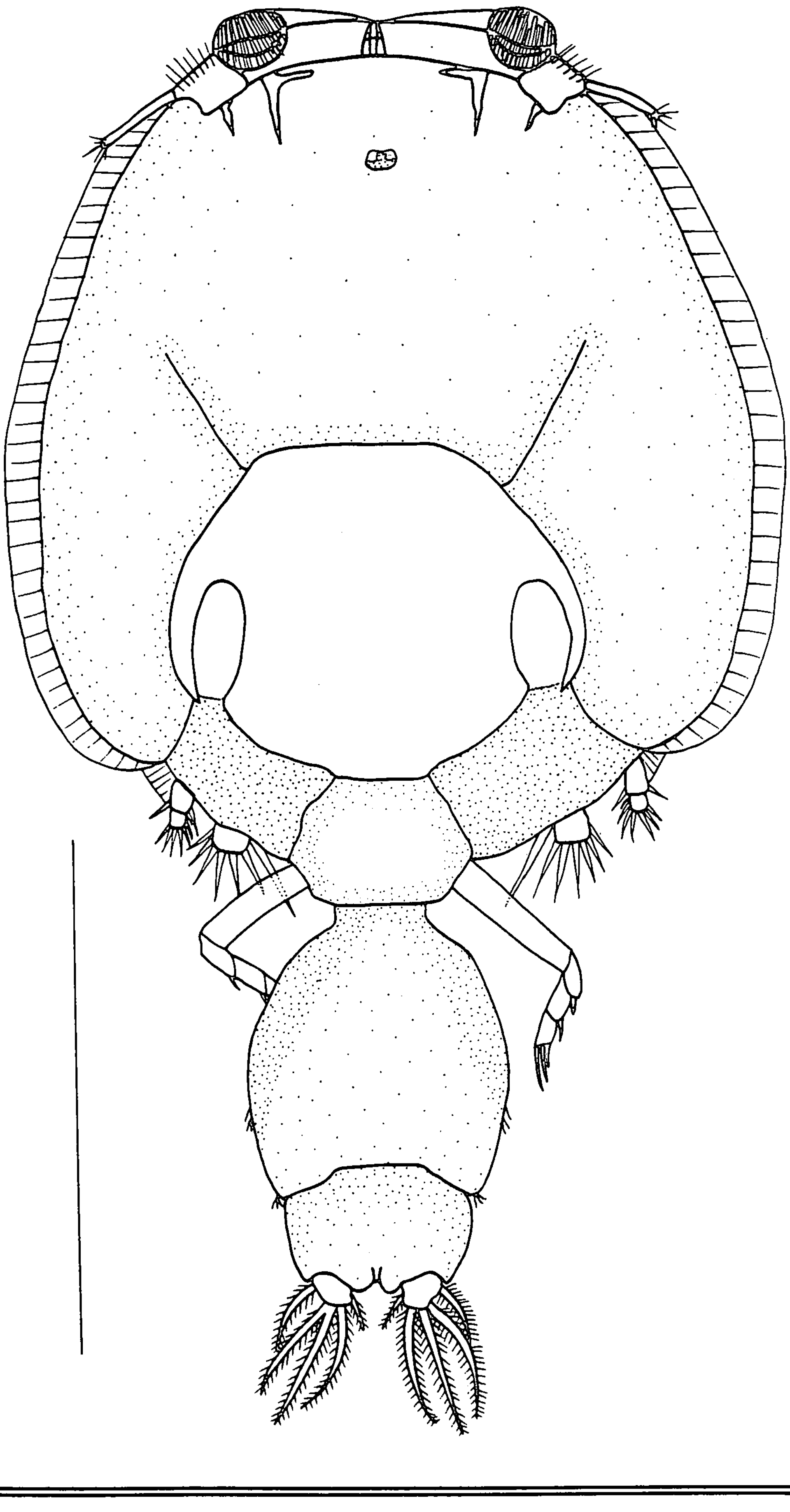


Figure 4.22

Microscope projection drawing of *Caligus confusus* Pillai, 1961 male (ventral) occurring on the fish host *Caranx sexfasciatus* Quoy and Gaimard, 1825, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa

Scale-bar: 1mm

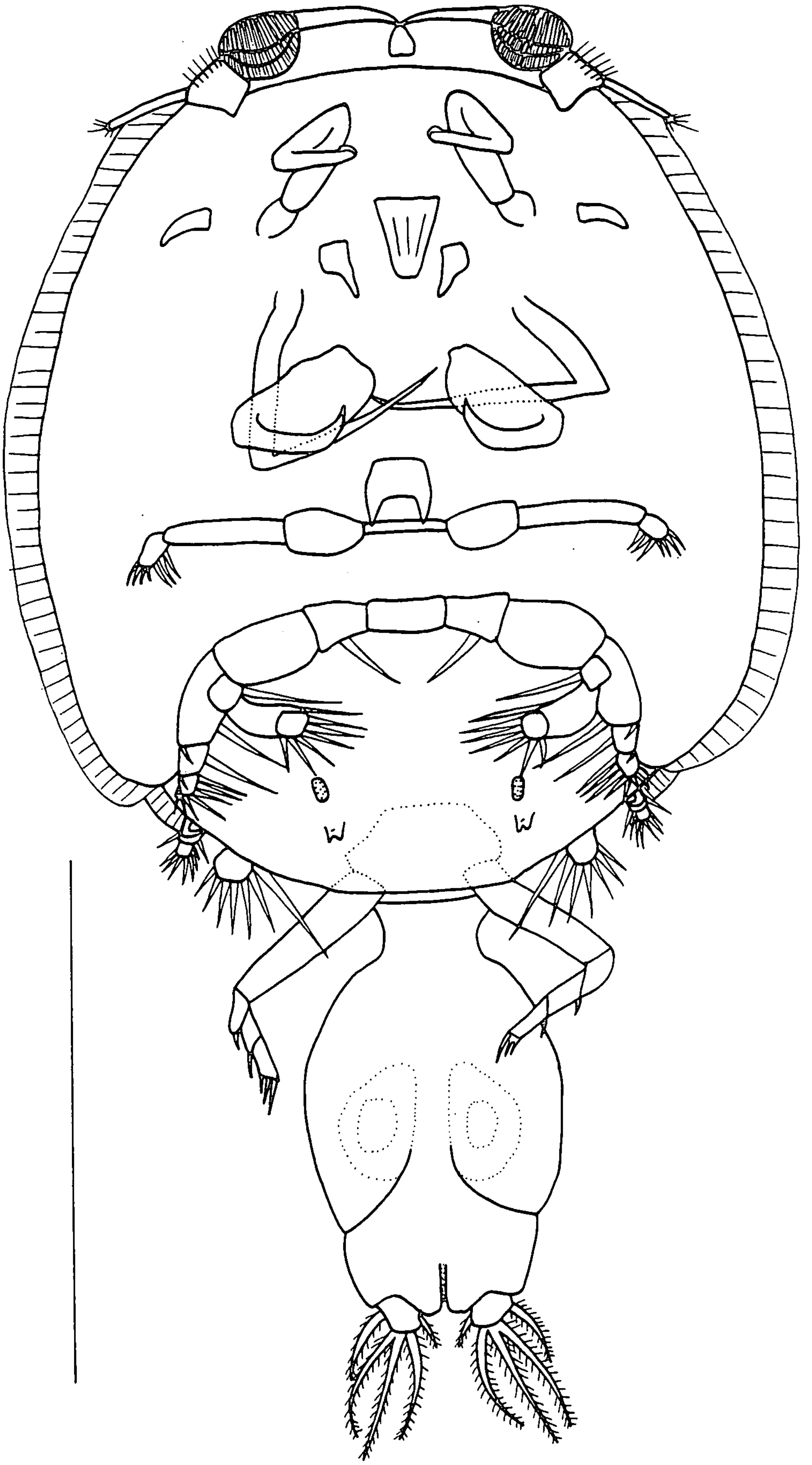


Figure 4.23

Microscope projection drawing of *Caligus confusus* Pillai, 1961 male occurring on the fish host *Caranx sexfasciatus* Quoy and Gaimard, 1825, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa

A. Antenna

B. Maxillule

C. Maxilliped

Scale-bar: A & C - 100µm. B - 10µm

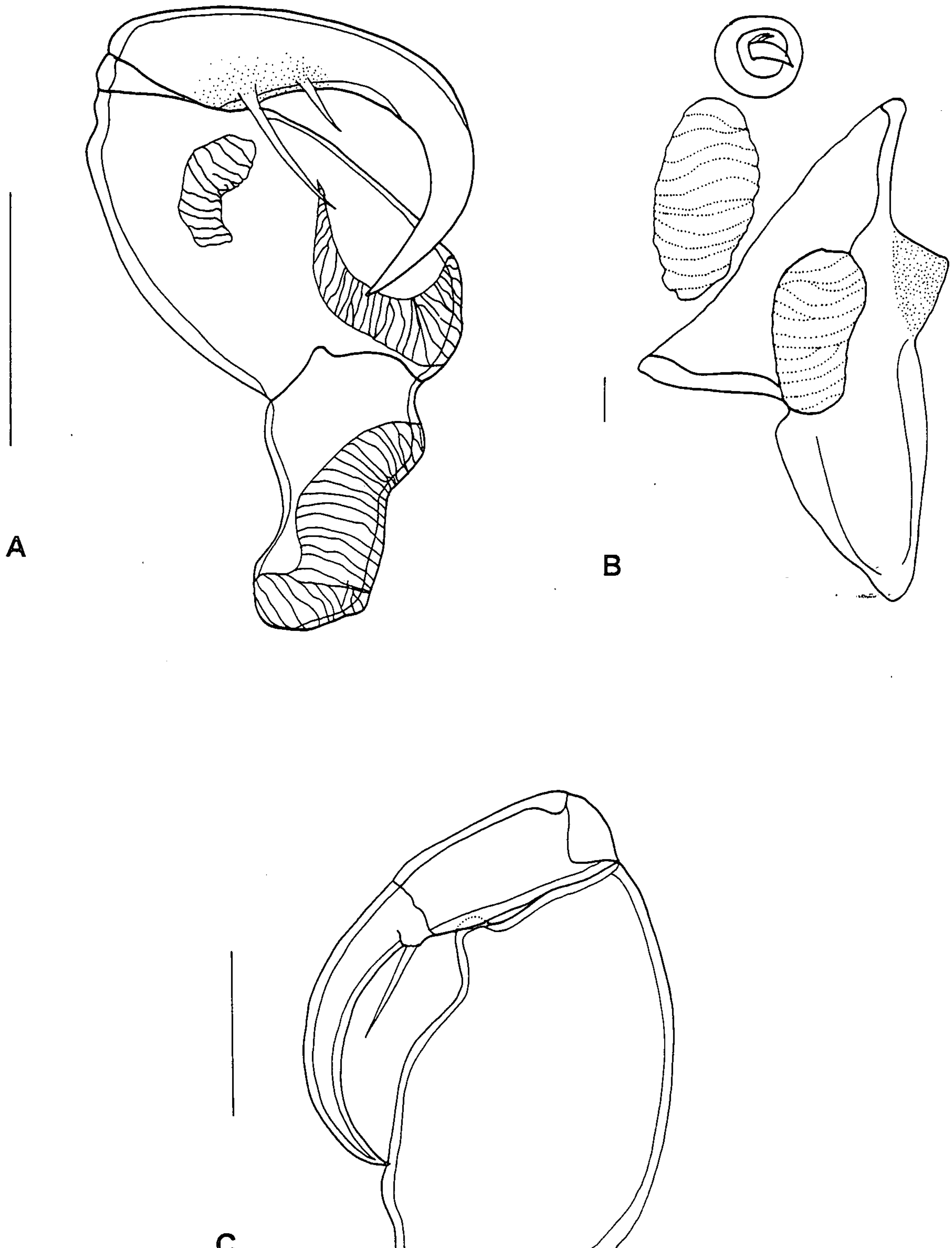

A
B
C

Figure 4.24

Scanning electron micrographs of *Caligus confusus* Pillai, 1961 female occurring on the fish host *Caranx sexfasciatus* Quoy and Gaimard, 1825, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Ventral view

B. Oral region and anterior part with frontal plates

C. Lunule

D. Caudal ramus

E. Antenna

F. Postantennary process

Scale-bar: A - 1mm. B & E - 100µm. C, D & F - 10µm

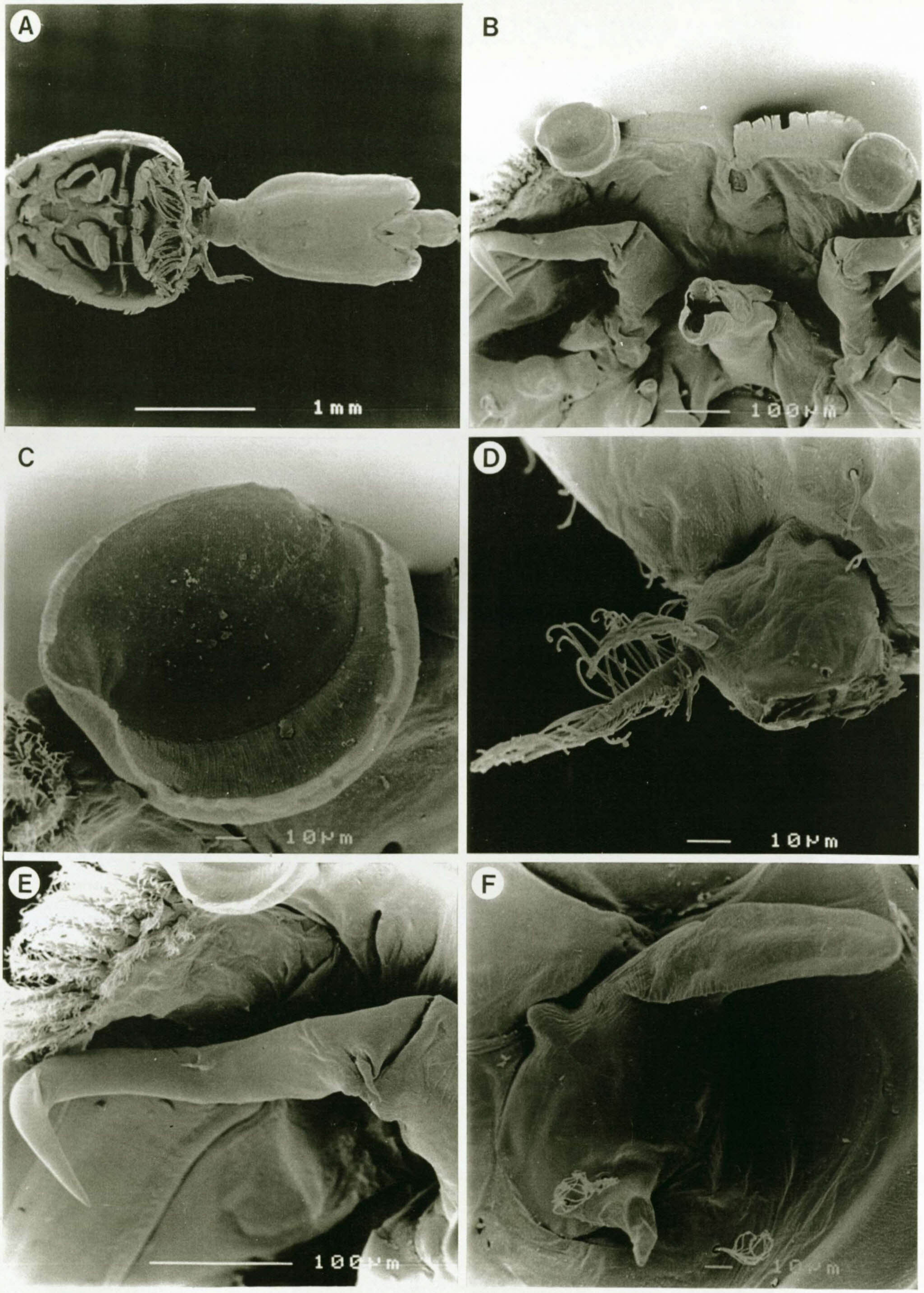

A
1 mm
B
100 µm
C
10 µm
D
10 µm
E
100 µm
F

Figure 4.25

Scanning electron micrographs of *Caligus confusus* Pillai, 1961 female occurring on the fish host *Caranx sexfasciatus* Quoy and Gaimard, 1825, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Spiniform processes on dorsal side of mouth opening

B. Spiniform process

C. Maxillule

D. Flabellum on branchium of maxilla

E. Maxilliped

F. Sternal furca

Scale-bar: E - 100μm. A, C, D & F - 10μm. B - 1μm

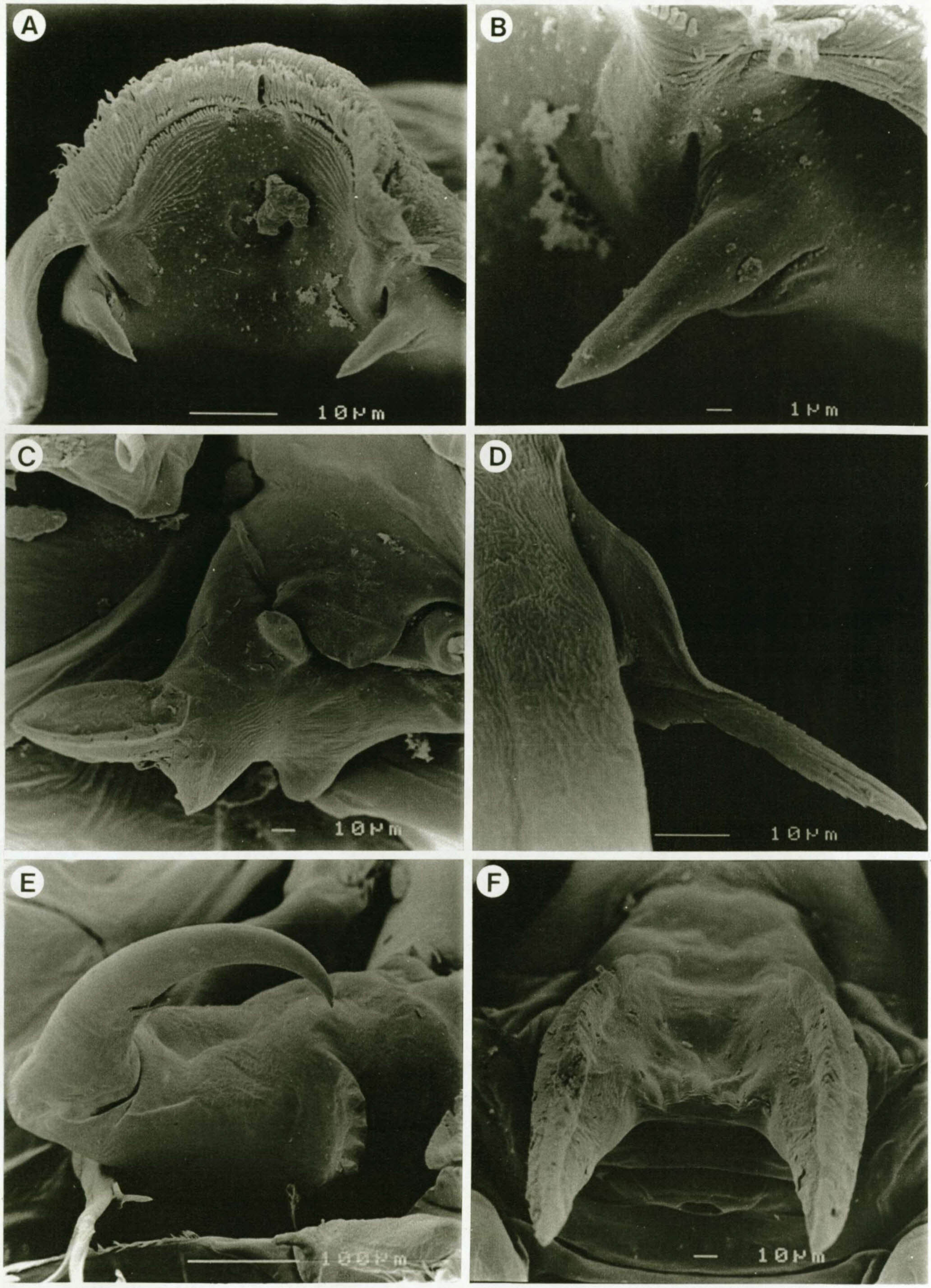

A
10µm
B
1µm
C
10µm
D
10µm
E
100µm
F
10µm

Figure 4.26

Scanning electron micrographs of *Caligus confusus* Pillai, 1961 female occurring on the fish host *Caranx sexfasciatus* Quoy and Gaimard, 1825, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Spine 2 and 3 with spiniform secondary process of leg 1 exopod

B. Strong teeth and bifid projecting rib above leg 3 endopod

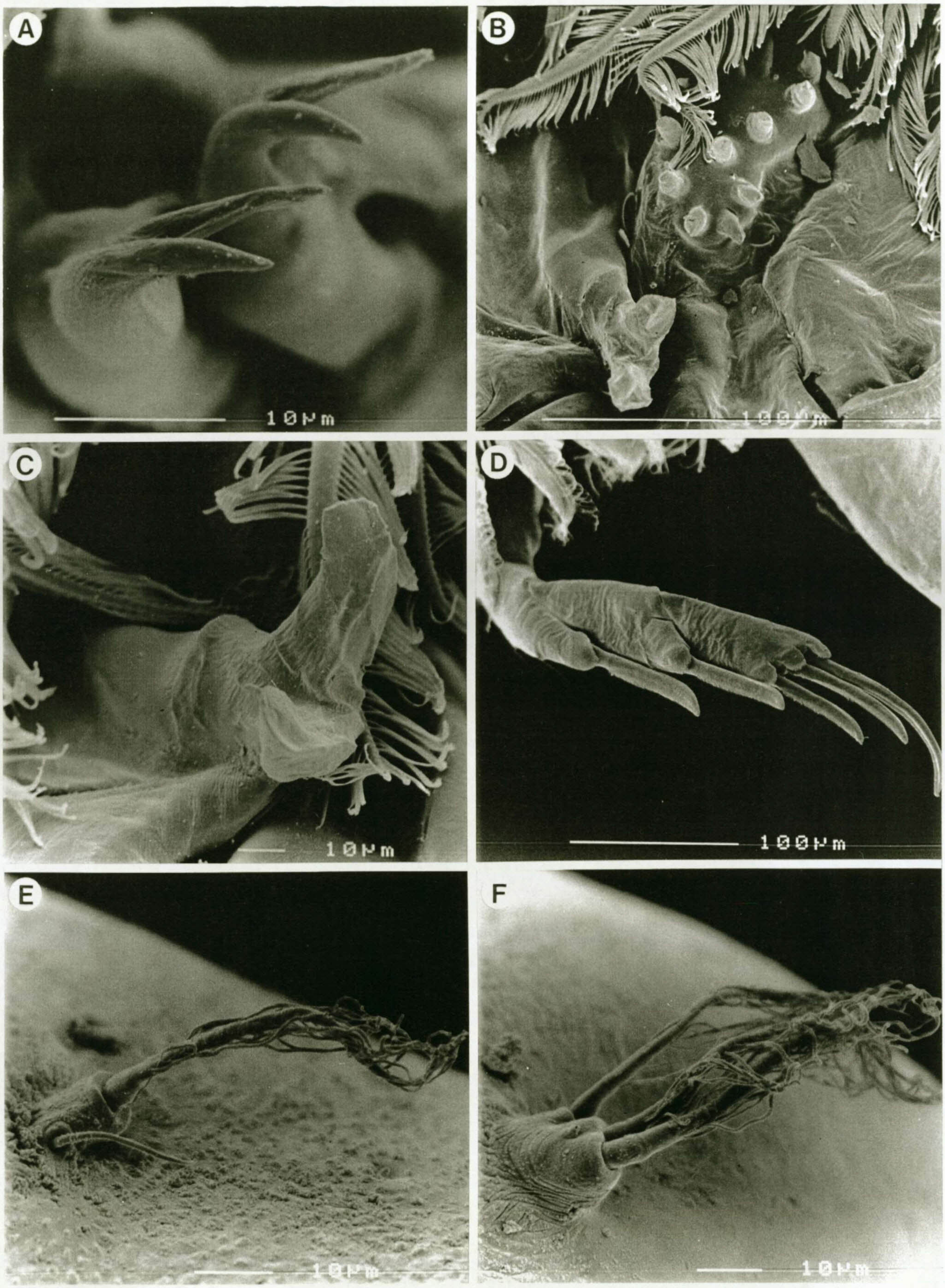
C. Bifid projecting rib

D. Leg 4

E. Leg 5

F. Leg 6

Scale-bar: B & D - 100µm. A, C, E & F - 10µm



A
10µm
B
100µm
C
10µm
D
100µm
E
10µm
F
10µm

Figure 4.27

Scanning electron micrographs of *Caligus confusus* Pillai, 1961 male occurring on the fish host *Caranx sexfasciatus* Quoy and Gaimard, 1825, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Dorsal view

B. Ventral view

C. Leg 5

D. Leg 6

E. Genital complex and abdomen

F. Setae on caudal ramus

Scale-bar: A, B & E - 100µm. C, D & F – 10µm

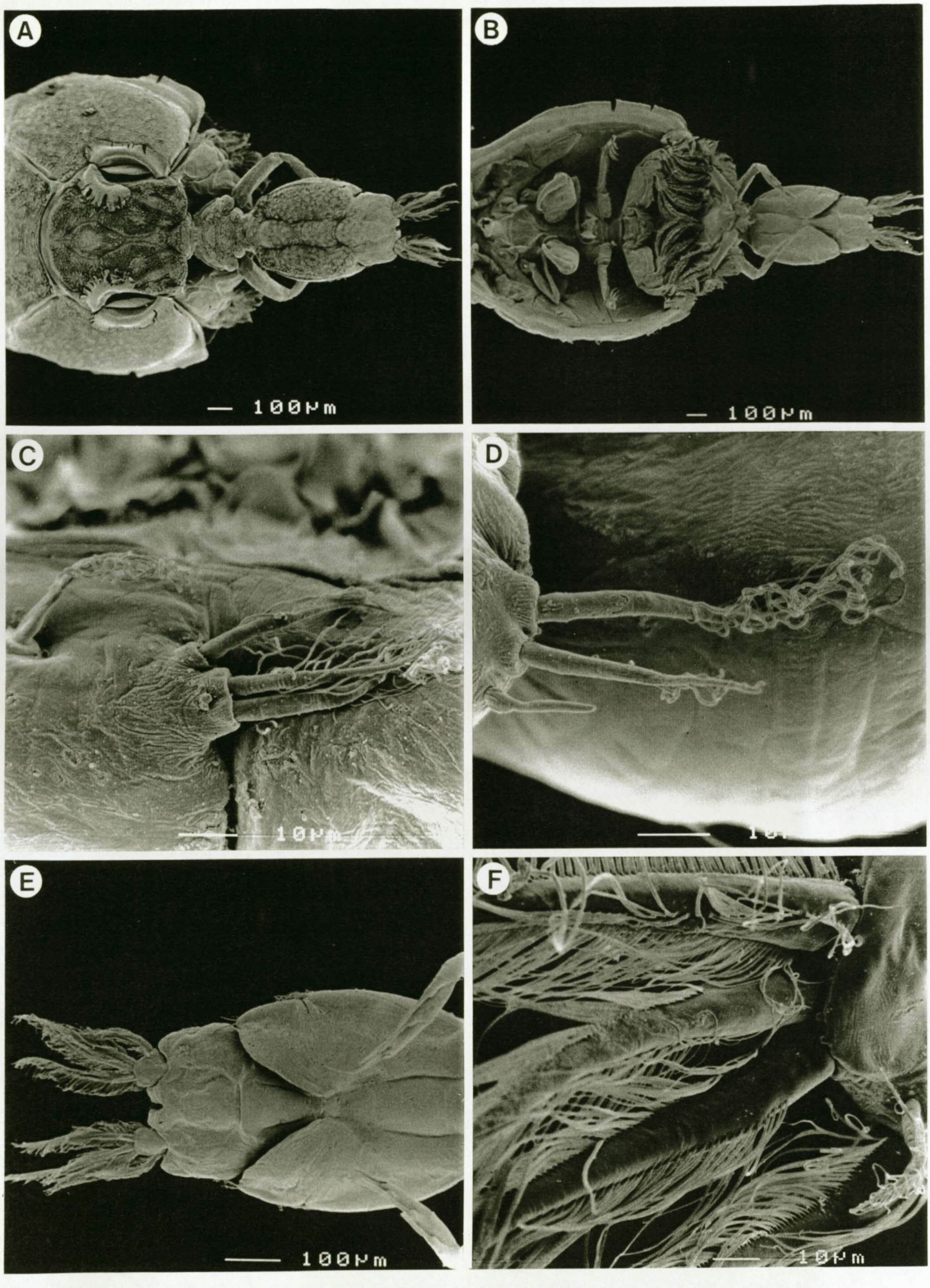

A
100 µm
B
100 µm
C
10 µm
D
E
100 µm
F
10 µm

Figure 4.28

Scanning electron micrographs of *Caligus confusus* Pillai, 1961 male occurring on the fish host *Caranx sexfasciatus* Quoy and Gaimard, 1825, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Antenna

B. Maxillule

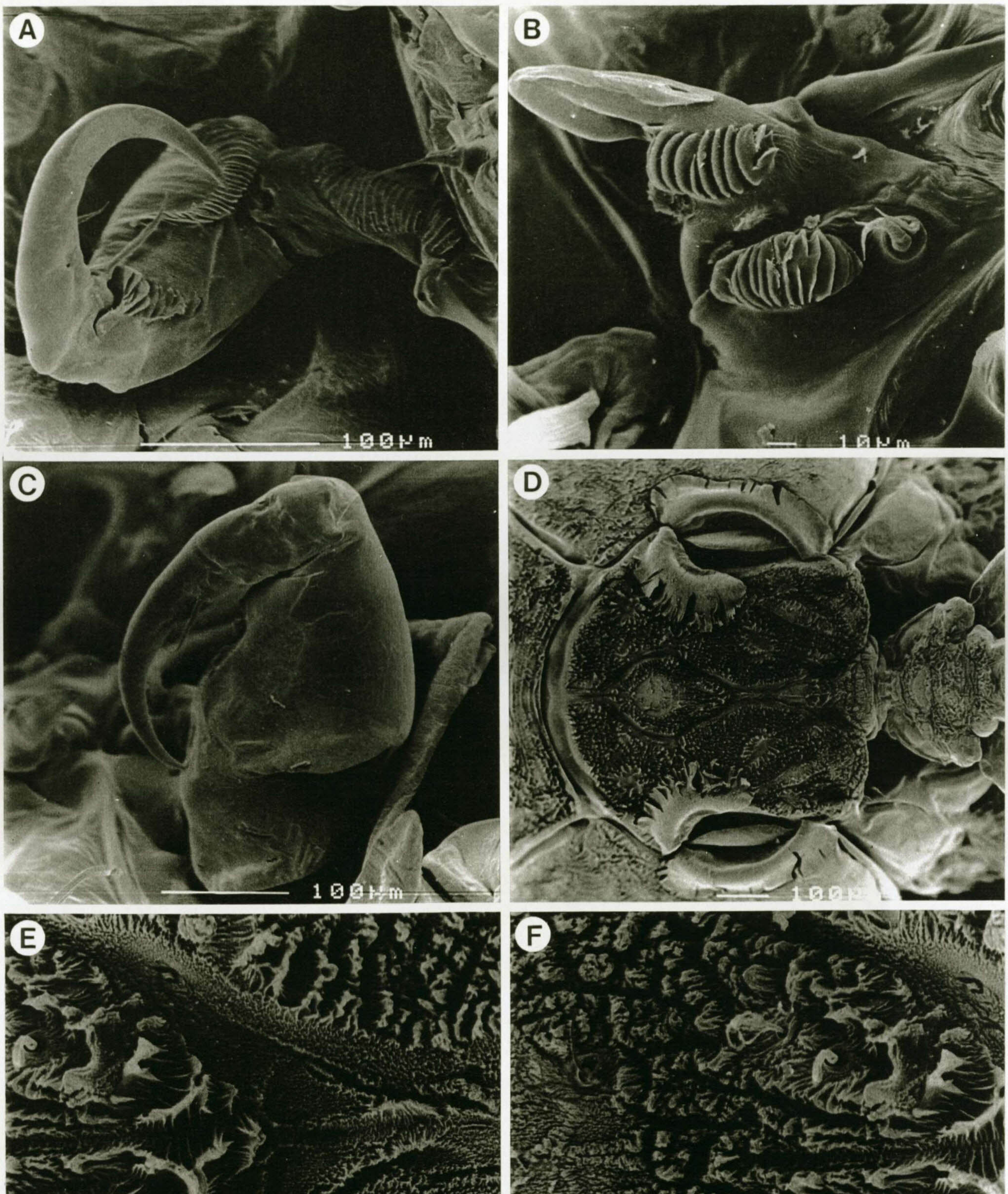
C. Maxilliped

D. Ornamental pattern on dorsal shield

E. Ornamental patterns

F. Ornamental patterns

Scale-bar: A, C & D - 100µm. B, E & F - 10µm


A
100µm
B
10µm
C
100µm
D
100µm
E
10µm
F
10µm

Caligus engraulidis Barnard, 1948

Figures 4.29 – 4.40

Hosts: Striped mullet *Liza tricuspidens* (Smith, 1935) and Flathead mullet *Mugil cephalus* Linnaeus, 1758.

Localities: Fanies Island and Charters Creek in Lake St Lucia.

Reference material: 9 / 045; 15 / 001; 17 / 4; 17 / 5; 17 / 6; 17 / 8; 17 / 9.

Material examined: Nine females and ten males were collected from the body surface of *Mugil cephalus*. One female was collected from the body surface of *Liza tricuspidens*.

Description of adult female: Body with typical appearance of *Caligus* (Figure 4.29, 4.30). Total length of female 5.83mm (5.28 - 5.99; n=5). Cephalothorax suborbicular, 1.1 times as wide as long. Frontal plates narrow; lunules small to medium (Figure 4.31A). Posterior sinuses medium to deep; lateral zones just reaching fourth pediger. Tip of antennule not reaching lateral limit of dorsal shield. Fourth pediger wider than long; distinctly separated from genital complex. Genital complex (Figure 4.38A) slightly wider than long; subquadrangular; posterolateral corners rounded, slightly produced. Abdomen a third of genital complex (Figure 4.38A); one-segmented; slightly longer than wide. Boundary between genital complex and abdomen distinct. Caudal rami three times as long as wide; slightly shorter than abdomen. Posterior margin of each ramus armed with one outer and one medial small seta and three large terminal setae. Egg sacs about two-thirds of total body length; containing 30 to 55 eggs.

Antennule: Two-segmented (Figure 4.31A, 4.38B). Proximal segment trapezoid, much broader than distal segment, with 13 large, stout, marginal setae, with 13 short, plumose ventral setae and two short, plumose dorsal setae (Figure 4.31B). Distal segment rod-shaped, much longer than wide; armed with 13 terminal setae and one subterminal aesthete on posterior margin.

Antenna: Three segmented (Figure 4.31C, 4.38C). Proximal segment with pointed posteromedial corner. Second segment largest, robust; armed medially with large corrugated patch. Terminal segment a strongly curved hook, bearing one basal seta and one marginal seta.

Postantennary process: Hook-like (Figure 4.31D, 4.38D), with two basal papillae each bearing three long setules and one similar papilla located nearby on sternum.

Maxillule: Dentiform (Figure 4.32A, 4.38E), sharply hook-like with papilla bearing three setae.

Maxilla: Two-segmented, brachiform (Figure 4.32B). Lacertus unarmed. Brachium slender with flabellum on medial margin bearing hyaline membrane. Calamus serrated on both margins. Canna serrated on both margins, shorter than calamus (Figure 4.38F).

Maxilliped: Three-segmented (Figure 4.32C). Proximal segment stout, unarmed. Second and terminal segments fused, forming strong claw with subterminal, medial seta.

Sternal furca: Base as long as wide (Figure 4.32D, 4.39A), with parallel and bluntly pointed tines. Tines as long as base and separated narrowly.

Leg 1: Biramous (Figure 4.33A, 4.39B). Protopod with one inner and one outer short, plumose seta. Exopod two-segmented; first segment with lateral distal spine; second segment with four terminal elements which appear the same; first spine simple and slightly longer than spines 2 or 3; spines 2 and 3 simple (Figure 4.39C); spine 4 same length as spine 1, robust, tapering and unarmed; three plumose, long setae on posterior margin of same segment. Endopod rudimentary, unarmed.

Leg 2: Large plumose seta on coxa (Figure 4.33B, 4.39D); basis with one small, naked lateral seta, one long medial setule and a striated membrane along medial margin. Exopod three-segmented; first segment with one outer spine with striated membrane on both margins, and one long, plumose inner seta; second segment with one outer, inward curving spine and one long, plumose inner seta; third segment with three external spines constructed unequally and five long, plumose setae; first outer spine minute; second outer spine same as first, larger; third outer spine with striated membrane along both margins. Endopod three-segmented; first segment with one long, plumose inner seta and prominent crest of hairs on outer margin; second segment with two long, plumose inner setae and a row of prominent hairs on outer margin and a row of hairs on the inner margin; third segment with six long, plumose terminal setae.

Leg 3: Adhesive pad on ventrolateral surface and striated marginal membranes (Figure 4.34A). Row of denticles above endopod. Exopod three-segmented; first segment with large basal claw with prominent lateral hump; second segment with one outer spine and one plumose inner seta; third segment with three spines of different length and four plumose setae of equal length. Second and third segment with rows of setules on lateral margins. Endopod two-segmented; first segment expanded laterally into velum on outer margin and bearing one long, plumose seta on medial margin; second segment with five long, plumose setae of different length.

Leg 4: Outer seta on protopod short and plumose. Long and slender exopod (Figure 4.34B, 4.39E), indistinctly two-segmented; first segment with short naked spine; second segment armed with two terminal spines covered by pectinated membrane; one long and one short terminal spine serrated on both margins (Figure 4.39F).

Leg 5: Represented by three short, plumose setae (Figure 4.40A) on posterolateral corner of genital complex.

Armature on rami of legs 1-4:

Leg 1	Exp 1-0; III, 1, 3	Enp (rudimentary)
Leg 2	Exp I-1; I-1; I, II, 5	Enp 0-1; 0-2; 6
Leg 3	Exp I-0; 1-1; 3, 4	Enp 0-1; 6
Leg 4	Exp I-0, II,	Enp (absent)

Description of adult male: Total length of male 5.41mm (4.98 – 5.67; n=5). Adult male slightly shorter than female (Figure 4.35, 4.36). Cephalothorax suborbicular, less than 1.1 times as long as wide. Fourth pediger wider than long. Genital complex with rounded posterolateral corners; slight indentation between posterolateral corner and abdomen. Genital complex with rudimentary leg 5 (Figure 4.40B) on rounded posterolateral margin. Leg 5 represented by three plumose setae. Abdomen one-segmented; longer than wide. Caudal rami armed as in female; different in size.

Antenna: Three-segmented (Figure 4.37A, 4.40C). Proximal segment unarmed. Second segment large; robust; armed with three corrugated patches; adhesion pads well developed. Terminal segment smallest; claw bifid, covered by overlapping cuticular flap; strong seta on each side of claw, close to base.

Maxilliped: Corpus broader than female (Figure 4.37B, 4.40D), bearing prominent shelf-like expansion in myxal area.

Postantennary process: Hook much longer and strongly curved (Figure 4.37C).

Remarks: Hypersymbionts were found associated with *Caligus engraulidis*, and will be discussed in Chapter 6. The tips of spines 2 and 3 on the exopod of leg 1 (Figure 4.39C) have striated ridges and may be of some sensory aid, or it may be used for accessory adhesion. Sensory hairs were found on both the dorsal side of the lunules (Figure 4.40E) and hyaline membrane of the dorsal shield (Figure 4.40F). As the lunules are sensory adaptations in assisting the antennules, sensory hairs are thus not uncommon. It aids in the sensory function of the lunules and helps the caligid in searching for either food or hosts. The function of the hairs on the hyaline membrane is not known, but it may be used in search of suitable hosts.

The most characteristic features of *C. engraulidis* are the possession of long and slender caudal rami, and a slender, one-segmented exopod bearing an armature of I, II on leg 4, with the two terminal spines serrated on both margins. No other *Caligus* species is known to have a serrated terminal spine on the exopod of leg 4. The function of the serrated spines (Figure 4.39F) is not fully known, and may be used for movements over the host` body surface. *C. engraulidis* was first recorded by Barnard in 1948 from the Zwartkops River, Algoa Bay. Barnard (1948) made a short species description of the female, and the male was not found until the present study. He mentioned the serrated spines on the exopod of leg 4, which is characteristic of this species, and also mentioned in the description of the female that no secondary or rudimentary fifth legs are present on the genital complex. The species found in this study do have rudimentary fifth legs, and are represented by three plumose setae. Barnard (1948) have either not seen the rudimentary fifth legs or the species found in the present study is a new species. For the moment the present species will be referred to as *C. engraulidis*. Barnard did deposit a type specimen of *C. engraulidis* in the South African Museum, but the specimen was disintegrated and it was not possible to verify the specific species with the species found in the present study.

Figure 4.29

Microscope projection drawing of *Caligus engraulidis* Barnard, 1948 female (dorsal) occurring on the fish host *Mugil cephalus* Linnaeus, 1758, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

Scale-bar: 1mm

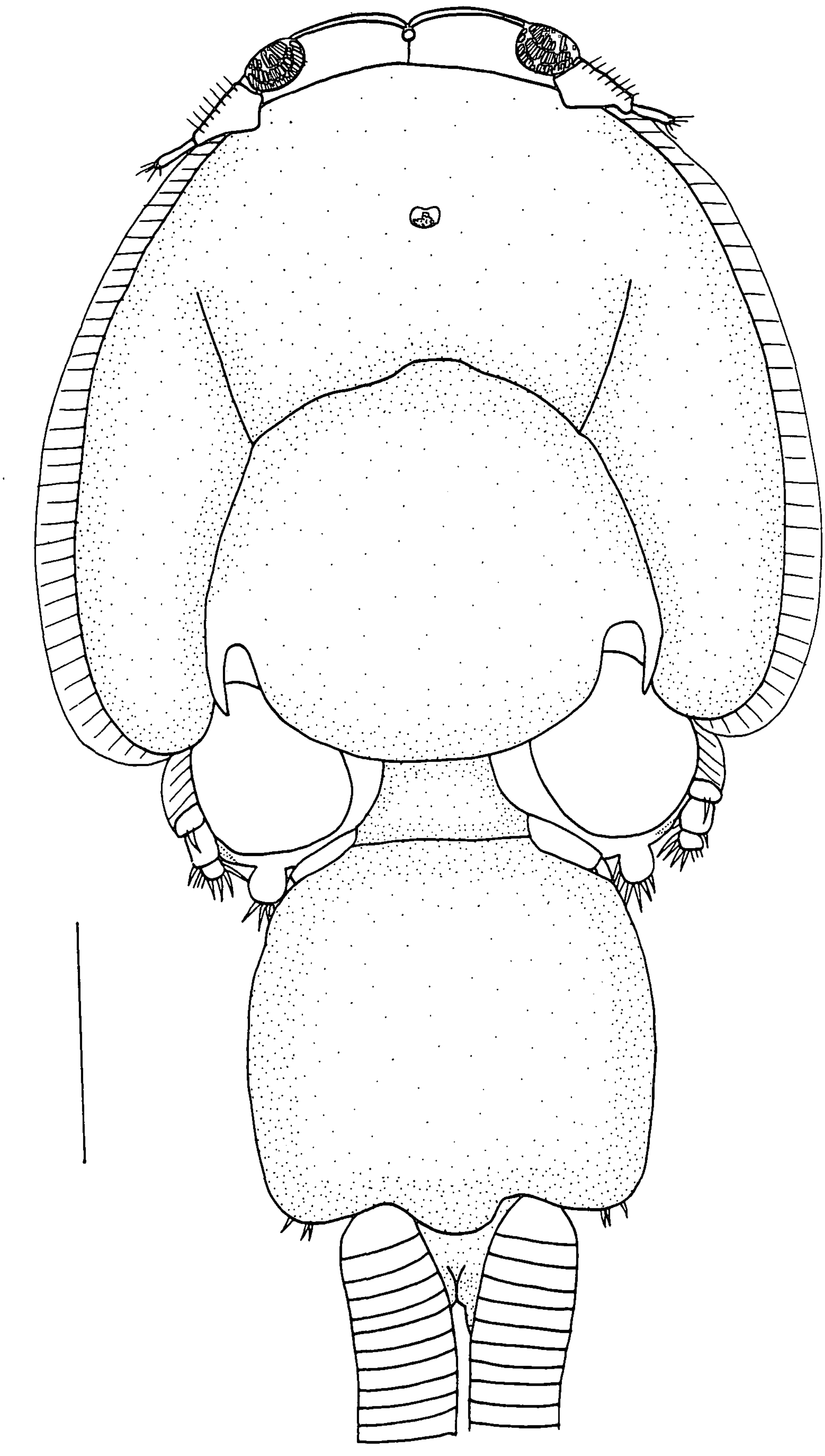


Figure 4.30

Microscope projection drawing of *Caligus engraulidis* Barnard, 1948 female (ventral) occurring on the fish host *Mugil cephalus* Linnaeus, 1758, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

Scale-bar: 1mm

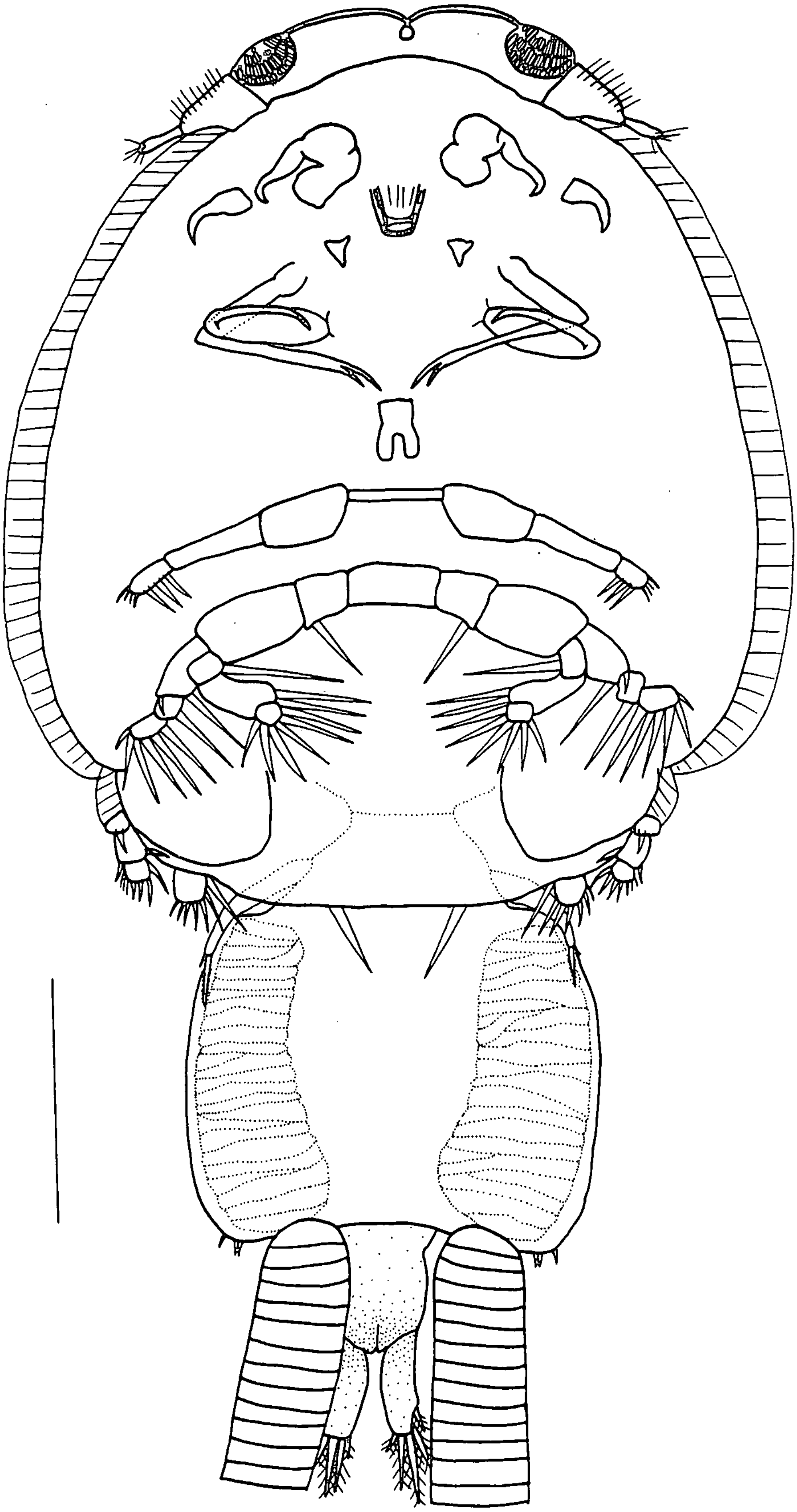


Figure 4.31

Microscope projection drawing of *Caligus engraulidis* Barnard, 1948 female occurring on the fish host *Mugil cephalus* Linnaeus, 1758, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Ventral view of lunule and antennule

B. Dorsal view of antennule

C. Antenna

D. Postantennary process

Scale-bar: A, B, C & D - 100μm

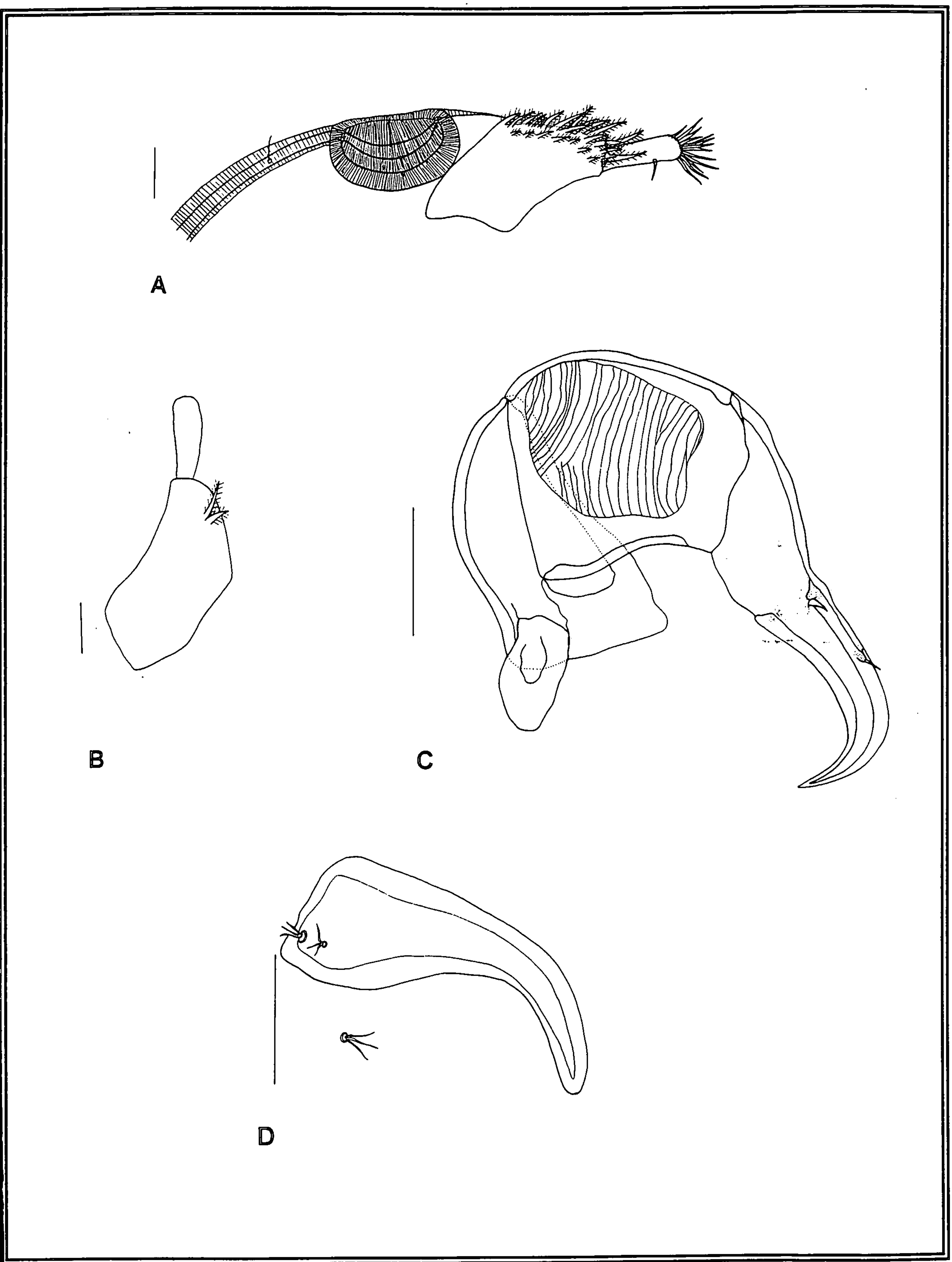

A
B
C
D

Figure 4.32

Microscope projection drawing of *Caligus engraulidis* Barnard, 1948 female occurring on the fish host *Mugil cephalus* Linnaeus, 1758, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

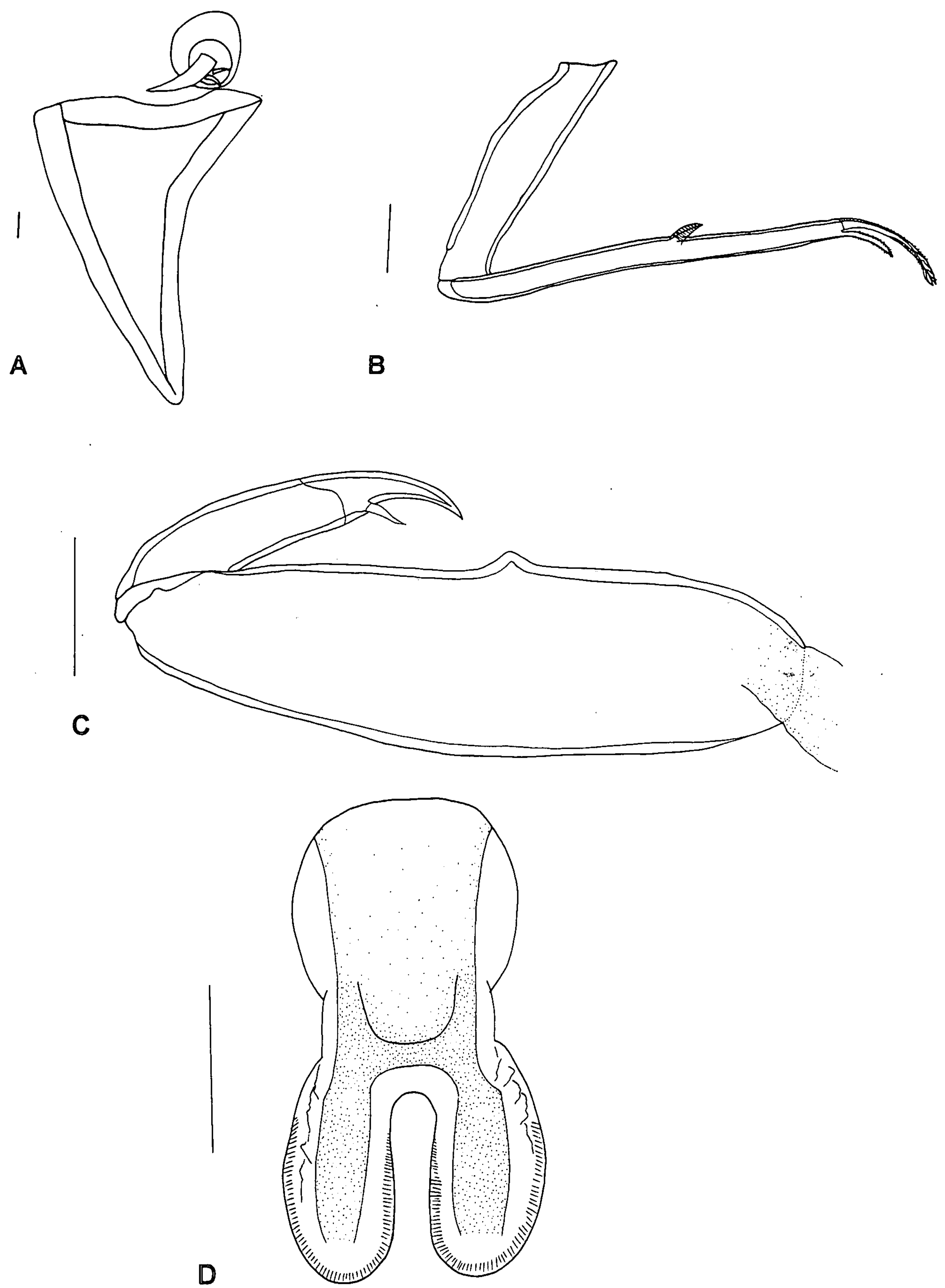
A. Maxillule

B. Maxilla

C. Maxilliped

D. Sternal furca

Scale-bar: B, C & D - 100µm. A - 10µm



A
B
C
D

Figure 4.33

Microscope projection drawing of *Caligus engraulidis* Barnard, 1948 female occurring on the fish host *Mugil cephalus* Linnaeus, 1758, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Leg 1

B. Leg 2

Scale-bar: A & B - 100µm

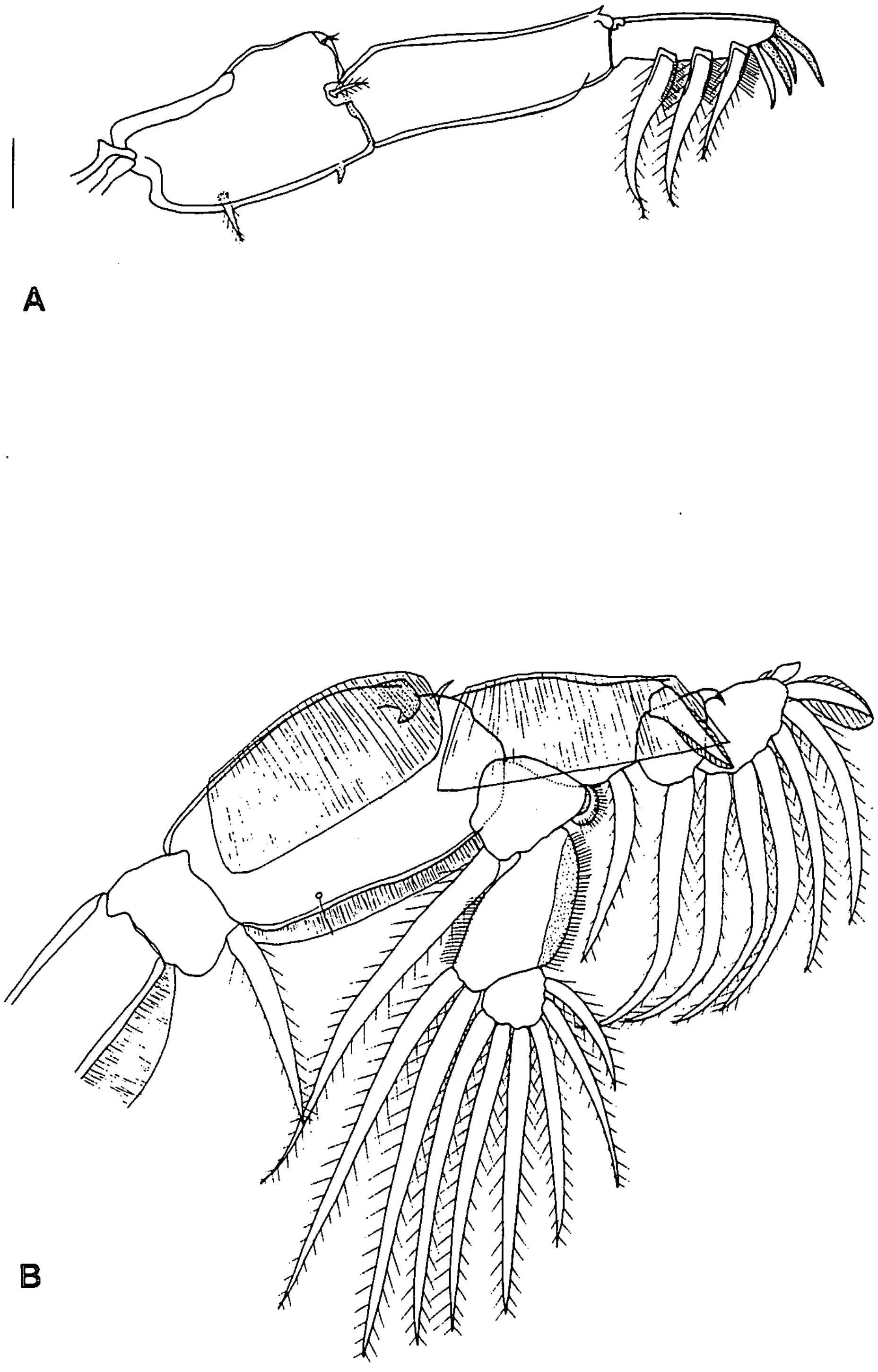

A
B

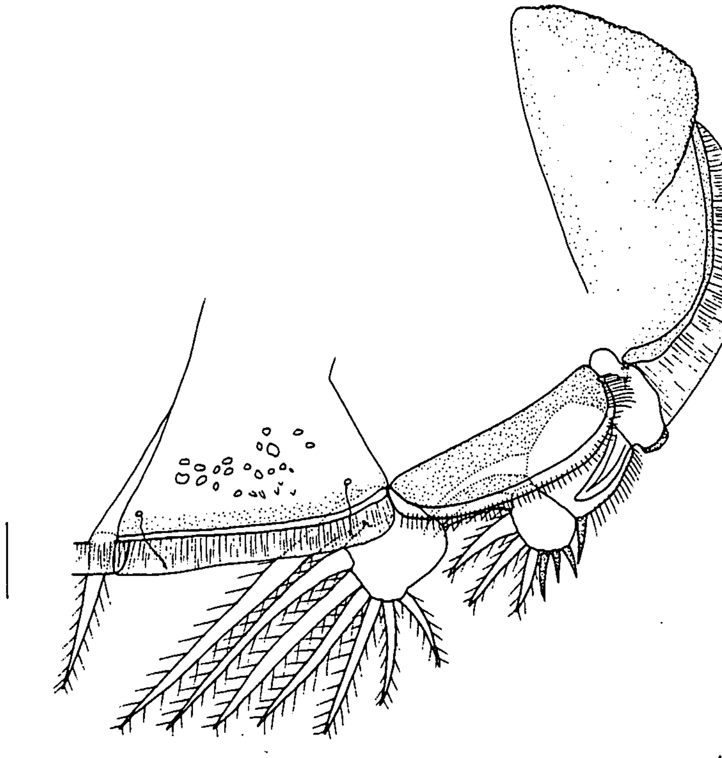
Figure 4.34

Microscope projection drawing of *Caligus engraulidis* Barnard, 1948 female occurring on the fish host *Mugil cephalus* Linnaeus, 1758, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

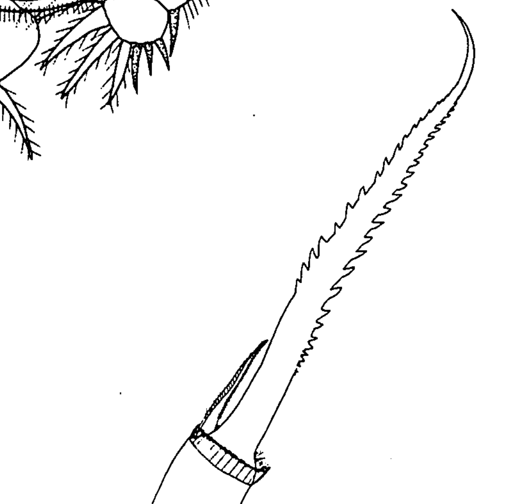
A. Leg 3

B. Leg 4

Scale-bar: A & B - 100µm



A



B

Figure 4.35

Microscope projection drawing of *Caligus engraulidis* Barnard, 1948 male (dorsal) occurring on the fish host *Mugil cephalus* Linnaeus, 1758, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

Scale-bar: 1mm

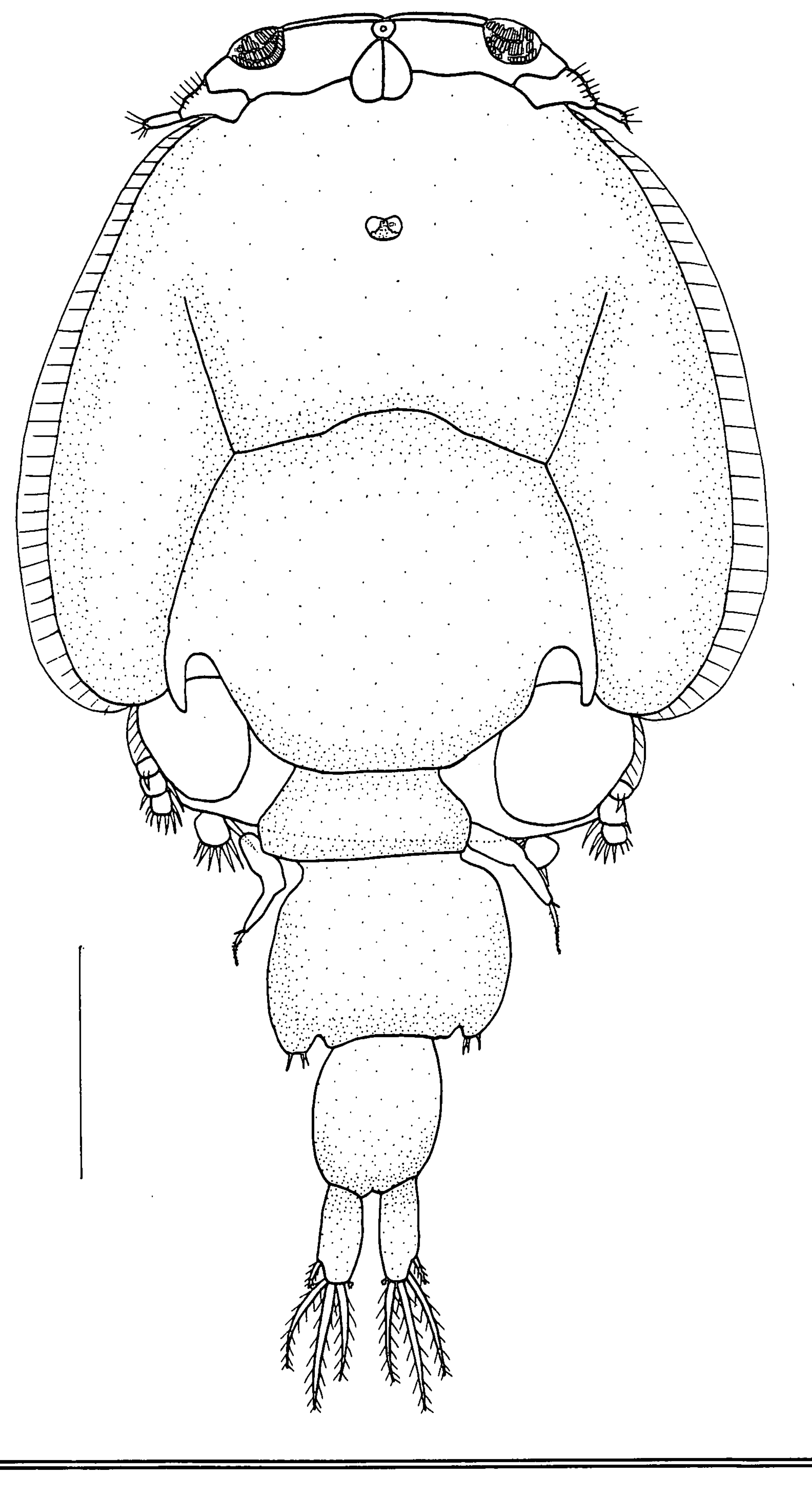


Figure 4.36

Microscope projection drawing of *Caligus engraulidis* Barnard, 1948 male (ventral) occurring on the fish host *Mugil cephalus* Linnaeus, 1758, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

Scale-bar: 1mm

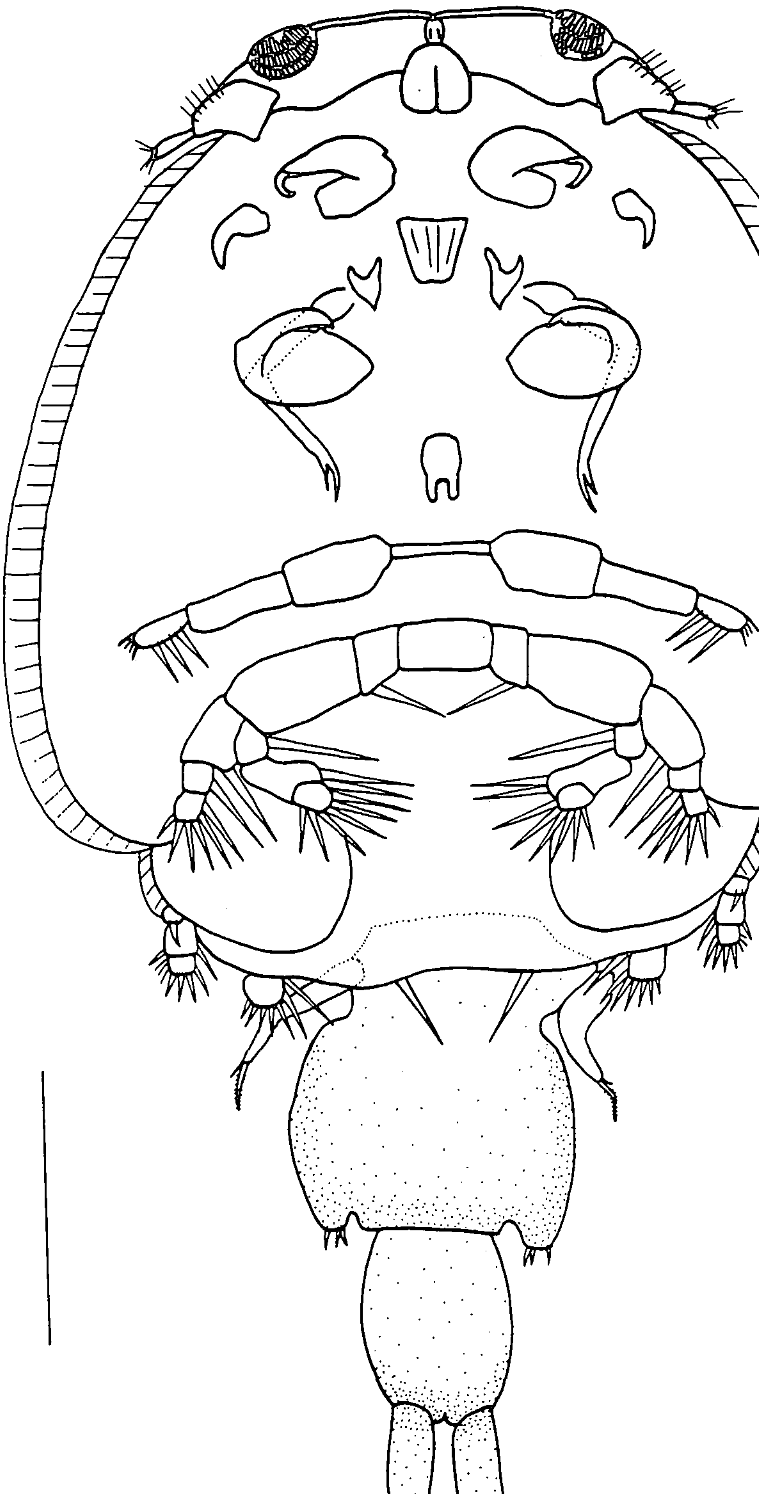


Figure 4.37

Microscope projection drawing of *Caligus engraulidis* Barnard, 1948 male occurring on the fish host *Mugil cephalus* Linnaeus, 1758, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Antenna

B. Maxilliped

C. Postantennary process

Scale-bar: A, B & C - 100μm

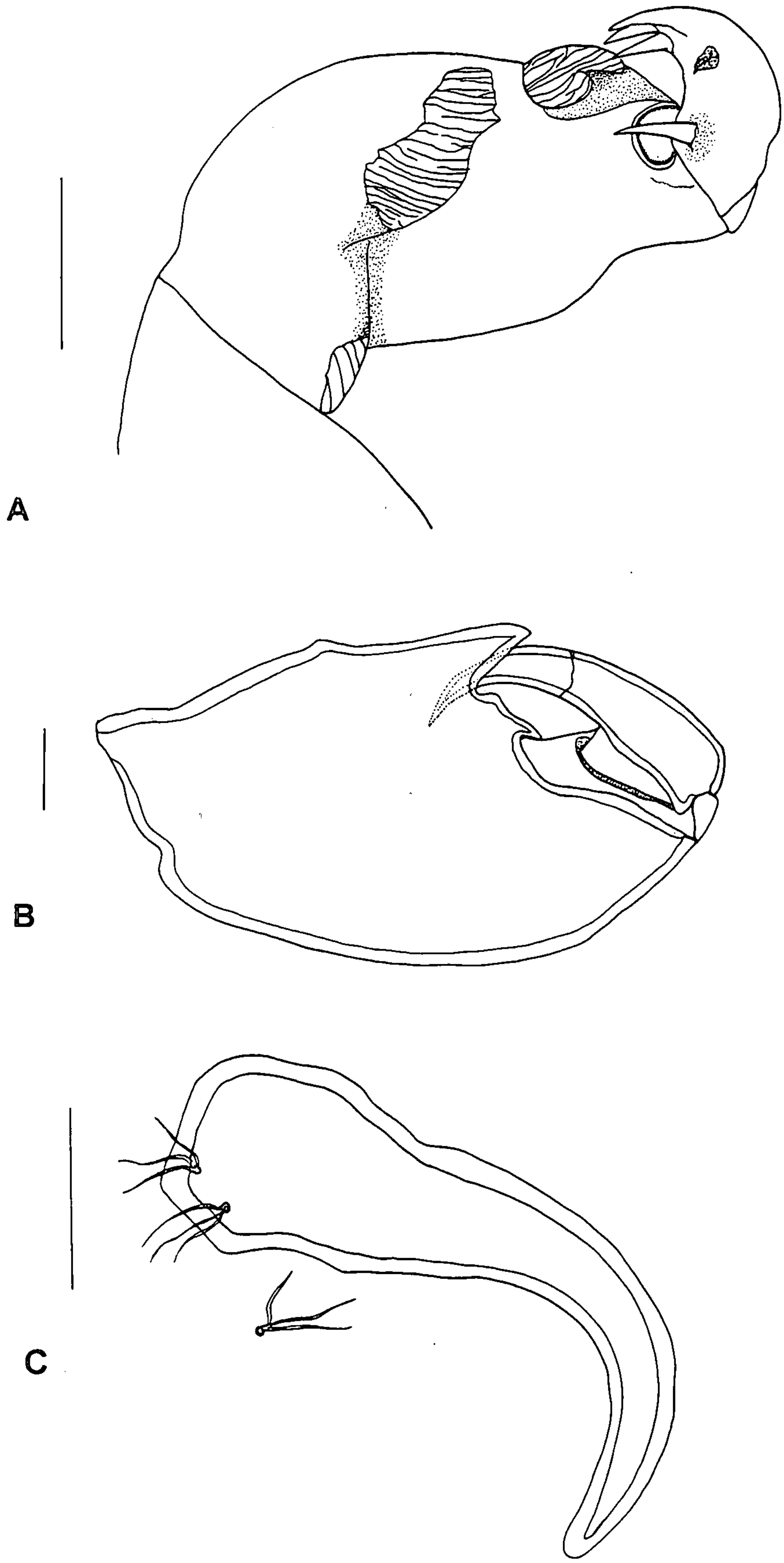

A
B
C

Figure 4.38

Scanning electron micrographs of *Caligus engraulidis* Barnard, 1948 female occurring on the fish host *Mugil cephalus* Linnaeus, 1758, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Ventral view of genital complex and abdomen

B. Ventral view of proximal segment of antennule

C. Tip of antenna

D. Postantennary process

E. Maxillule

F. Calamus and canna of maxilla

Scale-bar: A & B - 100µm. C, D, E & F - 10µm

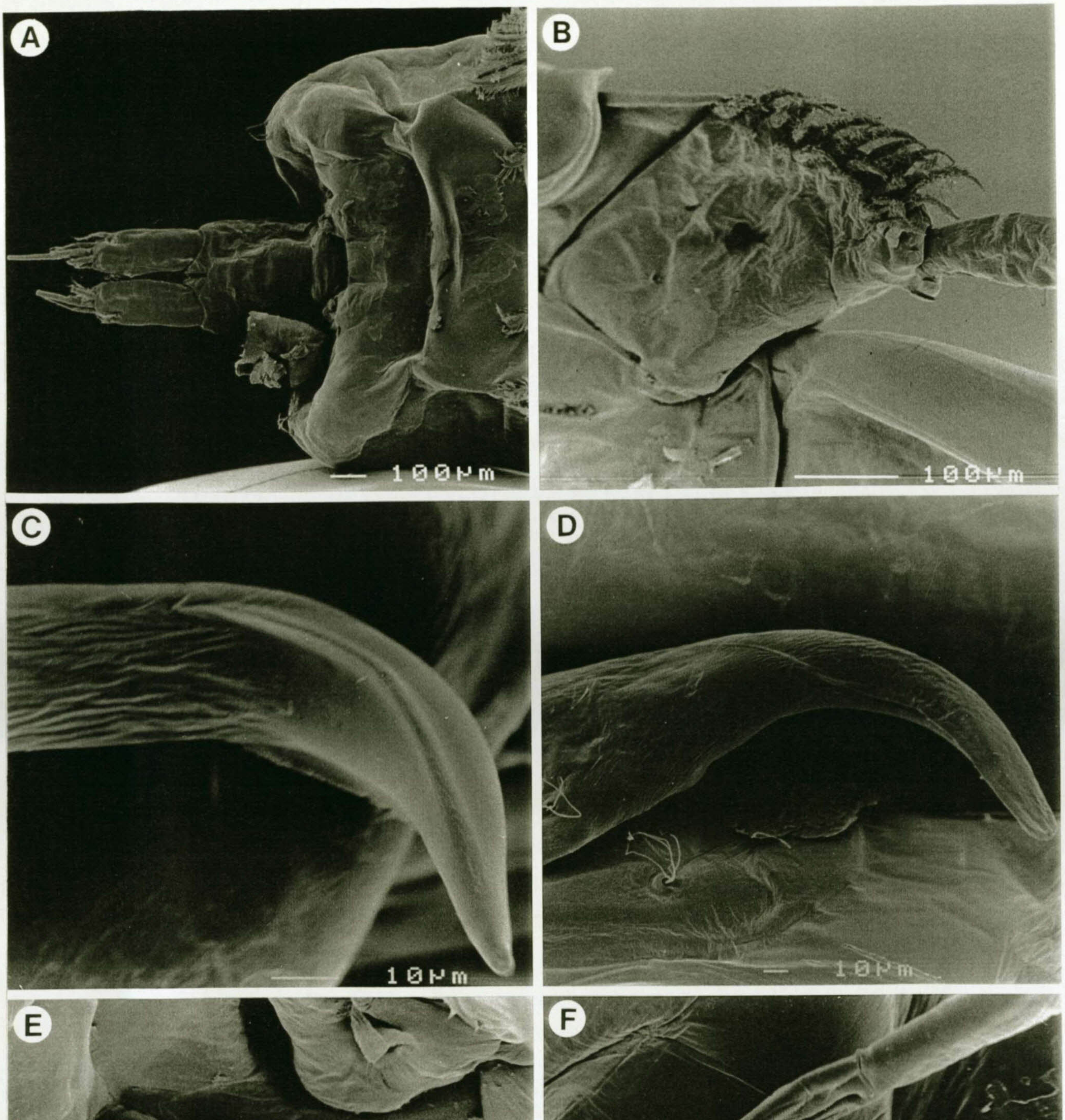

A
100µm
B
100µm
C
10µm
D
10µm
E
10µm
F
10µm

Figure 4.39

Scanning electron micrographs of *Caligus engraulidis* Barnard, 1948 female occurring on the fish host *Mugil cephalus* Linnaeus, 1758, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Sternal furca

B. Leg 1

C. Spines on exopod of leg 1

D. Leg 2

E. Leg 4

F. Serrated terminal spine of leg 4

Scale-bar: A, B, D & E - 100µm. F - 10µm. C - 1µm

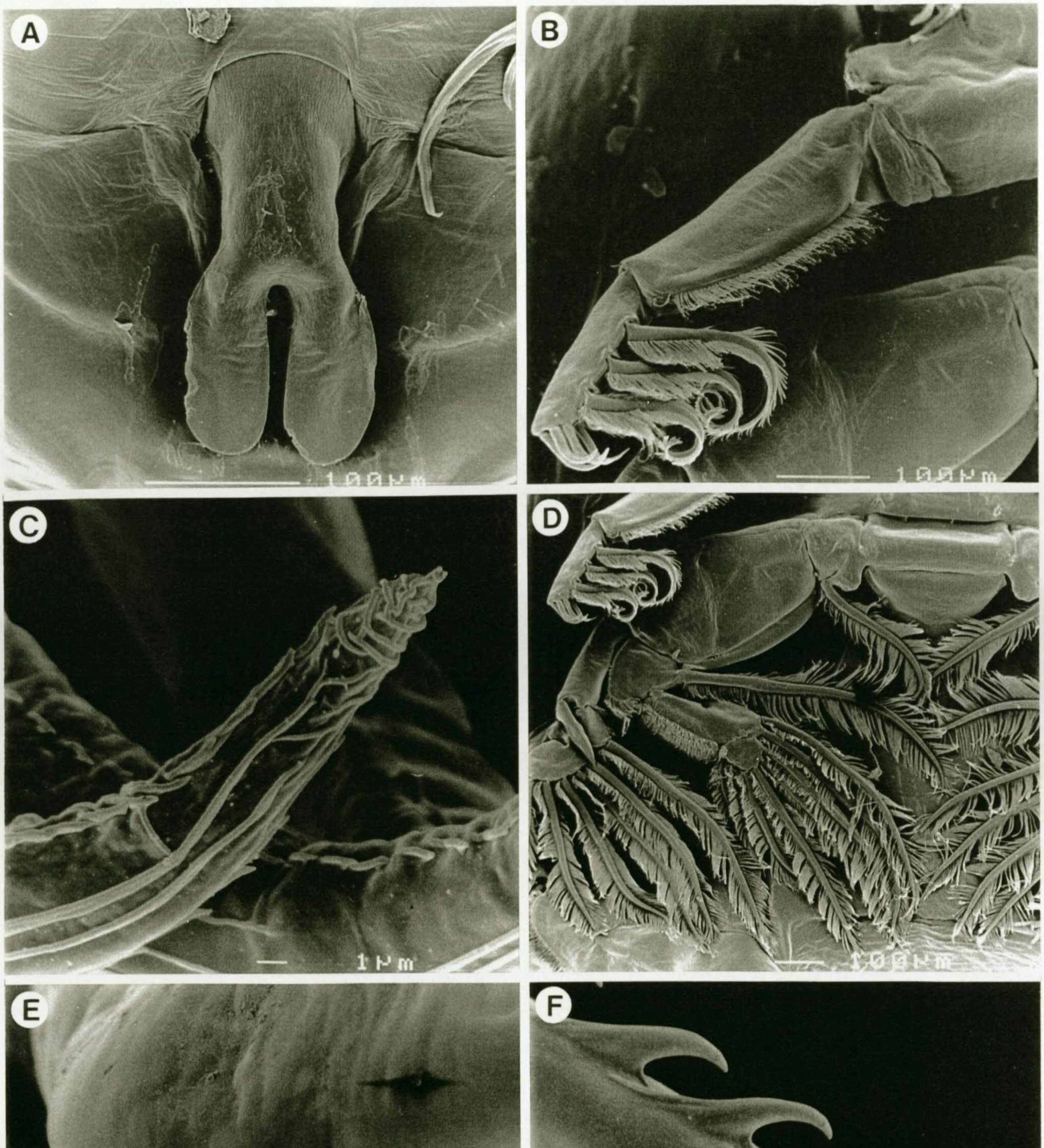

A
100µm
B
100µm
C
1µm
D
100µm
E
100µm
F
10µm

Figure 4.40

Scanning electron micrographs of *Caligus engraulidis* Barnard, 1948 female (A) and male (B-F) occurring on the fish host *Mugil cephalus* Linnaeus, 1758, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Leg 5

B. Leg 5

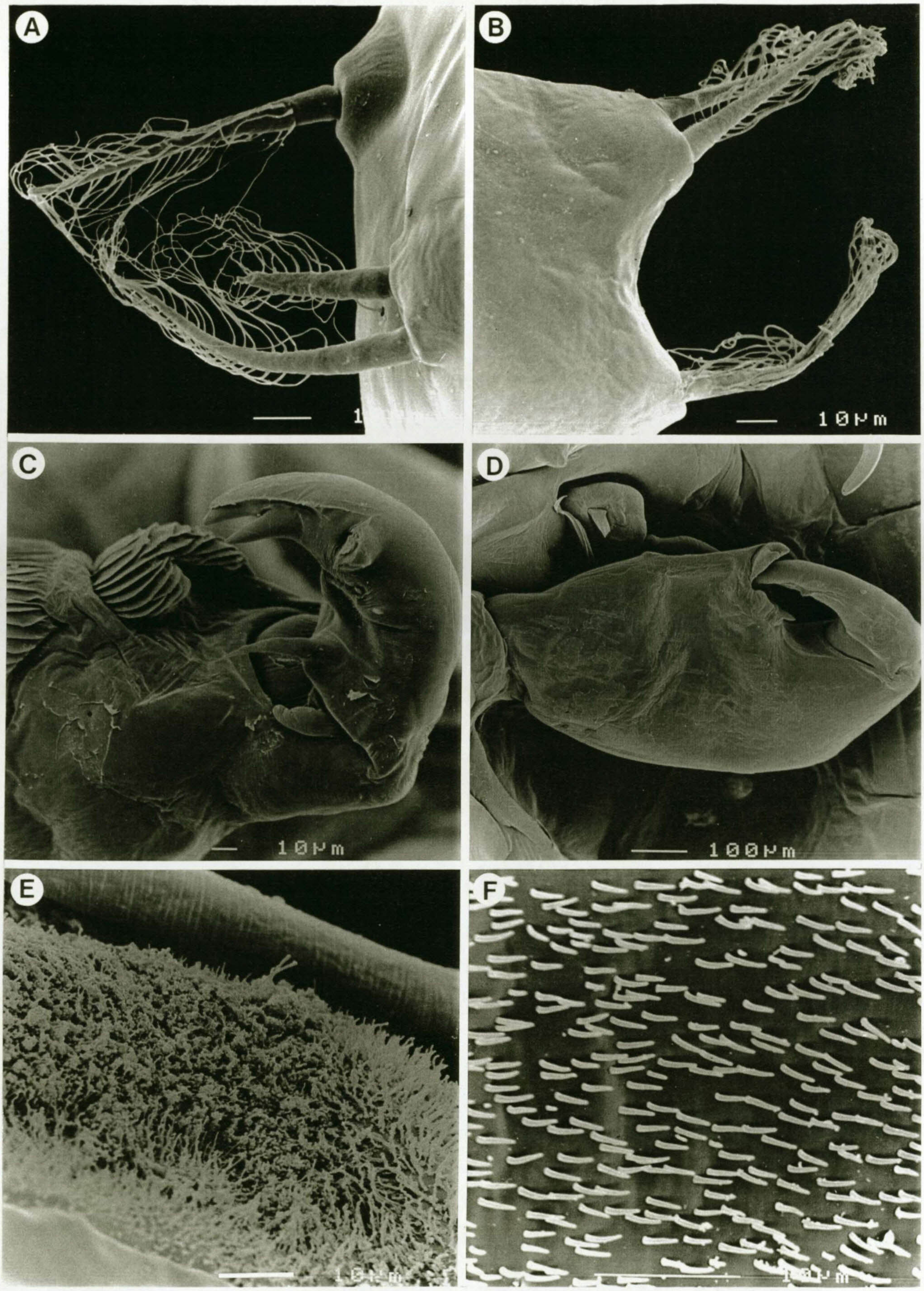
C. Tip of antenna

D. Maxilliped

E. Sensory hairs on dorsal side of lunule

F. Sensory hairs on hyaline membrane of dorsal shield

Scale-bar: A & B - 100µm. C, D, E & F - 10µm


A
B
10µm
C
10µm
D
100µm
E
F

Caligus mortis Kensley, 1970

Figures 4.41 – 4.52

Hosts: Super klipfish *Clinus superciliosus* (Linnaeus, 1758); Bluntnose klipfish *Clinus cottoides* Valenciennes, 1836 and Rocksucker *Chorisochismus dentex* (Pallas, 1769).

Localities: Jeffreys Bay and De Hoop Nature Reserve.

Reference material: 97 / 02 / 22 – 01; 97 / 04 / 07 – 03; 98 / 04 / 07 – 07; 98 / 04 / 10 – 02; 99 / 01 / 18 – 02; 99 / 03 / 22 – 04.

Material examined: 13 females and eight males were collected from the body surface of *Clinus superciliosus*. Three females were collected from the body surface of *Clinus cottoides*. Three females were collected from the body surface of *Chorisochismus dentex*.

Description of adult female: Body with typical appearance of *Caligus* (Figure 4.41, 4.42). Total length of female 2.56mm (2.38 – 2.69; n=5). Cephalothorax suborbicular, 1.1 times as wide as long. Frontal plates well developed, lunules medium. Posterior sinuses deep; lateral zones not reaching fourth pediger; posterolateral corner of lateral zone with conspicuous sensory pit. Tip of antennule not reaching lateral limit of dorsal shield. Fourth pediger wider than long; distinctly separated from genital complex. Genital complex 1.2 times wider than long; tapered anteriorly, and bearing a small, triangular, posteroventral process between abdomen and egg sac attachment area. Abdomen a quarter of genital complex; one-segmented; slightly wider than long. Border between genital complex and abdomen distinct. Caudal rami longer than wide; shorter than abdomen. Posterior margin of each ramus armed with two outer, one small, medial plumose and three large terminal plumose setae (Figure 4.52B). Egg sacs about as long as total body length; containing 35 to 55 eggs.

Antennule: Two-segmented (Figure 4.43A, 4.50A). Proximal segment trapezoid, much broader than distal segment, with 14 large, stout, marginal setae, with 13 short, plumose ventral setae and two short, plumose dorsal setae (Figure 4.43B). Distal segment rod-shaped, much longer than wide; armed with 13 terminal setae and one subterminal aesthete on posterior margin.

Antenna: Three-segmented (Figure 4.43C, 4.50B). Proximal segment with pointed posteromedial corner. Second segment largest, robust; unarmed and without usual dorsal corrugated patch. Terminal segment a strongly curved hook, bearing one basal and one marginal seta, and two minute hyaline papillae.

Postantennary process: Hook-like (Figure 4.43D, 4.50C) with two basal papillae, bearing one and two long setules respectively and one similar papilla located nearby on sternum bearing two long setules.

Maxillule: Dentiform (Figure 4.44A, 4.50D), sharply hook-like with papilla bearing three setae.

Maxilla: Two-segmented, brachiform (Figure 4.44B). Lacertus unarmed. Brachium slender with flabellum on medial margin bearing hyaline membrane. Calamus serrated on both margins. Canna serrated on both margins, shorter than calamus.

Maxilliped: Three-segmented (Figure 4.44C). Proximal segment stout, unarmed. Second and terminal segments fused, forming strong claw. Second segment with small, hyaline, setiform process in small pit and one naked seta on inner distal corner. Terminal segment with minute accessory tooth near inner distal end.

Sternal furca: Base small (Figure 4.44D, 4.50E). Tines not tapered, curving inward, slightly flared, and truncate at tip.

Leg 1: Biramous (Figure 4.45A). Protopod with one inner and one outer short, plumose seta. Exopod two-segmented; first segment with lateral distal spine and medial row of setules; second segment with four terminal elements which appear differently; first spine simple and slightly longer than spines 2 or 3; spines 2 and 3 with spiniform secondary process, equaling half the length of spines (Figure 4.51A); spine 4 two times as long as spine 1, robust, tapering and unarmed; three plumose, long setae on posterior margin of same segment, different in size. Endopod rudimentary, unarmed.

Leg 2: Large plumose seta on coxa and one setule near intercoxal plate (Figure 4.45B, 4.51B, C & D); basis with one long medial setule and a striated membrane along medial margin. Exopod three-segmented; first segment with one outer slightly curved spine and one long, plumose inner seta; second segment with one outer spine and one long, plumose inner seta; both spines with serrated membranes along two-thirds the length of outer and inner margins; third segment with three external spines constructed unequally and five long, plumose setae; first outer spine minute; second outer spine with hyaline membrane and row of hairs on inner margin; third outer spine with striated membrane along outer margin and setae on inner margin. Endopod three-segmented; first segment with one long, plumose inner seta; second segment with two long, plumose inner setae and a crest of prominent hairs on outer margin; third segment with six long, plumose terminal setae and a patch of hairs on outer margin.

Leg 3: Small adhesive pad on ventrolateral surface and striated marginal membranes (Figure 4.46A, 4.51E). Exopod three-segmented; first segment with large basal claw bearing an outer membrane; second segment with one outer spine and one plumose inner seta; third segment with three spines of different length and four plumose setae of equal length. Endopod two-segmented; first segment expanded laterally into velum on outer margin and bearing one long, plumose seta on medial margin; second segment with five long, plumose setae of different length and rows of hair on lateral margin.

Leg 4: Protopod bearing two setules (Figure 4.46B); outer seta on protopod short and plumose. Long and slender exopod, indistinctly two-segmented; first segment with spine almost as long as terminal spine, naked and bearing pectinate membrane at base; second segment with two spines of different size; first spine relatively short, naked, not highly sclerotized, without pectinate membrane; terminal spine with two rows of serrated membranes and equipped with pectinate membrane at base (Figure 4.51F).

Leg 5: Represented by two setiferous lobes; anterior lobe with one plumose seta (Figure 4.52A); posterior lobe with two plumose setae.

Armature on rami of legs 1-4:

Leg 1	Exp 1-0; III, 1, 3	Enp (rudimentary)
Leg 2	Exp I-1; I-1; I, II, 5	Enp 0-1; 0-2; 6
Leg 3	Exp I-0; 1-1; 3, 4	Enp 0-1; 6
Leg 4	Exp I-0; I, I	Enp (absent)

Description of adult male: Total length of male 1.88mm (1.66 – 1.93; n=5). Adult male much smaller than female (Figure 4.47, 4.48). Cephalothorax suborbicular, less than 1.1 times as wide as long. Frontal plates well developed, large; lunules large (Figure 4.52C). Fourth pediger wider than long. Genital complex with slightly rounded posterolateral corners with rudimentary leg 5 (Figure 4.52D) on lateral margin, and rudimentary leg 6 (Figure 4.52E) on rounded posterolateral corners. Leg

5 represented by three plumose setae; leg 6 represented by two plumose setae. Abdomen one-segmented; wider than long. Caudal rami armed as in female; different in size.

Antenna: Three-segmented (Figure 4.49A). Proximal segment unarmed. Second segment large; robust; armed with two corrugated patches; adhesion pads well developed. Terminal segment smallest; claw bifid (Figure 4.52F); strong seta on each side of claw, close to base.

Maxillule: Dentiform (Figure 4.49B); similar to female, with small band of striations on middle of process.

Remarks: The marginal membrane of *Caligus mortis* is equipped with sensory hairs (Figure 4.50F) and may be used for host recognition. The most characteristic features of *C. mortis* are the shape of the sternal furca and the two-segmented exopod of leg 4 bearing an armature of I-0; I, I. The majority of *Caligus* species possess three terminal spines on the exopod of leg 4. Only nine species of the over 200 known species of this genus have been described as bearing two spines at the tip of leg 4. Only five species have a two-segmented exopod of leg 4 with the formula I-0; I, I. *Caligus mortis* can be distinguished from the other four species by the shape of the sternal furca, and the morphology and relative lengths of the exopodal spines of leg 4, particularly the setiform nature of spine 2, and spine 1 almost equal in length to the terminal spine.

Only the female of *C. mortis* was known prior to the present study. The male is described for the first time and is new to science. *Caligus mortis* shows a preference for the host *Clinus superciliosus*, but was also found on *C. cottoides* and *Chorisochismus dentex*. As these three hosts are found in intertidal pools, *C. mortis* may be found on some other intertidal pool fish hosts if the main host *Clinus superciliosus* is not found. The preference for *Clinus superciliosus* can not be explained, but it may be due to the fact that *Clinus superciliosus* are found in the low water intertidal pools.

Figure 4.41

Microscope projection drawing of *Caligus mortis* Kensley, 1970 female (dorsal) occurring on the fish host *Clinus superciliosus* (Linnaeus, 1758), collected from the De Hoop Nature Reserve, South Africa.

Scale-bar: 1mm

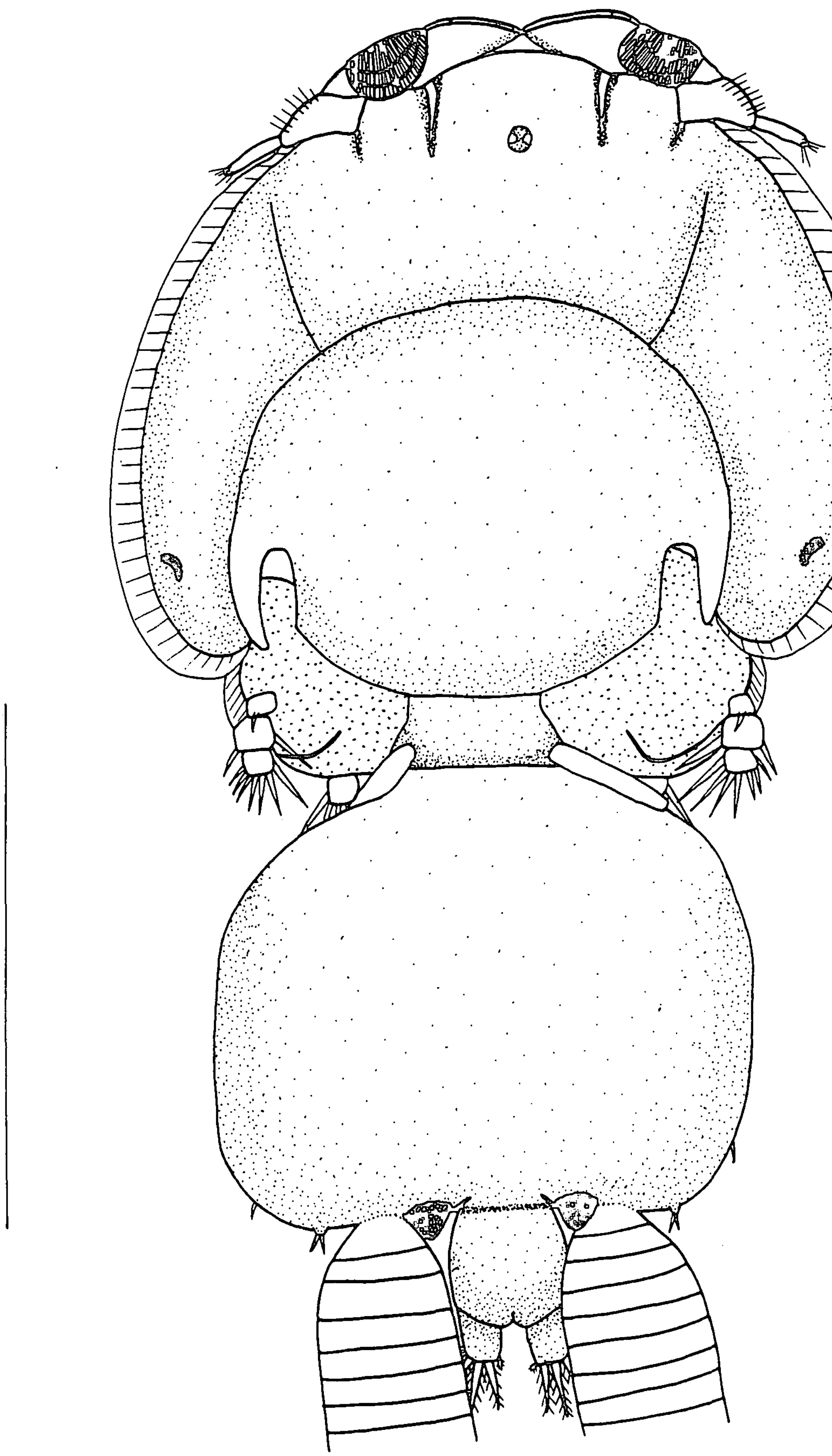


Figure 4.42

Microscope projection drawing of *Caligus mortis* Kensley, 1970 female (ventral) occurring on the fish host *Clinus superciliosus* (Linnaeus, 1758), collected from the De Hoop Nature Reserve, South Africa.

Scale-bar: 1mm

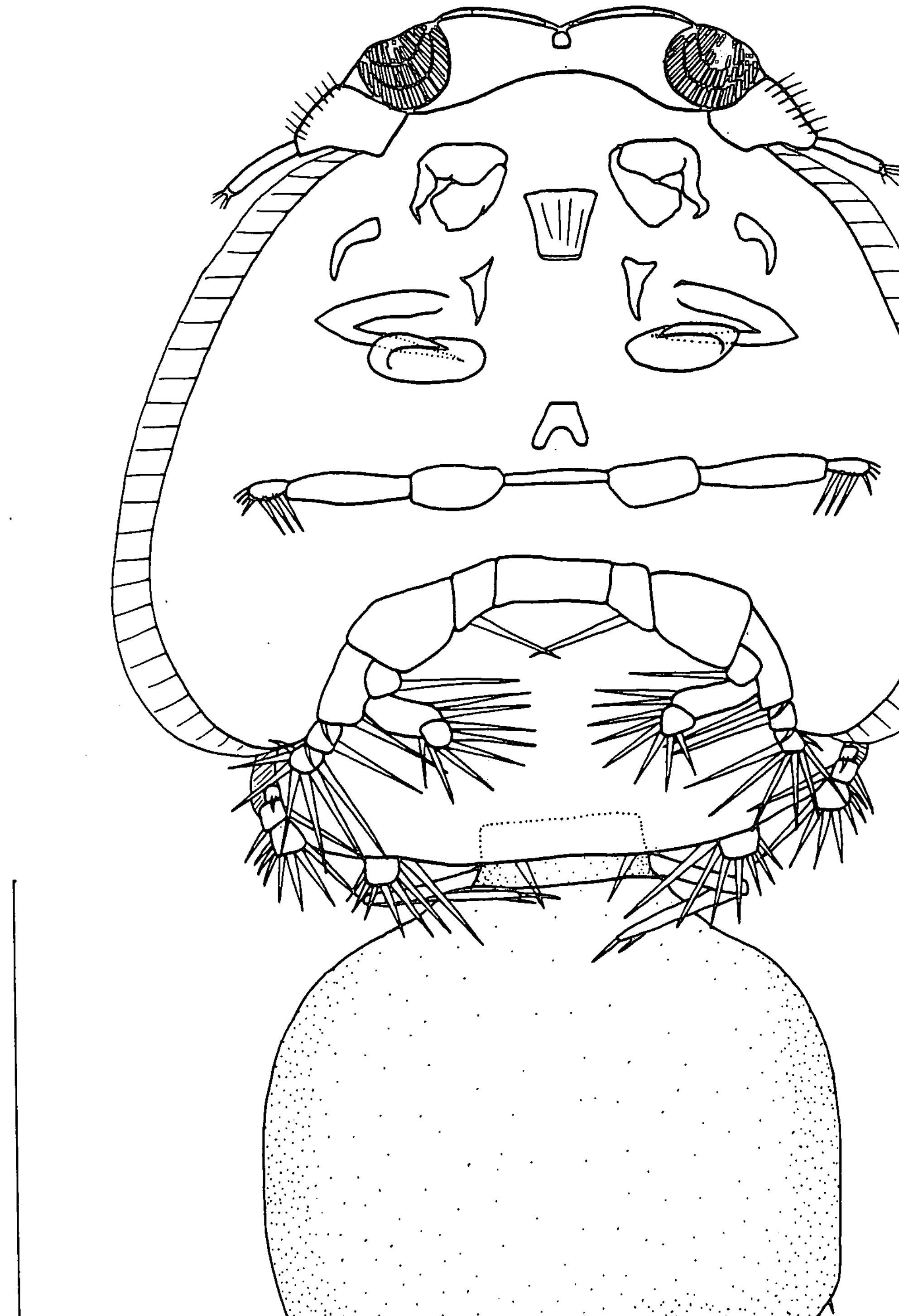


Figure 4.43

Microscope projection drawing of *Caligus mortis* Kensley, 1970 female occurring on the fish host *Clinus superciliosus* (Linnaeus, 1758), collected from the De Hoop Nature Reserve, South Africa.

A. Ventral view of antennule

B. Dorsal view of antennule

C. Antenna

D. Postantennary process

Scale-bar: A, B & C - 100µm. D - 10µm

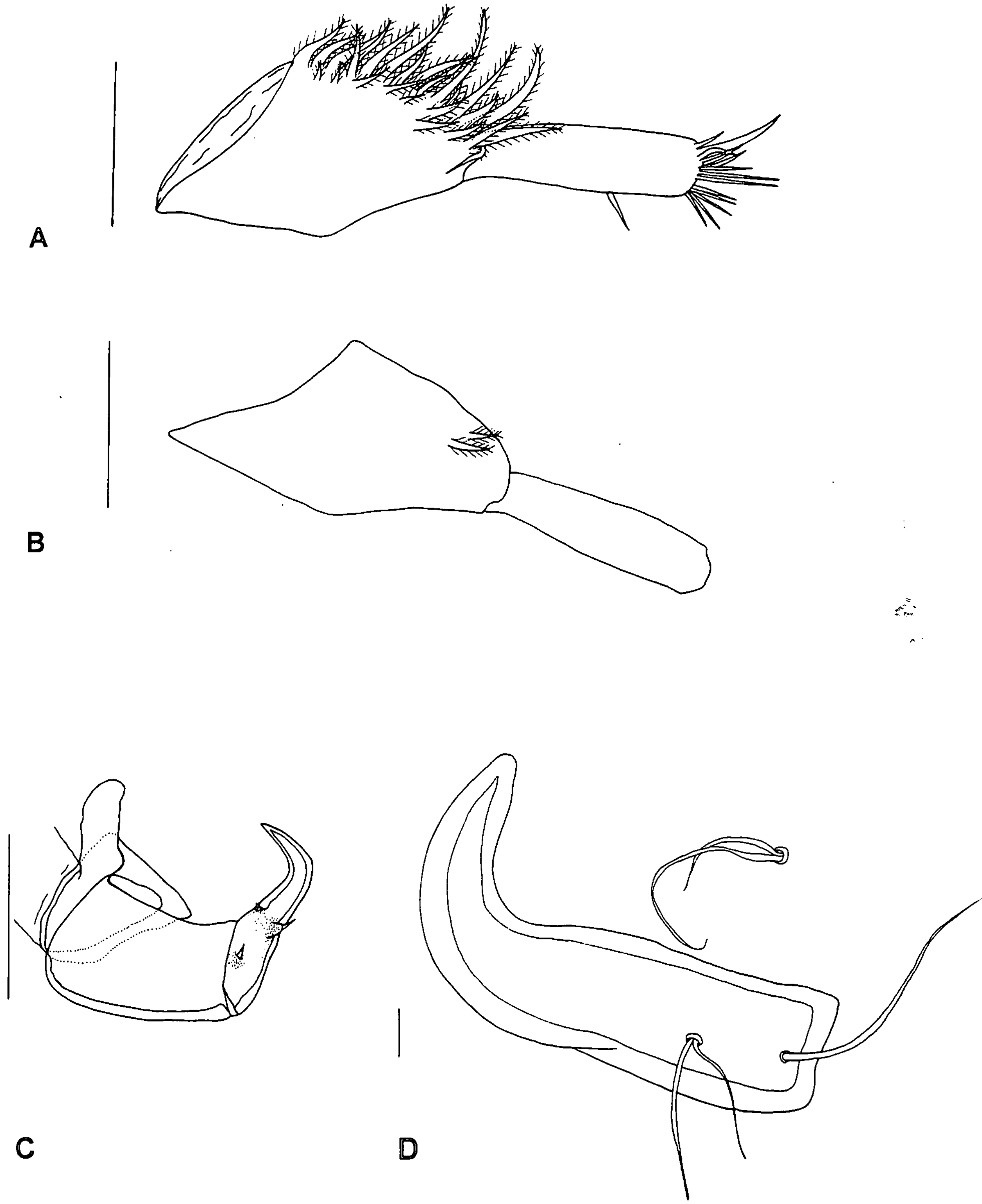

A
B
C
D

Figure 4.44

Microscope projection drawing of *Caligus mortis* Kensley, 1970 female occurring on the fish host *Clinus superciliosus* (Linnaeus, 1758), collected from the De Hoop Nature Reserve, South Africa.

A. Maxillule

B. Maxilla

C. Maxilliped

D. Sternal furca

Scale-bar: B & C - 100µm. A & D - 10µm

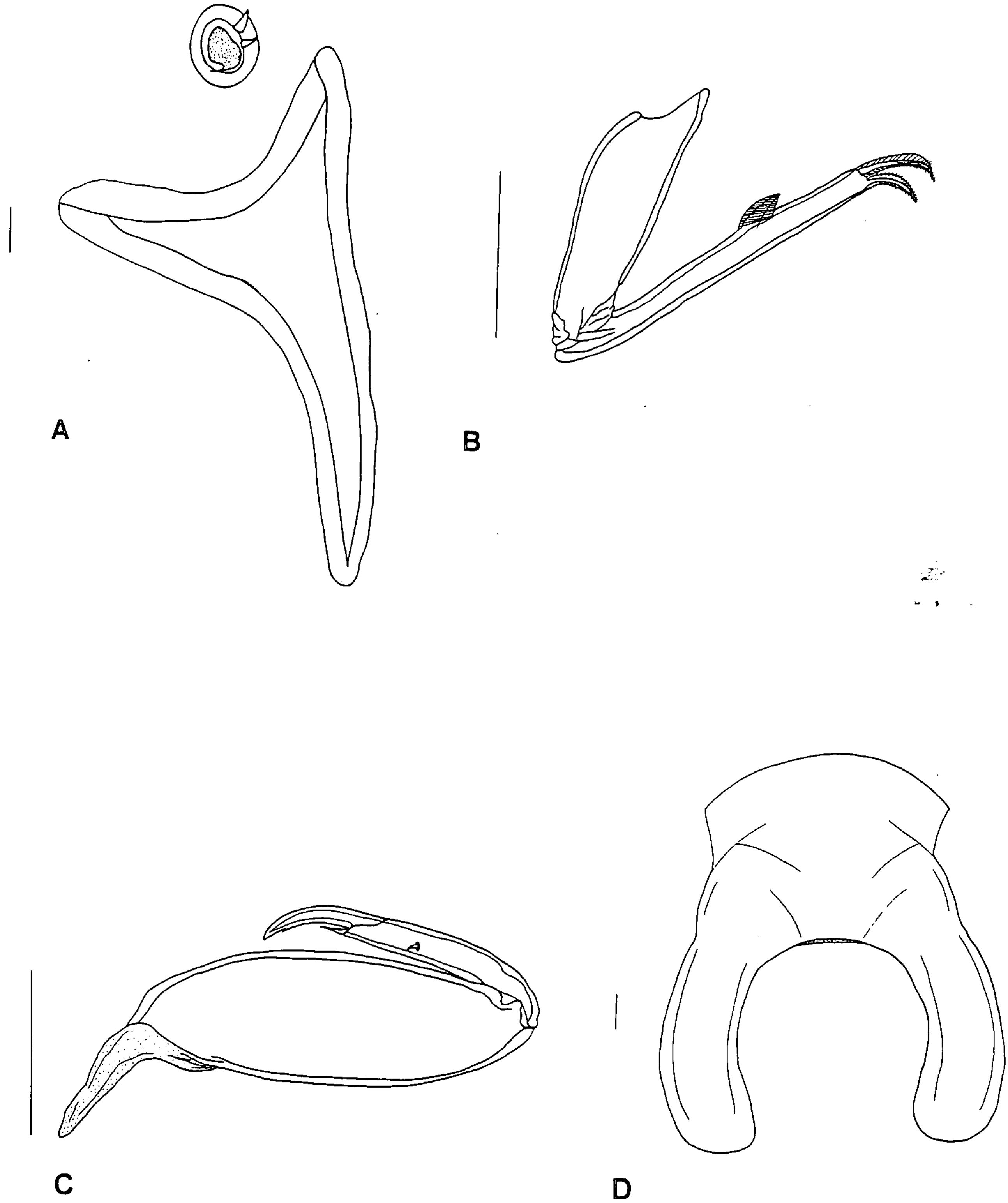

A
B
C
D

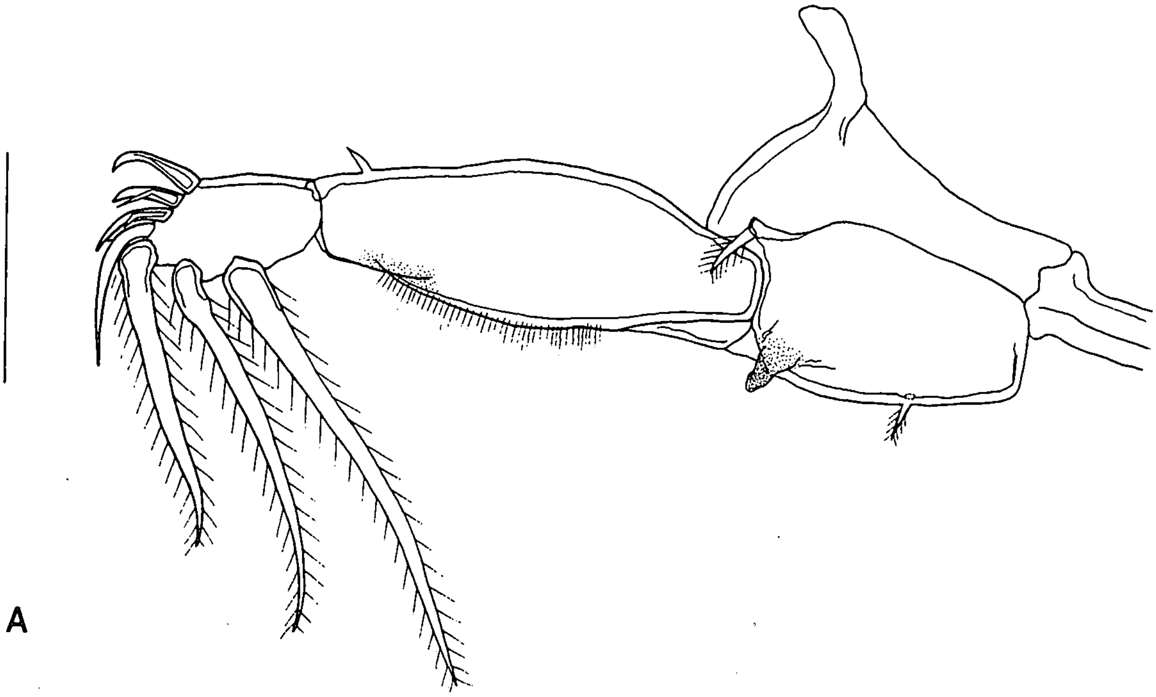
Figure 4.45

Microscope projection drawing of *Caligus mortis* Kensley, 1970 female occurring on the fish host *Clinus superciliosus* (Linnaeus, 1758), collected from the De Hoop Nature Reserve, South Africa.

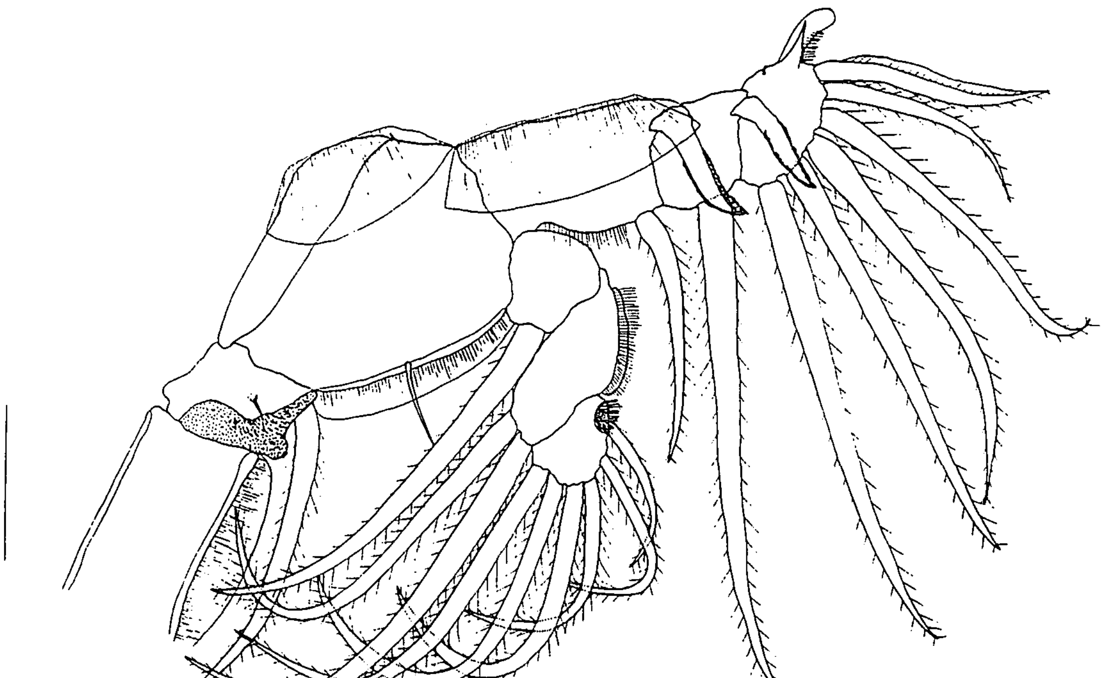
A. Leg 1

B. Leg 2

Scale-bar: A & B - 100µm



A



B

Figure 4.46

Microscope projection drawing of *Caligus mortis* Kensley, 1970 female occurring on the fish host *Clinus superciliosus* (Linnaeus, 1758), collected from the De Hoop Nature Reserve, South Africa.

A. Leg 3

B. Leg 4

Scale-bar: A & B - 100µm

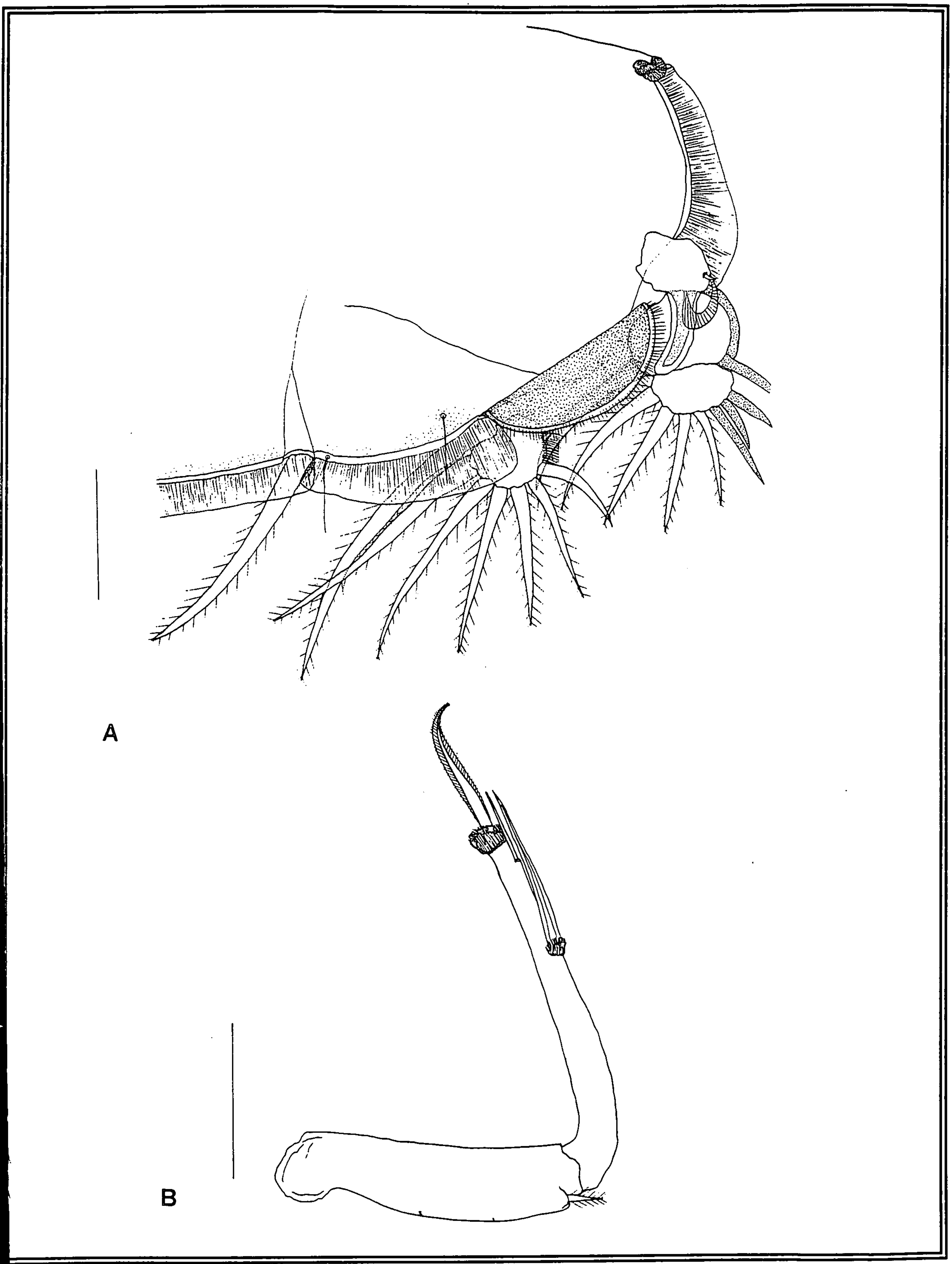

A
B

Figure 4.47

Microscope projection drawing of *Caligus mortis* Kensley, 1970 male (dorsal) occurring on the fish host *Clinus superciliosus* (Linnaeus, 1758), collected from the De Hoop Nature Reserve, South Africa.

Scale-bar: 1mm

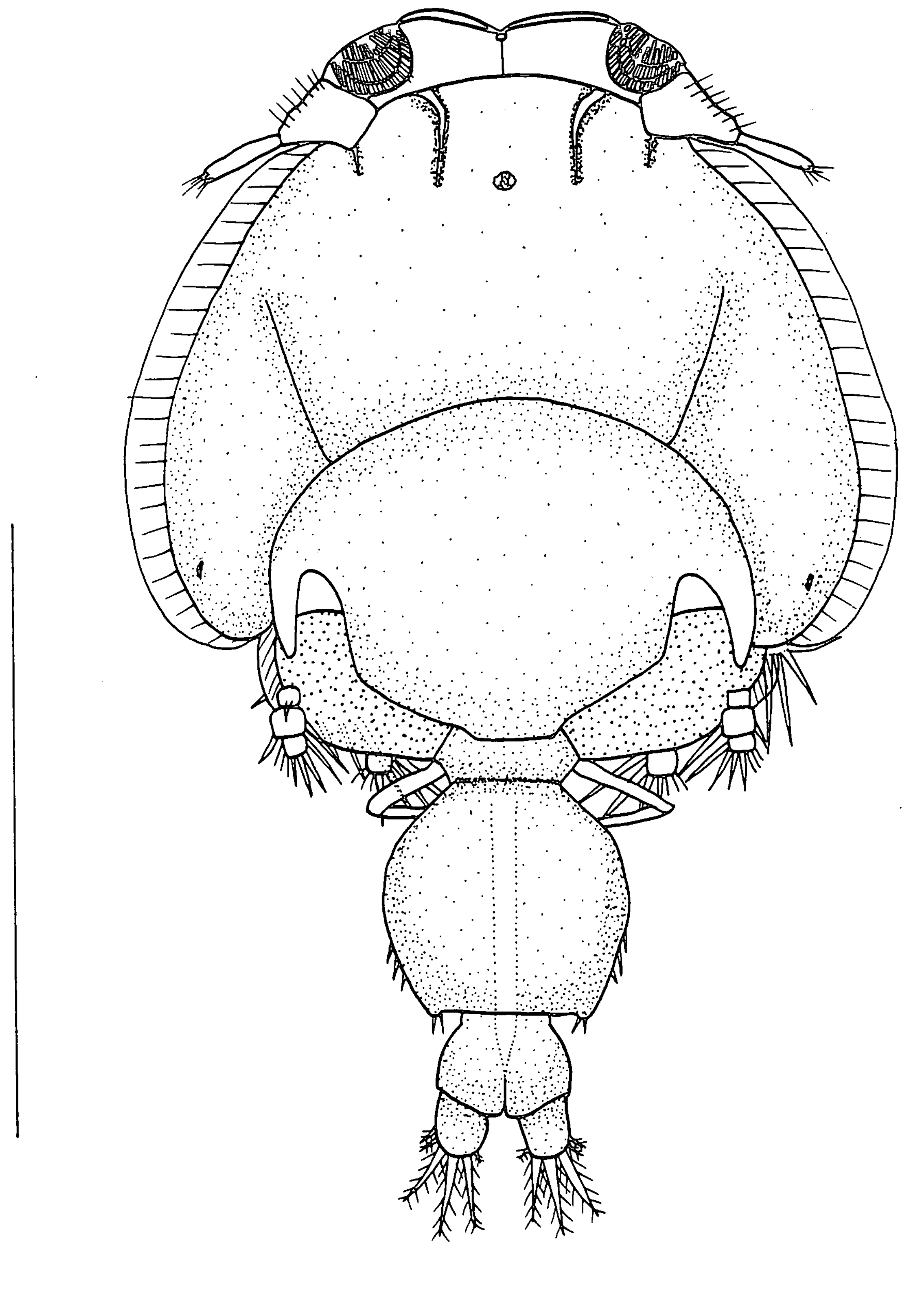


Figure 4.48

Microscope projection drawing of *Caligus mortis* Kensley, 1970 male (ventral) occurring on the fish host *Clinus superciliosus* (Linnaeus, 1758), collected from the De Hoop Nature Reserve, South Africa.

Scale-bar: 1mm

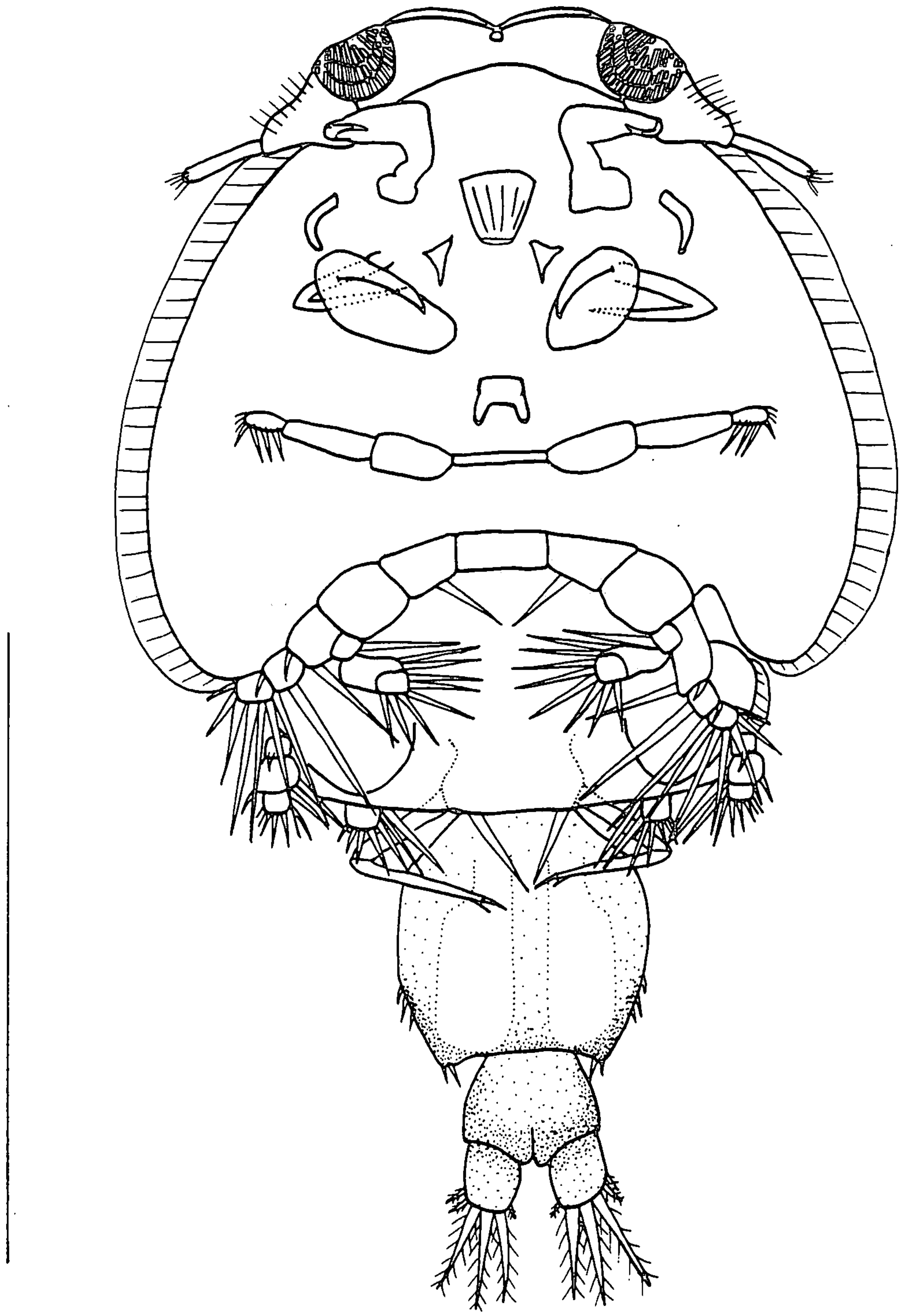


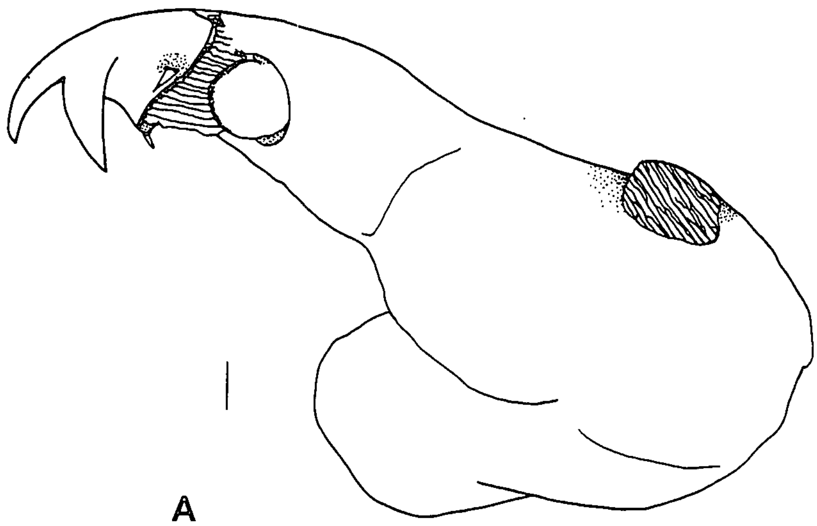
Figure 4.49

Microscope projection drawing of *Caligus mortis* Kensley, 1970 male occurring on the fish host *Clinus superciliosus* (Linnaeus, 1758), collected from the De Hoop Nature Reserve, South Africa.

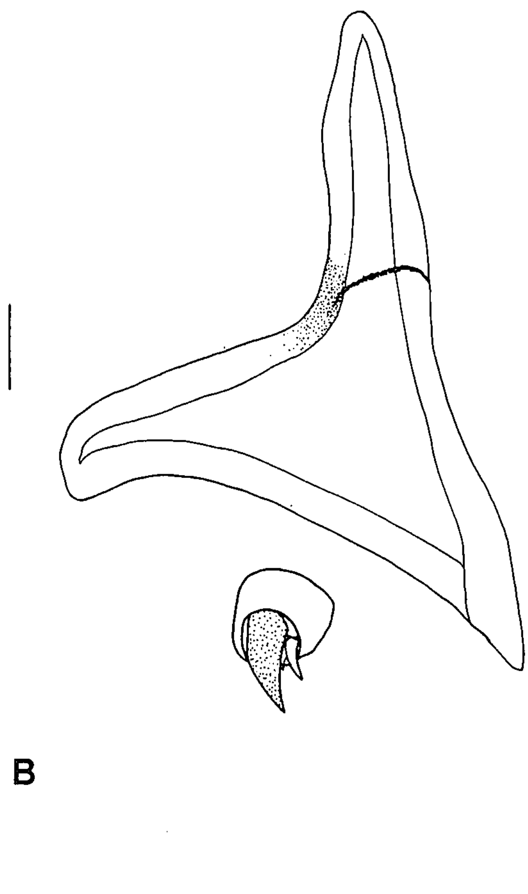
A. Antenna

B. Maxillule

Scale-bar: A & B - 10µm



A



B

Figure 4.50

Scanning electron micrographs of *Caligus mortis* Kensley, 1970 female occurring on the fish host *Clinus superciliosus* (Linnaeus, 1758), collected from the De Hoop Nature Reserve, South Africa.

A. Ventral view of antennule

B. Antenna

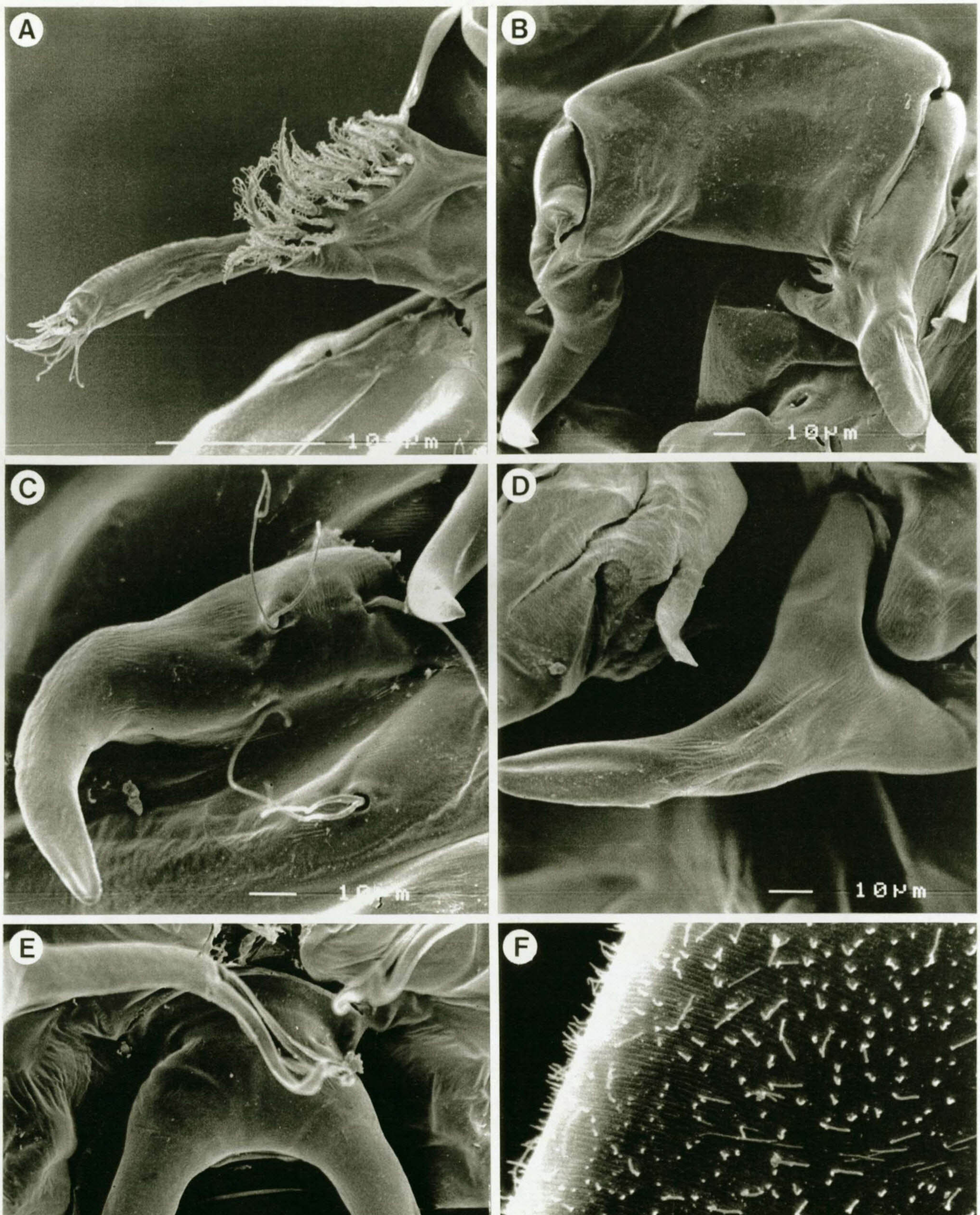
C. Postantennary process

D. Maxillule

E. Sternal furca

F. Sensory hairs on marginal membrane of dorsal shield

Scale-bar: A - 100µm. B, C, D, E & F - 10µm



A
B
C
D
E
F
10μm
10μm
10μm
10μm
10μm

Figure 4.51

Scanning electron micrographs of *Caligus mortis* Kensley, 1970 female occurring on the fish host *Clinus superciliosus* (Linnaeus, 1758), collected from the De Hoop Nature Reserve, South Africa.

A. Tip of exopod of leg 1

B. Leg 2

C. Hairs on endopod of leg 2

D. Exopod of leg 2

E. Leg 3

F. Tip of exopod of leg 4

Scale-bar: B, D & E - 100μm. A, C & F - 10μm

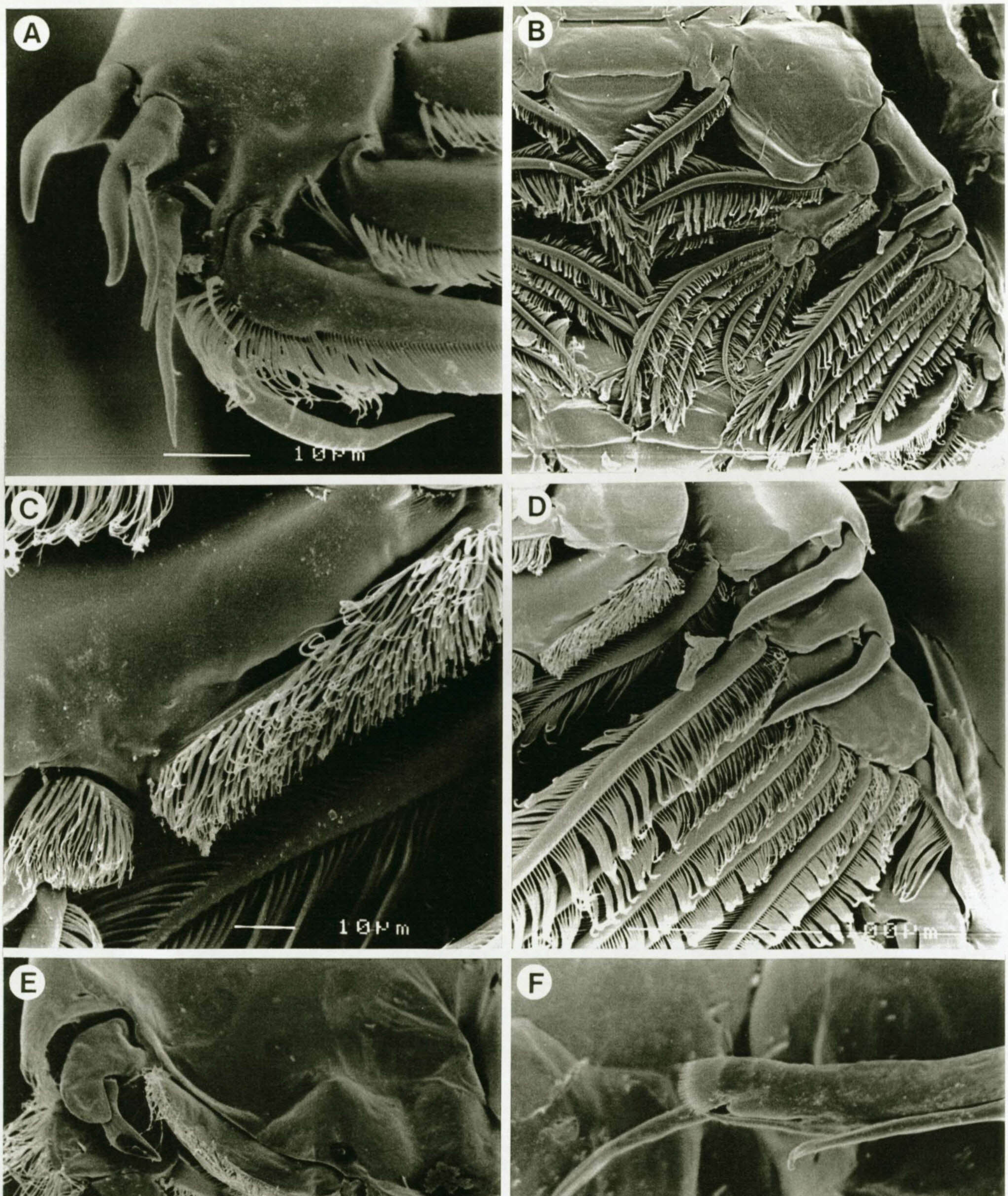

A
10µm
B
C
10µm
D
100µm
E
100µm
F
10µm

Figure 4.52

Scanning electron micrographs of *Caligus mortis* Kensley, 1970 female (A-B) and male (C-F) occurring on the fish host *Clinus superciliosus* (Linnaeus, 1758), collected from the De Hoop Nature Reserve, South Africa.

A. Leg 5

B. Plumose setae on caudal ramus

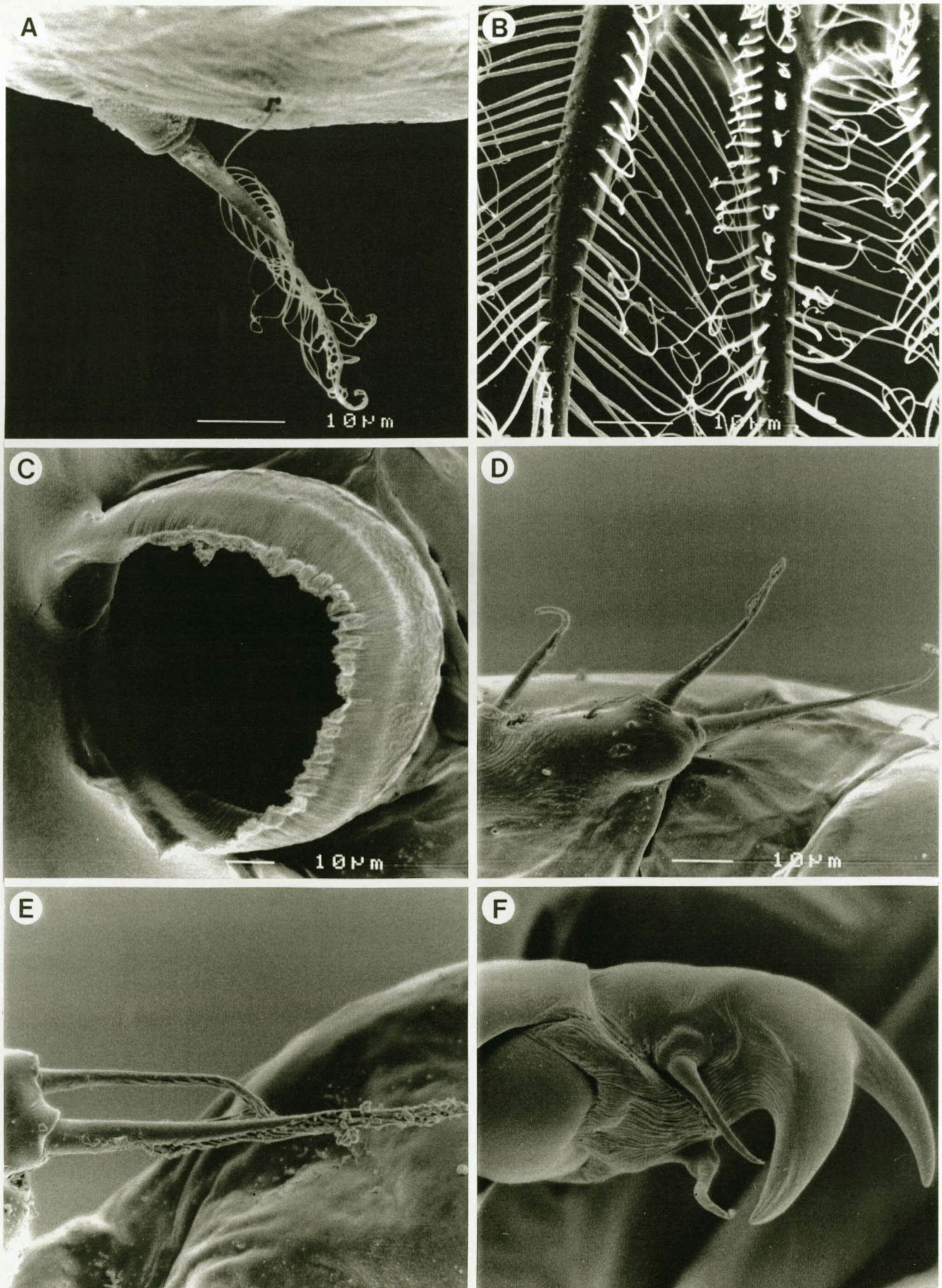
C. Lunule

D. Leg 5

E. Leg 6

F. Tip of antenna

Scale-bar: A, B, C, D, E & F - 10μm


A
10 µm
B
10 µm
C
10 µm
D
10 µm
E
10 µm
F
10 µm


5

Parasite/Host associations with notes on the life cycle of a *Caligus* species

Aspects of Parasite/Host Associations

Tidal pool species

The rich and varied fauna and flora of the southern African coast could partly be attributed to the extreme contrast between the water masses on the east and west coasts (Branch, *et al.* 1994). The uniqueness of the southern African coastline is also demonstrated by the intertidal fish fauna. According to Prochazka and Griffiths (1992) the intertidal fish fauna of southern Africa is rich in species and exhibits a high degree of endemism. Most of the research done on the intertidal fish were either taxonomic or were checklists, recording presence, absence or relative abundance (Penrith, 1969; Penrith & Kensley, 1970; Kensley & Penrith, 1973; Penrith, 1976). Other studies such as those by Bennett and Griffiths (1984), and Beckley (1985) and Bennett (1987), are quantitative collections of intertidal fishes. The only recent studies on the parasites of intertidal pool fish were carried out by one of the students in our Aquatic Parasitology Research Group. In his work, Loubser (1994) concentrated on representatives of ectoparasitic Peritrichida found on the South African intertidal fish.

Gibson (1982) and Beckley (1985) suggested that tidal pool fish could be classified as either **resident** or **transient**. The residents include various species of the families Clinidae, Gobiidae and Bleniidae as well as the giant clingfish, *Chirosochismus dentex* (Pallas, 1769). The transient species include juveniles of the families Sparidae, Cheilodactylidae and Mugilidae.

Transient tidal pool species

Estuaries of the world are widely recognised as valuable nursery areas for many commercially and recreationally important fish species. Beckley (1985) found that this is also true for tidal pools along the southern African coast. He found that the juveniles of *Chirodactylus brachydactylus* (Cuvier, 1830), *Cheilodactylus fasciatus* Lacepède, 1803 and *Sparodon durbanensis* (Castelnau, 1861) occur in tidal pools and are absent from other coastal habitats, thus suggesting that they could be dependant on tidal pools as nursery areas. The fact that tidal pools play an important role in the life history of certain fish highlights the importance of a better understanding of the parasites found on fishes in tidal pools.

Residential tidal pool species

As already mentioned the resident species of tidal pools consist mainly of various species of Gobiidae, Blenniidae and Clinidae as well as species such as *Chorisochismus dentex*.

The family Gobiidae constitutes the largest single family of marine fishes. Most gobies are small and have an elongated body with a bluntly rounded head. The pelvic fins are particularly well developed and are fused to form a sucking disc. According to Migdalski and Fichter (1976) gobies are commonly found resting on the bottoms of sandy tidal pools. The most common gobies in southern African tidal pools are *Caffrogobius nudiceps* (Valenciennes, 1827) and *C. caffer* (Günther, 1874). Bennett and Griffiths (1984) found that the highest percentage of *C. caffer* is found in tidal pools situated between the mean tidal level and low water mark.

Members of the family Blenniidae are small, elongated scaled fish with blunt, rounded heads and prominent eyes. According to Van der Elst (1988) blennies are rather similar to gobies in looks and habits. *Antennablennius bifilum* (Günther, 1861) and *Helcogramma obtusirostre* (Klunzinger, 1871) were the most common blennies collected during the present study.

The southern African Clinidae are represented by 39 species which are endemic to this region (Branch *et al.*, 1994). These small, elongated fishes are similar to blennies, but are readily distinguished by the distinct scales that cover the body. The variegated body colours of these fishes enable them to blend well with their surroundings of mainly kelp and eel grass. According to Veith (1979) and Bennett and Griffiths (1984) *Clinus superciliosus* (Linnaeus, 1758) is the most common clinid found along the south and west coasts of southern Africa.

Marine and estuarine species

A checklist of the marine fishes found from, and expected to be found between St Lucia and Kosi Bay on the east coast of KwaZulu-Natal was published by Bruton and Cooper (1980). The marine fishes are abundant in every niche except the midwater zone where food is scarce. There are numerous fishes such as moonfishes (Monodactylidae) and the goby *Glossogobius giuris* (Hamilton-Buchanan, 1822) that ascend to, or almost to, fresh water. Estuarine fishes like representatives of the Ambassidae, Gerreidae, the kob *Argyrosomus hololepidotus* (Lacepède, 1801), the spotted grunter *Pomadasys commersonni* (Lacepède, 1801) and 12 of the 15 mullets (family Mugilidae) occur in these estuarine sanctuaries. These fishes are frequently caught in the fish traps built by the indigenous fishermen in Kosi Bay. *Diplodus sargus capensis* (Smith, 1844) and *Lithognatus mormyrus* (Linnaeus, 1758) are equally at home in the estuary mouth or in the surf zone.

The large predators or game fishes swim actively seeking other fish or food. The kingfishes (Carangidae) and tunas (Scombridae) are two predators and their food consists of two types, namely the shoaling fishes such as sardines or pilchards which enter the Natal waters every winter from the south, or other from the tropical waters like the fusiliers.

Fish species collected at De Hoop Nature Reserve and Jeffreys Bay

The warm temperate south coast marine region stretches from Port St Johns to about Cape Point according to Branch and Branch (1995). Few tropical species occur here, while there are many species unique to this area. The collections carried out at the De Hoop Nature Reserve and Jeffreys Bay represent tidal pool fish species typical of this marine region.

A total of eight species belonging to five families were collected during the three excursions to the De Hoop Nature Reserve (Table 5.1). Specimens of seven species of tidal pool fishes belonging to five families were collected from Jeffreys Bay during the three excursions (Table 5.2).

Table 5.1 A summary of the fish species and families collected during three field trips to the De Hoop Nature Reserve as well as their distribution on the southern African coast according to Smith and Heemstra (1986).

Fish species collected	**Distribution**
CLINIDAE	
Clinus cottoides Valenciennes, 1836	Olifants River Mouth - Kei River
Clinus superciliosus (Linnaeus, 1758)	18°59'S West Coast - Kei River
GOBIIDAE	
Caffrogobius nudiceps (Valenciennes, 1827)	Walvis Bay - East London
MUGILIDAE	
Liza richardsonii (Smith, 1846)	West Coast - St Lucia
GOBIESOCIDAE	
Chorisochismus dentex (Pallas, 1769)	Port Nolloth - Northern KwaZulu\Natal
SPARIDAE	
Diplodus sargus capensis (Smith, 1844)	Angola - Mozambique
Sarpa salpa (Linnaeus, 1758)	Eastern Atlantic - Southern Mozambique
Sparodon durbanensis (Castelnau, 1861)	Cape - KwaZulu\Natal

Table 5.2 A summary of the fish species and families collected during three field trips to Jeffreys Bay, as well as their distribution on the southern African coast according to Smith and Heemstra (1986).

Fish species collected	**Distribution**
CLINIDAE	
Clinus cottoides Valenciennes, 1836	Olifants River Mouth - Kei River
Clinus superciliosus (Linnaeus, 1758)	18°59'S west coast - Kei River
GOBIIDAE	
Caffrogobius caffer (Günther, 1874)	False Bay - KwaZulu\Natal
MUGILIDAE	
Mugil cephalus Linnaeus, 1758	Cosmopolitan
GOBIESOCIDAE	
Chorisochismus dentex (Pallas, 1769)	Port Nolloth - northern KwaZulu\Natal
SPARIDAE	
Diplodus sargus capensis (Smith, 1844)	Angola - Mozambique
Rhabdosargus holubi (Steindachner, 1881)	Cape - KwaZulu\Natal

Fish species collected at Lake St Lucia

The east coast of southern Africa supports a particular high species diversity, because a large suite of tropical Indo-Pacific species contributes to its fauna and flora (Branch, *et al.* 1994). The importance of Lake St Lucia as a nursery and feeding ground for marine, estuarine and freshwater fish species must be emphasised in the light of environmental degradation along the KwaZulu-Natal coast. The survey done at Lake St Lucia represents data from the east coast marine region.

During field trips to Lake St Lucia in KwaZulu-Natal, seven different estuarine and marine fish species, belonging to five families, were collected. A summary of all the different species of fish collected and their distribution is presented in Table 5.3.

Table 5.3 A summary of the fish species and families collected during field trips to Lake St Lucia, as well as their distribution on the southern African coast according to Smith and Heemstra (1986).

Fish species collected	**Distribution**
CARANGIDAE	
Caranx sexfasciatus Quoy & Gaimard, 1825	KwaZulu-Natal - Indo-Pacific
HAEMULIDAE	
Pomadasys commersonnii (Lacepède, 1801)	Indian Ocean to False Bay, Cape estuaries, Algoa Bay
LEIOGNATHIDAE	
Leiognathus equula (Forsskål, 1775)	Indo-Pacific, KwaZulu-Natal to East London
MUGILIDAE	
Liza tricuspidens (Smith, 1935)	Mossel Bay - Kosi Bay
Mugil cephalus Linnaeus, 1758	Cosmopolitan
SPARIDAE	
Acanthopagrus berda (Forsskål, 1775)	Tropical Indo-Pacific, Mozambique, estuaries in KwaZulu-Natal, Swartvlei at Knysna
Rhabdosargus holubi (Steindachner, 1881)	Cape - KwaZulu\Natal

As *Caligus mortis* were the only species collected at Jeffreys Bay and De Hoop Nature Reserve with adequate infestation statistics, the results of these infestation is presented in Table 5.4. The infestation prevalence for *C. mortis* is displayed in Figure 5.1.

Table 5.4 Infestation statistics of *Caligus mortis* Kensley, 1970, from different species of intertidal fish collected at two different localities on the South African south coast.

Jeffreys Bay (1997, 1998 & 1999)								
Fish host		N	S (mm)	Inf.	TP	P (%)	I	MI
Clinus superciliosus	R	18	86 - 182 (124)	5	5	27.7	1	1
Clinus cottoides	R	3	98 - 107 (102)	1	1	33.3	1	1
Chorisochismus dentex	R	4	143 - 264 (203)	2	2	50	1	1
Liza richardsonni	T	9	110 - 141 (127)	0				
Sarpa salpa	T	8	49 - 74 (58)	0				
De Hoop Nature Reserve (1997, 1998 & 1999)								
Clinus superciliosus	R	31	73 - 219 (129)	7	16	51.6	1 - 8	2.29
Clinus cottoides	R	13	57 - 173 (90)	2	2	15.38	1	1
Chorisochismus dentex	R	1	135	1	1	100	1	1
Liza richardsonii	T	171	33 - 210 (99)	1	1	0.58	1	1
Sarpa salpa	T	44	107 – 214 (122)	1	1	2.27	1	1
Rhabdosargus holubi	T	25	54 - 121 (78)	0				

N - Total number of fish collected
S - Size interval of hosts and mean size
Inf. - Number of hosts infested
TP - Total number of parasites
T - Transient tidal pool species
P - Prevalence expressed as a percentage
I - Intensity
MI - Mean intensity (parasites per host)
R - Residential tidal pool species

No statistical data will be given for collections of fish species at Lake St Lucia. The data in the possession of the author is only of the caligids removed from a host species, and no records of the total fish species collected are available. As the variation of salinity in Lake St Lucia is crucial for the existence of many organisms, the salinity for the various collection localities will be given in Table 5.5.

Table 5.5 A summary of the salinity values at various localities in Lake St Lucia, as well as the fish hosts caught (mm) in the specific areas, and the number of caligids per host (in brackets).

Date	Locality	Salinity (ppt)	Host and total parasites collected	Length (mm)
March 1992	Fanies Island	22	*Caranx sexfasciatus* (5)	375
October 1992	Fanies Island	34	*Caranx sexfasciatus* (1)	-
			Rhabdosargus holubi (3)	313
			Rhabdosargus holubi (2)	348
March 1993	Charters Creek	40	*Leiognathus equula* (1)	210
			Liza tricuspidens (1)	523
			Pomadasys commersonnii (1)	331
May 1993	Charters Creek	50	*Caranx sexfasciatus* (2)	562
			Caranx sexfasciatus (13)	563
May 1993	Hell`s Gate	22	*Rhabdosargus holubi* (201)	281-308
August 1994	Fanies Island	32	*Mugil cephalus* (7)	537
			Rhabdosargus holubi (241)	303
November 1994	Hell`s Gate	33	*Acanthopagrus berda* (5)	262-316
			Rhabdosargus holubi (3)	109-352

ppt = parts per thousand; mm = millimetres

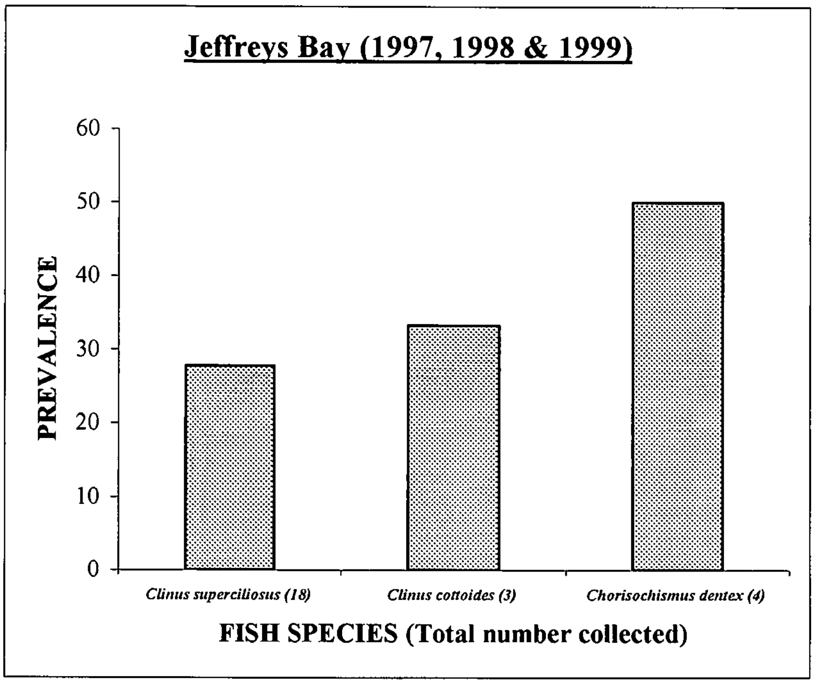
Caligids were collected from the intertidal fish species, but the data is not enough to draw any significant conclusions. Specimens of *Caligus mortis* were found on 12 of the 49 *Clinus superciliosus* collected at both Jeffreys Bay and De Hoop Nature Reserve. As *C. mortis* was recorded by Kensley (1970) from the super klipfish *Clinus superciliosus*, collections of *Clinus cottoides* were also made to investigate the occurrence of *C. mortis* on these hosts. Only 16 *Clinus cottoides* hosts were caught during the present study, and three individual *C. mortis* specimens were found on three of the 16 host specimens. As five and eight specimens of *C. mortis* were collected from two host specimens of *Clinus superciliosus* respectively, it appears that *C. mortis* has a preference for this specific host species. In their study of vertical distribution of *Clinus superciliosus*, Prochazka and Griffiths (1992) noted that large individuals are more abundant in lower tidal pools. The abundance of large individuals in these pools will increase the contact with caligids also more common in tidal pools closer to the low water mark. Five caligids were collected from a host of 145 mm in length, and eight caligids were collected from a host of 173 mm in length.

Chorisochismus dentex is almost always well-hidden in rock crevices and is seldom collected at Jeffreys Bay and De Hoop Nature Reserve. Three of the five specimens collected of this host species were infested with *Caligus mortis*. This fish attaches to the rock surface by means of a ventral sucker, and is most likely more abundant than reflected in the data and is probably only collected by chance in most cases. Due to the small sample size of *C. dentex* examined, the infestation statistics are not really meaningful.

The most abundant fish species collected was the southern mullet *Liza richardsonii*. This specific host was collected for the observation of another copepod family, and of 180 hosts collected, a single caligid specimen was found on *Liza richardsonii*. It is most likely that the caligid copepod attached to the mullet by chance, as this host species is not an ideal host for *Caligus mortis*.

The same can be said for the strepie, *Sarpa salpa*. A total of 44 specimens of *Sarpa salpa* were collected from De Hoop Nature Reserve for the observation of another copepod family. Only one specimen of *Caligus mortis* was collected, and this host is probably also not suitable for *C. mortis*.

Clinus superciliosus is without doubt the main host for *Caligus mortis* and is also more abundant than other residential pool fish. The infestation prevalence of *C. mortis* collected at both Jeffreys Bay and De Hoop Nature Reserve is illustrated in Figure 5.1.



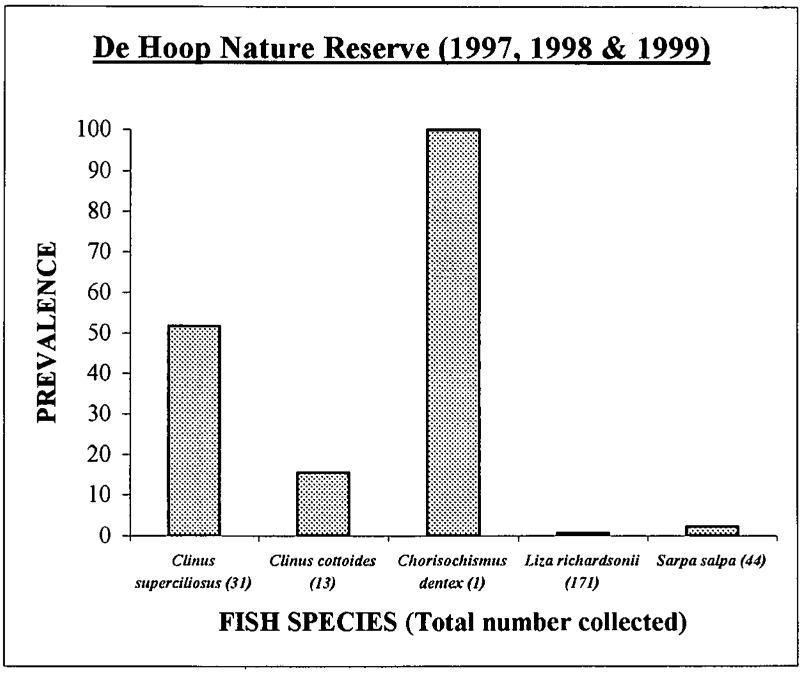


Figure 5.1 Histogram of the infestation prevalence (%) of *Caligus mortis* Kensley, 1970 on different species of tidal pool fish, collected during six field surveys at Jeffreys Bay and De Hoop Nature Reserve (1997, 1998 & 1999).

General Life Cycle of the Genus *Caligus* Müller, 1785

Notwithstanding the fact that more than 200 species of *Caligus* are known, the complete life cycle is known for only ten species (Lin, Ho & Chen 1997). Studies on the life cycle of different *Caligus* species was done by authors such as Kabata (1972), Piasecki & MacKinnon (1995) and Lin, Ho & Chen (1996 & 1997). Most *Caligus* species studied, pass through eight stages (two nauplii, one copepodid, four chalimus, and one preadult) before reaching the adult stage. *Caligus epidemicus* Hewitt is unusual in its development with two more chalimus stages.

The first nauplius has an irregular oval body with truncated anterior and posterior margins and no external segmentation. The second nauplius is barely distinguishable from the first. It is longer and its balancers are relatively smaller, but otherwise the two stages are very much alike. Nauplius larvae have only three paired appendages. The only certain way to tell them apart is by finding within them the outlines of the following stage, which in the second nauplius is an unmistakable copepodid. The bodies of copepodids consist of two tagmata.

Sometime after attaching to fish (by means of antennae) a tightly coiled frontal filament appear in the anterior portion of the cephalothorax and gives rise to the first chalimus stage. The first chalimus stage is characterised by the absence of distinct segmentation. There is some measure of external segmentation regained in the second chalimus stage. The third chalimus stage approaches the typical *Caligus*-form, and the sexes can now be distinguished by external appearance. The male differs from the female by having a slightly slimmer genital region and by the structure of its second antenna (Kabata 1972). In general appearance the fourth chalimus stage is characterised by the presence of all adult features. The main differences between chalimus IV and the preadult are in the proportions of various parts (Kabata 1972).

The developing lunules in the frontal plate become visible through the cuticle during chalimus IV. The preadult stage differs from that of the adult only in the relatively poorly developed genital complex. Mate-guarding found in the life history of *Caligus epidemicus* by Lin and Ho (1993) was also observed by Lin, Ho and Chen (1997) in the development of *Caligus multispinosus* Shen. Lin, *et al.* (1997) found that the youngest female being guarded by an adult male was chalimus III, where as in *C. epidemicus*, it was chalimus V.

The main differences among species are in the relative sizes of the four component tagmata, particularly the shape and size of the genital complex and the length and segmentation of the abdomen. The differences between sexes are mainly confined to the genital complex and abdomen (Kabata 1972). The male second antenna is always, and first maxilla sometimes, different from those of the female.

The larval development of *Caligus epidemicus* comprises ten stages: two nauplii, one copepodid, six chalimus, and one preadult (young adult) (Lin, Ho & Chen 1996). As the developmental stages of larval *Caligus* parasites are basically uniform, the larval development of *C. epidemicus* is used to show the different developmental stages of the female (Figure 5.2), that differs only in a few aspects from the male.

The first documented record of a caligid copepod utilising a frontal filament was by Burmeister (1835) who collected some external copepod parasites that were attached by the frontal threads to mackerel. Unaware of the identity of the larval specimens, Burmeister (1835) described them a new species within a new genus, *Chalimus*. Since the 1860's, when Burmeister's mistake was confirmed and widely accepted, the obsolete generic name, *Chalimus*, has become a convenient term to designate attached siphonostome copepod larvae in general (Piasecki & MacKinnon 1993).

The frontal filament is a larval prehensile organ, being an evolutionary achievement of the majority of Siphonostomatoida parasitic on fishes. The shape of the frontal filament is highly variable among families and sometimes even among related species. The filament is an acellular structure produced by a cement gland located inside the anterior part of the cephalothorax. In the present study a chalimus IV larval stage of *Caligus acanthopagri* were found and will be described below, using scanning electron microscopy.

Figure 5.2

Diagram illustrating the life cycle of *Caligus epidemicus* Hewitt, redrawn from Lin, Ho and Chen (1996)

n1 – nauplius 1

n2 – nauplius 2

co – copepodid

ch1 – chalimus 1

ch2 – chalimus 2

ch3 – chalimus 3

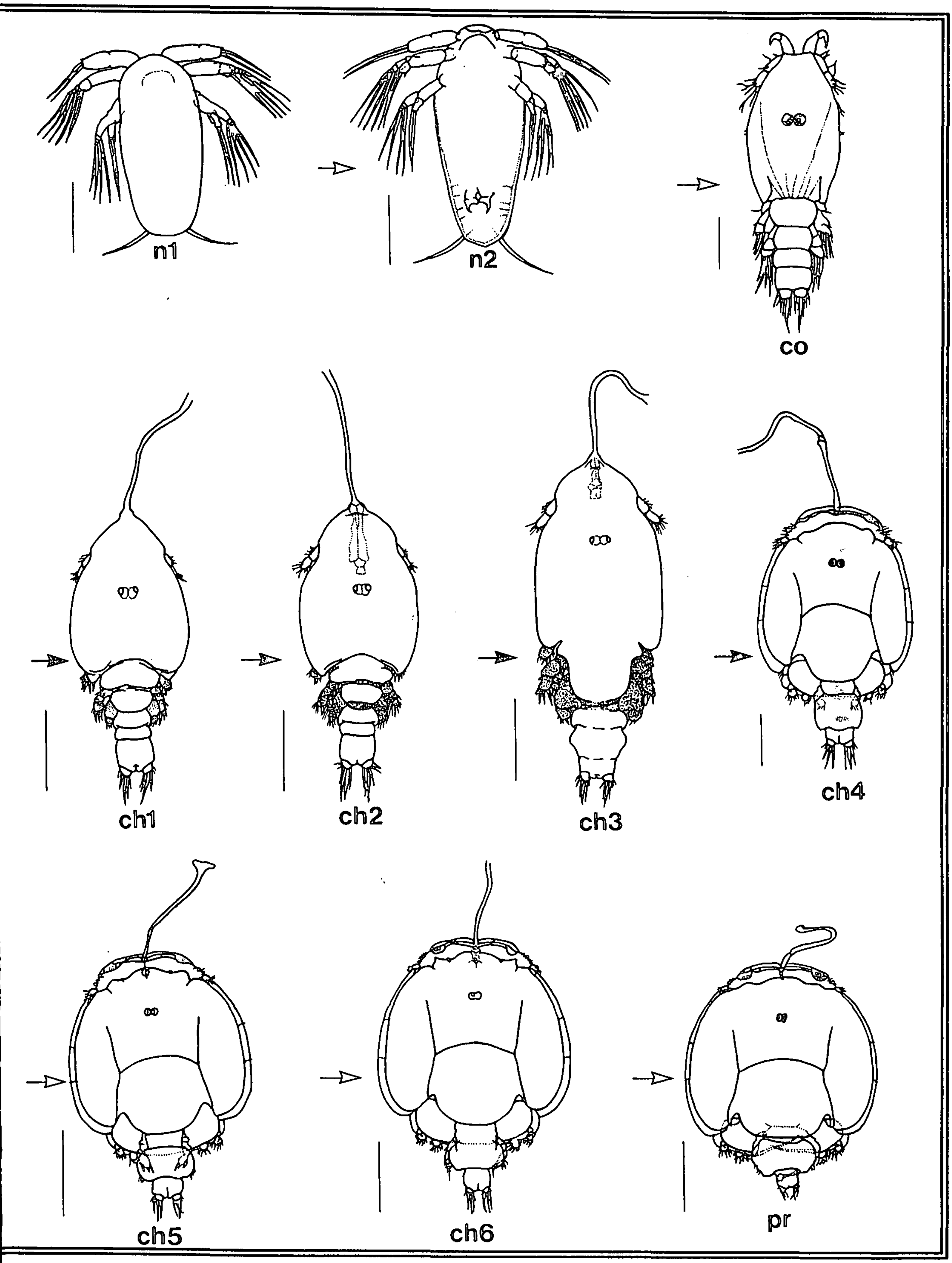
ch4 – chalimus 4

ch5 – chalimus 5

ch6 – chalimus 6

pr – preadult

Scale-bar: n1, n2 & co -100μm. ch1-ch4 - 200μm. ch5 & ch6 - 400μm. pr - 500μm


n1
n2
co
ch1
ch2
ch3
ch4
ch5
ch6
pr

Chalimus IV larva of *Caligus acanthopagri*

Host: Riverbream *Acanthopagrus berda* (Forsskål, 1775).

Locality: Fanies Island.

Reference material: 16 / 017

Material examined: Different developmental stages of *Caligus acanthopagri* were collected from the body surface of the host mentioned. Many of the developmental stages were damaged due to their small size and not knowing that developmental stages were collected. As a result of the damage to the nauplius and chalimus stages, only a SEM description of the chalimus stage will be presented below.

Description of chalimus stage: Body with typical appearance of chalimus (Figure 5.3A & 5.4C). No morphological measurements were taken.

Frontal filament: The shape of the frontal filament (Figure 5.3A & B) are used to identify the specific chalimus stage. When chalimus I approaches, the cuticle delaminates and the next stage is visible inside. Also, the surface of the frontal organ delaminates, leaving its old secretory pads with the old cuticle. The filament is still attached to the secretory pads of chalimus I. Under the old cuticle, the frontal organ produces a new extension part to the filament lobe. It is round, regularly shaped, and deeply concave anteriorly. It is firmly attached ventrally to the two secretory pads of the frontal organ. The cement gland secretion forming the lobe is apparently elastic and sticky. It is assumed that it hardens rapidly in contact with water. After the moult into chalimus II, the new lobe totally covers the filament lobe of the previous stage.

The similar process of reattachment is repeated during the next moults. Each time an extra lobe is added to the base of the frontal filament. Chalimus II has one visible element at the proximal end of the filament, chalimus III has two, chalimus IV has three, and chalimus V has four. The real number of lobes is actually more than one, since the very first element attributed to chalimus I is totally covered by the lobe produced by chalimus II. Thus, the real number of elements at the proximal end of the filament corresponds with the chalimus stage number.

Each subsequent cup-shaped lobe of the filament is slightly bigger than the previous one. Each has two connecting pads which are cemented to the secretory pads of the frontal organ until the reattachment process is complete. Then the old cuticle is discarded. The surface of those connecting pads reflects the shape and external structure of the secretory pads of the frontal organ of sequential stages. The fine structure of the surface of the connecting pads indicates that the secretory pads remain structurally similar throughout all the stages, and consist of uniform, densely packed villiform papillae. The connecting pads of chalimus IV are shown in Figure 5.3C, and the tip of the frontal filament is shown in Figure 5.3D.

Antennule: Two-segmented (Figure 5.3E). The antennule does not have all the plumose setae as in the adult stage, and will acquire all the setae in the following developmental stages.

Maxilla: Ornamentation on calamus and canna is reduced (Figure 5.3F), and will be acquired in the following developmental stages. Two rows of spinules are visible on the calamus and the canna has a marginal, denticulate membrane.

Maxilliped: Two-segmented (Figure 5.4A); proximal segment unarmed; distal segment forming claw; shaft of distal segment armed with spine.

Sternal furca: Small and just beginning to form (Figure 5.4B); bluntly pointed parallel tines.

Leg 1: Reminiscent of those in adult (Figure 5.4D); ornamentations not clearly visible yet.

Leg 2: Reminiscent of those in adult (Figure 5.4E); ornamentations not clearly visible yet.

Leg 3: Reminiscent of those in adult (Figure 5.4F); apron-shaped; ornamentations faintly visible.

Remarks: As the life cycle of *Caligus acanthopagri* is not yet known, further studies must be done to understand the full life cycle of this diverse species.

Figure 5.3

Scanning electron micrographs of the chalimus IV stage of *Caligus acanthopagri* Lin, Ho and Chen, 1994 occurring on the fish host *Acanthopagrus berda* (Forsskål, 1775), collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Anteroventral view of chalimus

B. Frontal filament

C. Base of frontal filament with connecting pads

D. Tip of frontal filament

E. Ventral view of antennule

F. Tip of maxilla

L1 – extension lobe of chalimus II; L2 – extension lobe of chalimus III; cp – connecting pad

Scale-bar: A & B - 100μm. C, D, E & F - 10μm

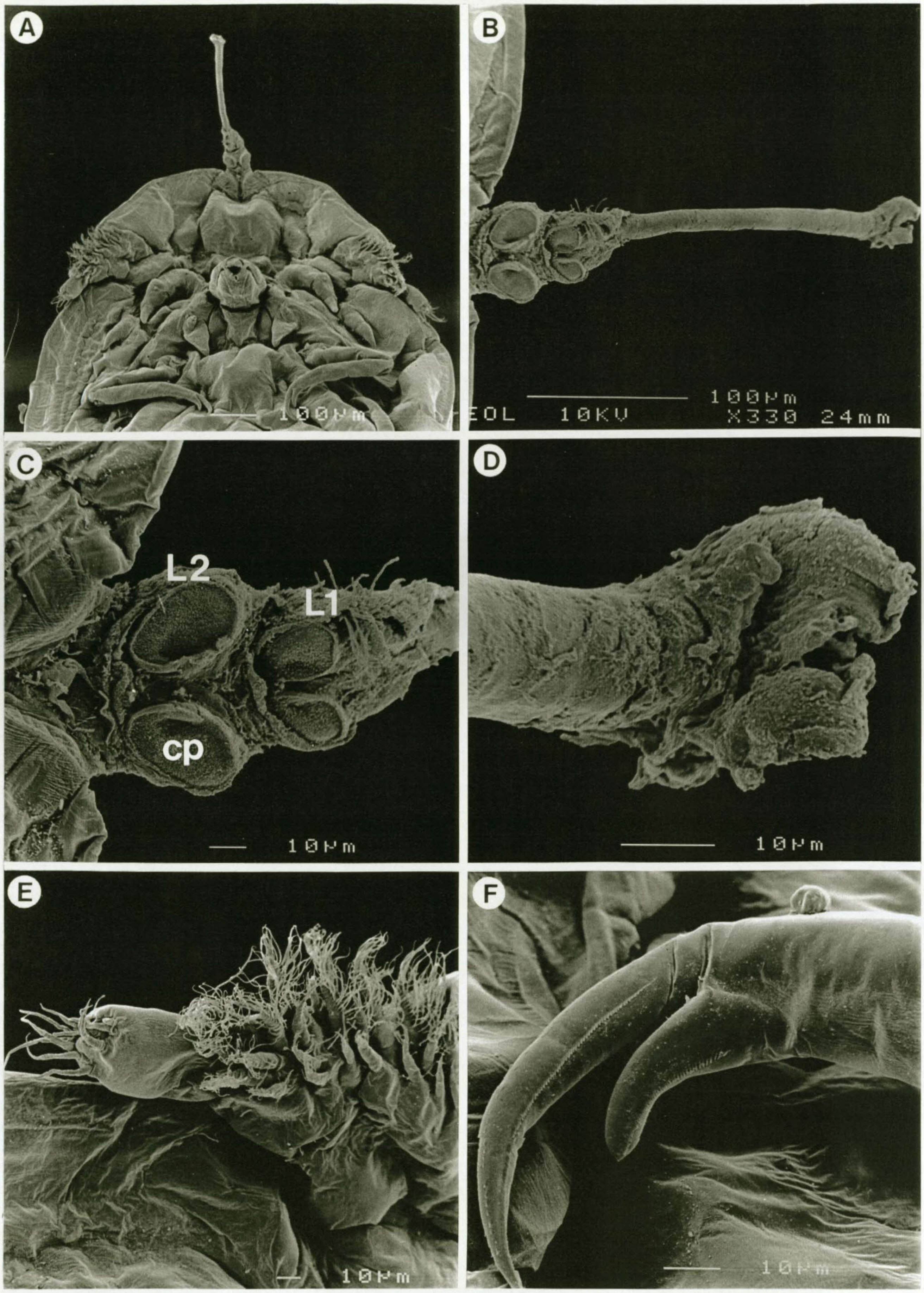

A
100µm
B
100µm
JEOL 10KV X330 24mm
C
L2
L1
cp
10µm
D
10µm
E
10µm
F
10µm

Figure 5.4

Scanning electron micrographs of the chalimus IV stage of *Caligus acanthopagri* Lin, Ho and Chen, 1994 occurring on the fish host *Acanthopagrus berda* (Forsskål, 1775), collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Maxilliped

B. Sternal furca

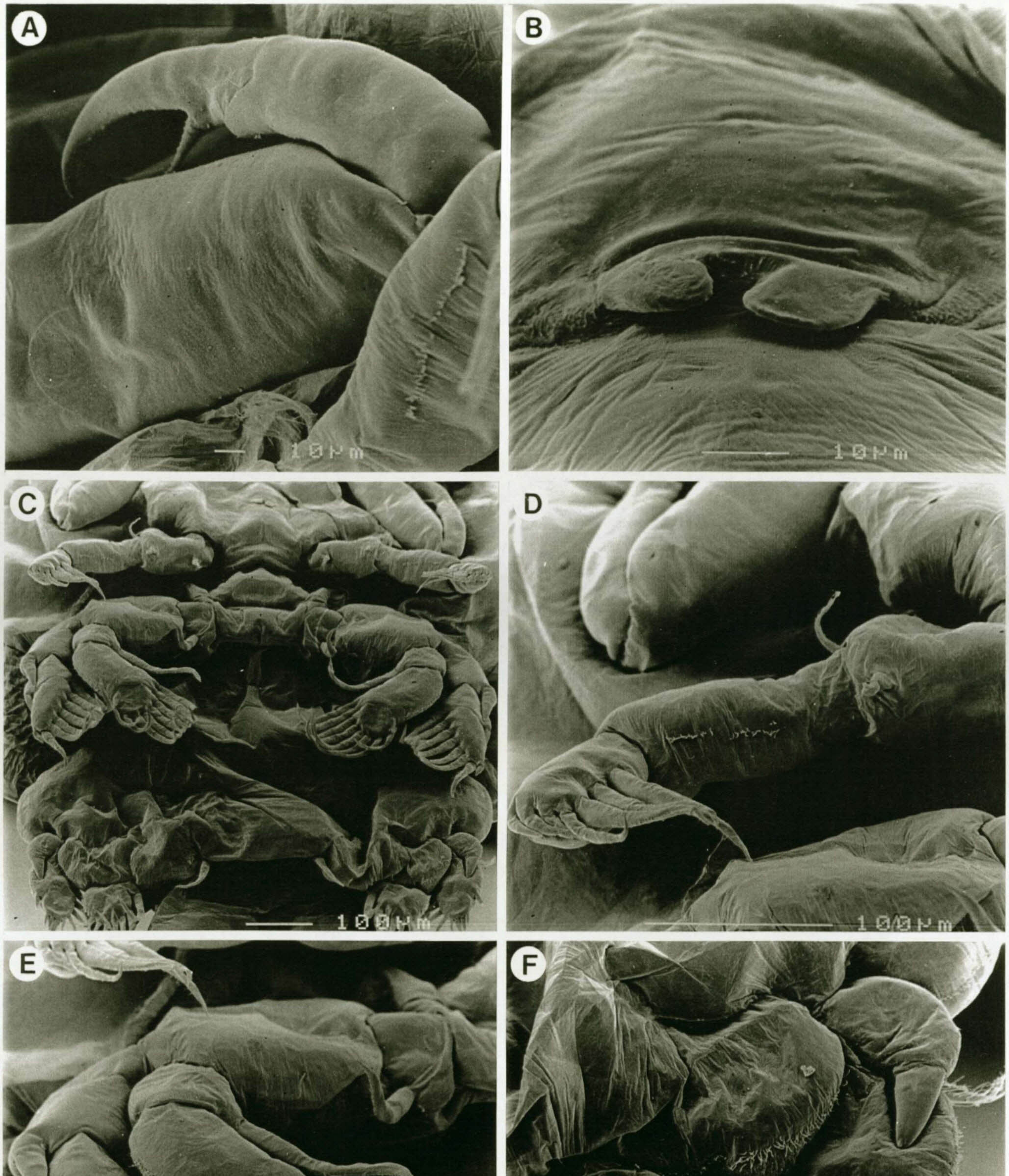
C. Posteroventral view of chalimus

D. Leg 1

E. Leg 2

F. Leg 3

Scale-bar: C, D & E - 100µm. A, B & F - 10µm


A
10µm
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C
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D
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F
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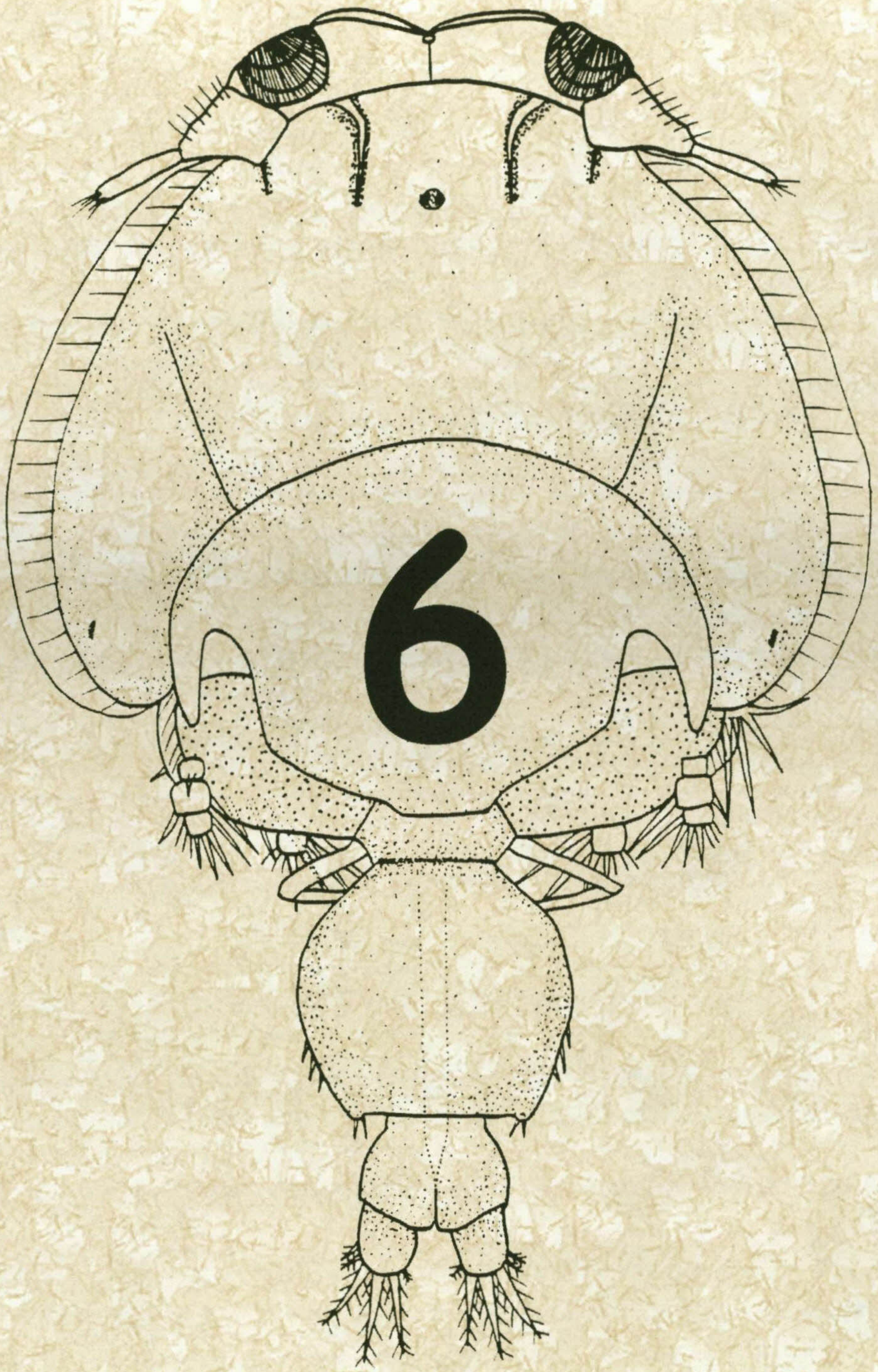

6

Hypersymbionts associated with *Caligus*

Ectosymbionts attach to a wide range of fish and crustaceans of commercial importance, especially ciliophorans (Lom 1973, Esch, Hazen, Dimock & Gibbons 1976, Vogelbein & Thune 1988, Conroy, Conroy, Dixon, Fukushima & Shimokawa 1989). These ciliophoran-host relationships have been either described as phoretic (Nagasawa 1988) where the host merely carries the epibiont, or as non-parasitic or ectocommensal (Lom 1973, Hazen, Raker, Esch & Fliermans 1978, Vogelbein & Thune 1988, Stone & Bruno 1989) where the epibiont benefits without damaging the host, for example by receiving fresh oxygenated water or extra nutrients.

No records of ciliophorans found on caligid copepods from marine fish from the southern African coast are known to date. The only documented information about sessiline ciliophoran associations with crustacean fish-ectoparasites in South Africa is that of Viljoen (1982) who found *Epistylis* spp. on *Lernaea barnimiana* Hartman, 1870, and Avenant (1983) who referred to the association of an *Epistylis* sp. on *Dolops ranarum* (Stuhlmann, 1891). But these ciliophorans are from freshwater fish parasites and the record of these ciliophorans on marine fish parasites is new to South Africa. Sessiline ciliophorans have been found on *Lernaea* species from other parts of the world, but no identification to species level has been done. Viljoen (1983) and Van As and Viljoen (1984) identified the sessiline ciliophorans of freshwater crustacean parasites to species level, but they used live specimens for the identification purposes. In this study ciliated protozoans of the genus *Epistylis* were found attached to the marginal membrane and ventral surface of *Caligus acanthopagri* and *C. engraulidis*. Scanning electron microscopy is used to provide detail of the fine structure of the ciliophorans and their attachment mechanisms.

Another interesting hypersymbiont was found attached to *Caligus engraulidis*. No records of udonellids found on *Caligus* species from marine fish from the southern African coast are known to date. Only five described species of *Udonella* are known and are found exclusively and commonly on caligid copepods parasitising marine fishes. Scanning electron microscopy is used to provide detail of the morphology, life cycle and species identification.

Ciliophorans – The Genus *Epistylis* Ehrenberg, 1830

Systematics of the genus *Epistylis* Ehrenberg, 1830

There are currently 14 phyla distinguished within the kingdom Protozoa, including the phylum Ciliophora. Listed below is an abridged version of the classification of *Epistylis* species adjusted from the classification of De Puytorac (1994).

Classification of the genus *Epistylis* Ehrenberg, 1830

Empire	Eukaryota
Kingdom	Protozoa Goldfuss, 1818
Phylum	Ciliophora Doflein, 1901
Subphylum	Epiplasmata De Puytorac *at el.*, 1993
Superclass	Membranellophora Jankowski, 1975
Class	Oligohymenophorea De Puytorac *et al.*, 1974
Subclass	Peritrichia Stein, 1859
Order	Peritrichida Stein, 1859
Suborder	Sessilida Kahl, 1933
Family	Epistylidae Kahl, 1935
Genus	*Epistylis* Ehrenberg, 1830

Presented below are the systematic characteristics of the relevant sessile ciliophoran, according to the thesis by Van As (1997).

Class Oligohymenophorea De Puytorac *et al.*, 1974

Oral apparatus distinct from somatic ciliature, comprised of well-defined paroral membrane plus several membranelles of peniculli located in buccal cavity or infundibulum situated on ventral side of body, with cytostome at base of the cavity;

inconspicuous cytopharynx; stomatogenesis parakinetal or buccokinetal; some variation in mode of fission; conjugation temporary and only in one group; free-living or symbiotic.

Subclass Peritrichia Stein, 1859

Body characteristically inverted bell- or goblet-shaped or conical-cylindrical; morphology dominated by adoral ciliary wreath of buccal ciliature, winding counterclockwise at apical pole and a scopula (holdfast derivatives: contractile stalk or complex adhesive disc) at antiapical pole; somatic ciliature reduced to subequatorial locomotor fringe (trocheal band); ciliated infundibulum, into which contractile vacuole empties, leading to cytostome; stomatogenesis buccokinetal, plane of fission parallel to major axis of body; dimorphism (migratory telotroch), colonies, loricae or thecae and cysts common to many species; conjugation (total) involves fusion of micro- with macroconjugant; very widespread aquatic distribution, free-living or symbionts on diverse host range, some commensals and even ecto- or endoparasites.

Order Sessilida Kahl, 1933

Sedentary or sessile (adults), commonly stalked (or with inconspicuous adhesive disc, scopula), with a few species secondarily mobile; many produce arboroid colonies; some entire groups loricate; mucocysts and pellicular pores universal; adults filter feed on bacteria (larval stage mouthless); habitats ranging from freshwater, brackish and marine, few species live as endozoic forms.

Family Epistylidae Kahl, 1935

Normally stalked individuals, stalk not contractile; body highly contractile; single or colonies; widespread in aquatic environment; free-living, some symbiotic with organisms.

Genus ***Epistylis*** Ehrenberg, 1830

Body inverted bell-shaped, always stalked, stalk not contractile; body highly contractile; stalk branched into two, always divides in two; always colonies, elongated macronucleus; habitats ranging from freshwater, brackish and marine, specific to substrate.

Epistylis sp. found on *Caligus acanthopagri* Lin, Ho & Chen, 1994 and *Caligus engraulidis* Barnard, 1948

Approximately 240 *Caligus acanthopagri* copepods were examined for ectosymbionts and about 30 specimens were found to be infected by *Epistylis* sp. Four specimens of 20 *Caligus engraulidis* copepods were found infected with *Epistylis* sp. Live specimens were not available for study, as all the *Caligus* specimens were fixed in either 70% ethanol or 10% neutral buffered formalin after removal from their hosts. All data presented here are thus from fixed material.

Epistylis sp. was found mainly on the marginal membrane and ventral surface (Figure 6.1A) of *Caligus acanthopagri* and *Caligus engraulidis*, especially the maxilliped (Figure 6.1B) and the second and third pair of legs. Specimens were also present around the oral region and the sternal furca. The epistylid was found individually, in pairs (Figure 6.1C) and as colonies (Figure 6.1D), representing different stages of maturity of the ciliophoran. In many instances, the colonies comprised over 50 individuals, or zooids, in a tight cluster (Figure 6.1E). The zooids were inverted bell-shaped to cylindrical in shape and approximately 30 μm wide. As the copepods were fixed in 70% ethanol and some specimens in 10% buffered neutral formalin, many zooids were contracted as the cilia were withdrawn into the peristome and enclosed by the peristomial lip. The zooids are attached to the host cuticle via a longitudinally striated, segmented stalk.

Nagasawa (1986) stated that peritrich ciliophorans do not depend upon copepods for nutrition because they are bacterial feeders. Ciliophorans are capable of colonising fish and attaching to the scales (Lom 1973, Esch *et al.* 1976, Hazen *et al.* 1978), so it is possible that ciliophorans could be transported from fish to fish by the copepods. The ciliophorans did not appear to damage the copepod hosts and were probably ectocommensal.

The incidence of ciliophoran attachment on the chalimus stages of the copepod life cycle is not known. Moulting may not necessarily result in the loss of the ciliophorans by the host. Several authors have noted that ciliophoran epibionts are able to respond to the moult cycle of the crustacean hosts by producing motile stages that are able to resettle on the new cuticle as it emerges (Walker, Roberts & Ushir 1986). *Epistylis* are generally regarded as ectocommensals since they are not known to cause deleterious effects to the hosts, either through their feeding habits or mode of attachment (Lom 1973, Hazen *et al.* 1978). In the case of *Epistylis*, Vogelbein and Thune (1988) concluded that any harmful effects to the decapod host are probably limited to a decrease in available respiratory surface area and disruption of normal water flow patterns.

As no evidence of pathogenicity by the ciliophorans was seen on any one of the infected copepods it would seem likely that the ciliophorans are harmless commensals. It would appear that the copepod cuticle is an excellent surface for ciliophorans to colonise.

Unidentified symbionts found on *Caligus acanthopagri* Lin, Ho & Chen, 1994 and *Caligus engraulidis* Barnard, 1948

Many of the infected copepods were also infected with bacteria and fungal hyphae. It is not clear whether this bacteria and fungal hyphae were originally attached to the fish hosts and attached to the copepod hosts as they are moving over the fish host' surface. The bacterial infection may be of a secondary infection on the fish host and were transferred to the copepod host. Some unidentified symbionts were also found attached on the ventral surface of *Caligus acanthopagri* and *C. engraulidis*. One of the symbionts (Figure 6.1F) is oval in shape and bears an outer surface which is covered by roundish dots. It is approximately 4.5 μm in length and was found individually and in small numbers on the ventral side of the copepod host. The second unidentified symbiont (Figure 6.1G) is much like the previous one mentioned, but does not bear any roundish dots on the outer surface. It is approximately 4.5μm in length, the outer surface is smooth and the one end bears a fine structure that could be used for attachment to the host. The third symbiont (Figure 6.1H) is spherical and bears some roundish dots on the outer surface. It is approximately 2.8μm in diameter. Further research will be done to identify these unknown symbionts. It is just speculation that these symbionts may be present on the fish host and are thus transported to the copepod parasite. These symbionts are a bit bigger than bacteria, and it is my opinion that these symbionts are living organisms, but their association with the copepod host are not known yet.

The bacterial and fungal hyphae were probably growing on fish mucus, which adheres to the surface of the copepod parasites. It is not known if the fungi observed were potentially pathogenic. However, bacteria are sometimes associated with ectocommensal ciliophorans and are capable of causing disease to the host (Hazen *et al.* 1978).

Figure 6.1

Scanning electron micrographs of *Epystilis* sp. (A-E) and unidentified symbionts (F-H) occurring on the copepod host *Caligus acanthopagri* Lin, Ho and Chen, 1994 collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Ventral view of *Caligus acanthopagri* with attached *Epistylis* sp.

B. Maxilliped with attached *Epistylis* sp.

C. *Epistylis* sp. in a pair

D. *Epistylis* sp. in a colony

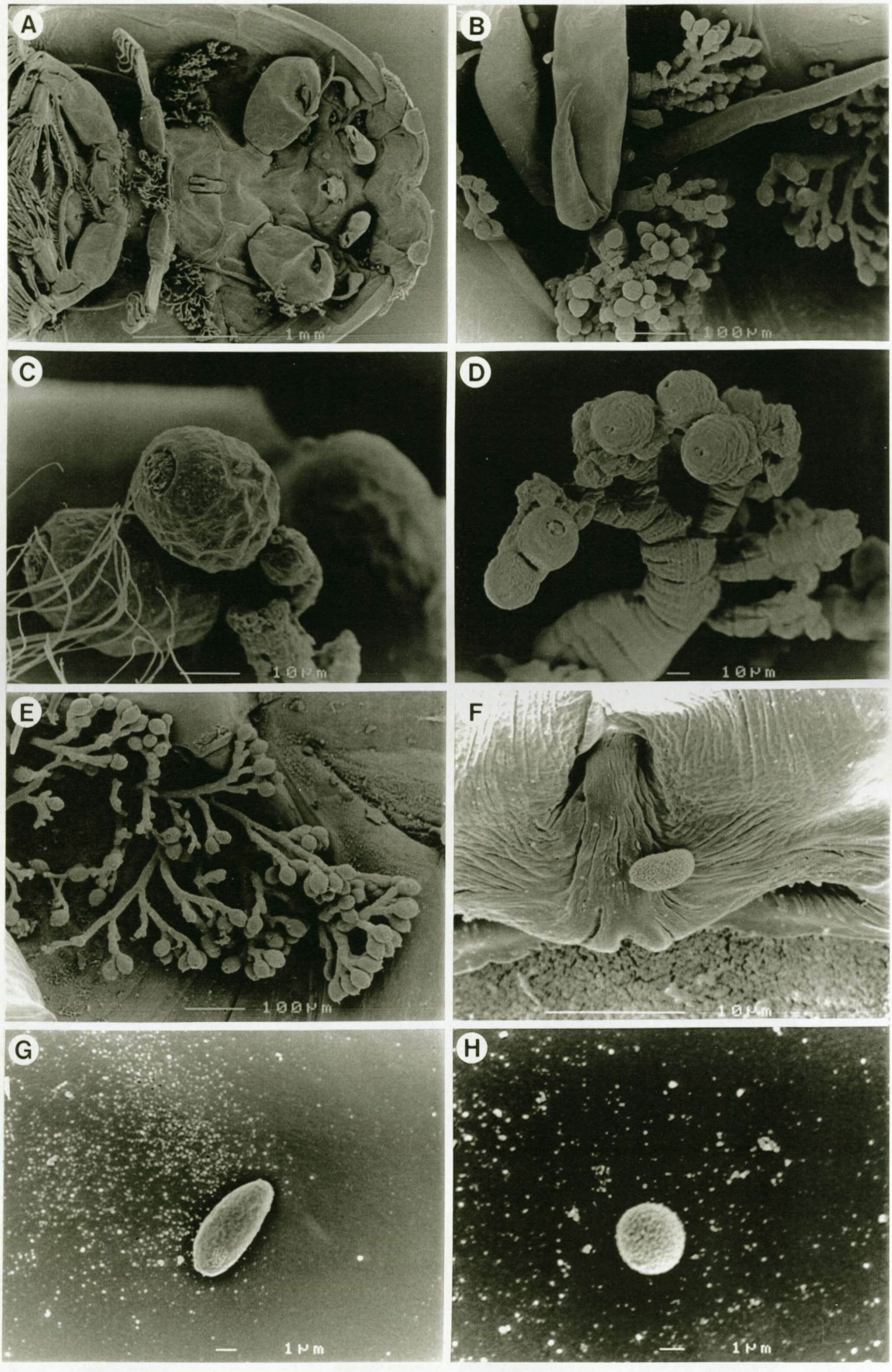
E. *Epistylis* sp. in a cluster

F. Oval-shaped symbiont with roundish dots on outer surface

G. Oval-shaped symbiont with smooth outer surface

H. Spherical symbiont with roundish dots on outer surface

Scale-bar: A - 1mm. B & E - 100µm. C, D & F - 10µm. G & H - 1µm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Caligid Monogenea – The Genus *Udonella* Johnston, 1835

Systematic problems with the genus *Udonella* Johnston, 1835

Systematists have been involved in much discussion about a certain helminth genus, namely *Udonella*. The five described species of *Udonella* are hyperparasites found exclusively and commonly on caligid copepods parasitising marine fishes, and these species are *Udonella caligorum* Johnston, 1835, *U. myliobati* (Guberlet, 1936), *U. ophiodontis* Kay, 1945, *U. papillifera* van der Land, 1967, and *U. murmanica* Kornakova and Timofeeva, 1981.

Guberlet (1936) described the species *Calinella myliobati* from the copepod *Trebius latifurcatus* Wilson, 1921 on the stingray *Myliobatis californica* in Monterey Bay, California. Price (1938) synonymised *Calinella* Monticelli, 1910 with *Udonella*, but did not comment specifically on the status of the species *Calinella myliobati* relative to the type species *Udonella caligorum*. Aken'Ova and Lester (1996) made an emended description of *Udonella myliobati*, making it a valid and fifth species of the genus *Udonella*.

When the surgeon George Johnston (Johnston 1835) originally described *Udonella caligorum* in 1835, he alluded to the problems systematists would have with the genus when he described it as a "leech" that "waves and contorts itself like a worm in pain" with its structure seemingly "allied to some intestinal worms" (Littlewood, Rohde & Clough 1998). In spite of their ubiquity, the phylogenetic position of *Udonella* has been discussed repeatedly since the type species was described as a monogenean platyhelminth. The genus *Udonella* was originally placed in a separate family, Udonellidae Taschenberg, 1879, and was upgraded later to a superfamilial status Udonelloidea Yamaguti, 1963, or even to be assigned to a new class Udonelloidea Ivanov, 1952. To date, some authors still include the genus in the Monogenea [(Van der Land 1967) as a special subclass Udonellida, (Lyons 1973, Justine, Lamberts & Mattei 1985)], although with uncertain affinities. Ehlers (1985) put the genus provisionally in the "Dalyellioidea" and stated that it probably does not belong to the

Neodermata (a clade consisting of the major groups of parasitic Platyhelminths). Kornakova (1987a, 1987b) examined the reproductive system of *Udonella* and concluded that "the comparative analysis of all systems of organs has revealed no features of specific similarity between Udonellida and Monogenea". Kornakova (1987a, 1987b) considered the genus belonging to the turbellarians, with ancestors among the Neorhabdocoela and most probably Typhloplanoida. Xylander (1987, 1988) considered it a typical neodermatan with an as yet unknown sister group within the Neodermata, based on the basis of EM studies of the tegument and sperm. Rohde, Watson and Roubal (1989) made an EM study of the flame bulbs, sensory receptors, tegument and sperm of *Udonella* and concluded that the genus is a typical neodermatan. In the structure of its protonephridial capillaries (lack of a septate junction), it resembles the cestodes, although similar capillaries were also found in a single polyonchoinean monogenean, *Anoplodiscus cirrusspiralis* (Rohde, Watson & Roubal 1992). Spermiogenesis of *Udonella* was examined by Rohde and Watson (1993) who concluded that it resembles that of polyonchoinean monogeneans.

The phylogenetic position of *Udonella* is of particular interest, since it has been claimed to be the sister group of the major classes of parasitic Platyhelminthes (Brooks & McLennan 1993), a view based on the comparison of superficially similar characters without prior homology assessment, but not supported by detailed morphological, including ultrastructural, studies of characters likely to be homologous (Rohde 1996). Littlewood, Rohde and Clough (1998) used phylogenetic analysis of molecular data from complete 18S rRNA and partial 28S rRNA genes of a variety of platyhelminths and placed the enigmatic *Udonella caligorum* firmly as a polyonchoinean monogenean. They used both maximum parsimony and a modified distance measure, operating under a maximum likelihood model, that gave identical solutions for each data set. These data further support morphological evidence from ultrastructural studies indicating the neodermatan affinities of *Udonella*, namely shared features in sensory receptors, surface tegument, sperm structure and spermiogenesis (Littlewood, Rohde & Clough 1998). Although only a few taxa are common to each data set, phylogenetic analysis of homologous ribosomal nuclear genes from a range of platyhelminths places *Udonella* as a polyonchoinean monogenean with possible sister group status with *Gyrodactylus* (order Gyrodactylidea), and certainly a member of a larger clade including the Capsalidea.

The classification of the class Monogenea is according to Boeger and Kritsky (1997), as this system is the most recent and most representative in terms of the phylogenetic relationships within the group. The genus *Udonella* will be included in the order Gyrodactylidea under the subclass Polyonchoinea (Table 6.1)

Since its description, the phylogenetic position of *Udonella* has been in doubt because of a number of peculiar characteristics. In particular, it lacks hooks at any stage of its development, whereas monogeneans (the group which it superficially resembles most closely in its ectoparasitic habit and possession of a posterior sucker) have hooks at least in the larval stage. However, the lack of hooks in *Udonella* may be a consequence of its attachment to copepods, whose hard exoskeletons are probably not suitable for penetration by hooks. Udonellids do not have ciliated larvae as in monogeneans, making it more confusing for placement in the class Monogenea. Furthermore, the tegument of the posterior sucker of *Udonella* is separated from that of the main body by a septate junction (Rohde & Watson 1995), as also found in the temnocephalans based on histological sections and staining of the protonephridial system.

TABLE 6.1 Classification of the class Monogenea (Van Beneden, 1858) adapted from Boeger and Kritsky (1997), with the inclusion of the family Udonellidae

SUBCLASS	ORDER	SUBORDER	INFRAORDER	SUPERFAMILY	FAMILY
Polyonchoinea (Bychowsky, 1937)	Monocotylidea				Monocotylidae
					Loimoidae
	Capsalidea				Dionchidae
					Capsalidae
	Motchadskyellidea				Montchadskyellidae
	Lagarocotylidea				Lagarocotylidae
	Gyrodactylidea				Bothitrematidae
					Tetraonchoididae
					Anoplodiscidae
					Udonellidae
					Gyrodactylidae
					Acanthocotylidae
	Dactylogyridea	Calceostomatinea			Calceostomatidae
		Neodactylodiscinea			Neodactylodiscidae
		Amphibdellatinea			Amphibdellatidae
		Tetraonchinea			Sundanonchidae
					Tetraonchidae
					Neotetraonchidae
		Dactylogyrinea			Dactylogyridae
					Diplectanidae
					Psuedomurraytrematidae
Polystomatoinea (Lebedev, 1986)	Polystomatidea				Polystomatidae
					Sphyranuridae
Oligonchoinea (Bychowsky, 1937)	Chimaericolidea				Chimaericolidae
	Diclybothriidea				Diclybothriidae
					Hexabothriidae
	Mazocraeidea	Mazocraeinea			Plectanocotylidae
					Mazoplectidae
					Mazocraeidae
		Gastrocoltylina	Anthocotylinea		Anthocotylidae
			Gastrocotylina		Psuedodiclidophoridae
				Protomicrocotyloidea	Allodiscocotylidae
					Psuedomazocraeidae
					Chauhaneidae
				Gastrocotyloidea	Bychowskycotylidae
					Gastrocotylidae
					Neothoracocotylidae
					Gotocotylidae
		Discocotylinea			Discocotylidae
					Diplozoidae
					Octomacridae
		Hexostomatinea			Hexostomatidae
		Microcotylinea		Microcotyloidea	Axinidae
					Diplasiocotylidae
					Heteraxinidae
					Microcotylidae
				Allopyragraphoroidea	Allopyragraphoridae
				Diclidophoroidea	Diclidophoridae
				Pyragraphoroidea	Pterinotrematidae
					Rhinecotylidae
					Pyragraphoridae
					Heteromicrocotylidae

Udonella caligorum Johnston, 1835

Figures 6.2 – 6.3

Host: *Caligus engraulidis* Barnard, 1948.

Localities: Fanies Island and Charters Creek in Lake St Lucia.

Reference material: 15 / 001.

Material examined: One adult and different developmental stages of *U. caligorum* were collected from the host mentioned. The adult *U. caligorum* specimen was found attached to the genital complex of the copepod host (Figure 6.2A). Eggs were also found on another three specimens of *C. engraulidis*, but no adult or pre-adult stages were found on these copepods. Eggs were found mostly on the genital complex and third pair of legs (Figure 6.2B & C).

Description of different udonellid developmental stages: Adult *U. caligorum* was attached to the lateral margin of the genital complex (Figure 6.2D) and is approximately 0.80 mm in length. Body elongated and cylindrical, cuticle with annulations. Two glandular head organs or pseudosuckers surrounded by blunt lobes on the anterior end of body. Haptor terminal, well-developed as a muscular, unarmed sucker, without septa (Figure 6.2E). Common lateral genital aperture (Figure 6.2F & G). Eggs (Figure 6.3A) relatively large with a thick membrane, which is extended into a long filament ending in an expansion or basal disc (Figure 6.3B) by which it is attached to the host. A structure on the ventrolateral surface (Figure 6.2H) is unidentified and may be annulations of the contracted specimen.

Basic life cycle

The worms attach to the host by means of a rounded posterior sucker (Figure 6.2E). The genital pore (Figure 6.2F & G) is about 20 μm in diameter and is situated laterally from where the eggs are released. Filamentous eggs (Figure 6.3A) were found attached to the genital complex of the caligid host. These filamentous eggs attach to the surface of the copepod host by means of a basal disc (Figure 6.3B). The genital complex and abdomen of *Caligus* are raised above the surface of the fish, when the latter is in motion. Suspended in midwater, they are bathed on all sides by the current, unlike any other part of the copepod. Possibly, conditions created by this uninterrupted flow are optimal for the processes of development and hatching. On hatching (Figure 6.3C & D), the young worm attaches itself to the copepod in the vicinity of the permanently anchored egg from which it has emerged. The pre-adult stages look like miniature adults, and the posterior rounded sucker can be seen on this newly hatched udonellid (Figure 6.3E). Another interesting characteristic of this species is the operculated eggs (Figure 6.3F). The operculum can easily be seen on the eggs in the present study and the eggs left by hatched worms were neatly severed where the operculum was situated (Figure 6.3G).

Notes on the filament of the eggs

Udonella species can be divided into two groups on the basis of the length of the filament. Group one contains four species that have the filament longer than the capsule; these are *U. caligorum* Johnston, 1835, *U. ophiodontis* Kay, 1945, *U. papillifera* van der Land, 1967, and *U. murmanica* Kornakova and Timofeeva, 1981. Group two contains one species with filaments shorter or equal to the capsule and this species is *U. myliobati* (Guberlet, 1936). The present species of *U. caligorum* belongs not to group one, but to group two, as the filament is shorter than the capsule of the egg. Byrnes (1986) and Schram and Haug (1988) reported specimens of *U. caligorum* with filaments of eggs shorter than the capsule itself. Whether the length of the filament may be used for species identification remains uncertain. Aken`Ova & Lester (1996) stated that the eggs of *U. myliobati* were nonoperculate. Schell (1972) drew an egg of *U. caligorum* with an operculum and mentioned pressure being exerted on the operculum by the worm prior to hatching. The eggs found in the present study were operculated as was found by Schell (1972).

Notes on feeding and transmission

If *Udonella caligorum* is not a harmless fellow-traveller subsisting on macerated tissues, as suggested by earlier writers, then it must obtain its food directly from the fish and not the copepod (Kabata 1973). Should this be the case, then the presence of the worm might aggravate the damage caused by the copepod. It appears thus that the udonellid worms do not feed on their host, but they rather rely on feeding from skin debris from the fish host. The preferred sites on the lateral margin of the dorsal shield give them easy access to the epidermis of the fish.

When feeding, all species of *Caligus* and related genera apply their mouths closely to the skin of the fish, sealing the orifice with a ring of marginal membrane. Any fragments of tissue rasped off the surface are taken up directly into the mouth cone. Small amounts could escape, when the mouth is detached at the end of a meal, but that would hardly be sufficient to sustain a population of worms. It can be presumed, therefore, that *U. caligorum* browses actively on the superficial tissues of the fish and that feeding on tissue debris, if it occurs, can be only of secondary importance.

The way of transmission of udonellids from one host to another is not known, but in heavy infestations of caligids on fish, transmission may take place when caligids are in close contact with each other. Direct contact between copepods appears necessary, and such contact is frequent on even large fish hosts, particularly when infestations are high (as many as 200 *Caligus elongatus* were found in a buccal cavity of a single cod) (Kabata 1973). Caligids are also known to swim free in the water in search of new hosts, but the possibility of the young worms attaching themselves to the free-swimming larvae of *Caligus* cannot be accepted. The newly hatched worm and the nauplius larvae are of about the same size, but before the copepod settles on a new host, the free-swimming stage involves two moults that would present insurmountable difficulties for the transfer of the worm. Eggs have been found on chalimus stages, but there is no proof that these eggs would eventually develop into mature adults. It is more probable that an adult *Caligus* transports *U. caligorum* when it changes its hosts. This could be a possible route for transmitting the udonellids.

Bacteria and fungi found on *Udonella caligorum*

As stated earlier in the chapter, bacteria and fungal infections were found on the udonellids (Figure 6.3H). These bacteria and fungi were present on a newly hatched udonellid, but were not present on the adult. No explanation for this occurrence can be given, except that the bacteria and fungi present may be from the copepod host or the fish host. Further studies will be done to identify the specific bacterial and fungal infestations.

Figure 6.2

Scanning electron micrographs of *Udonella caligorum* Johnston, 1835 occurring on the copepod host *Caligus engraulidis* Barnard, 1948, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Udonellid attached to dorsal side of genital complex of caligid host

B. Cluster of egg cases on leg 3

C. Egg cases on leg 3

D. Dorsal view of *Udonella caligorum*

E. Rounded posterior sucker

F. Genital pore and head organ

G. Genital pore

H. Unidentified structure on ventrolateral surface

Scale-bar: A, B, C & D - 100μm. E, F, G & H - 10μm.

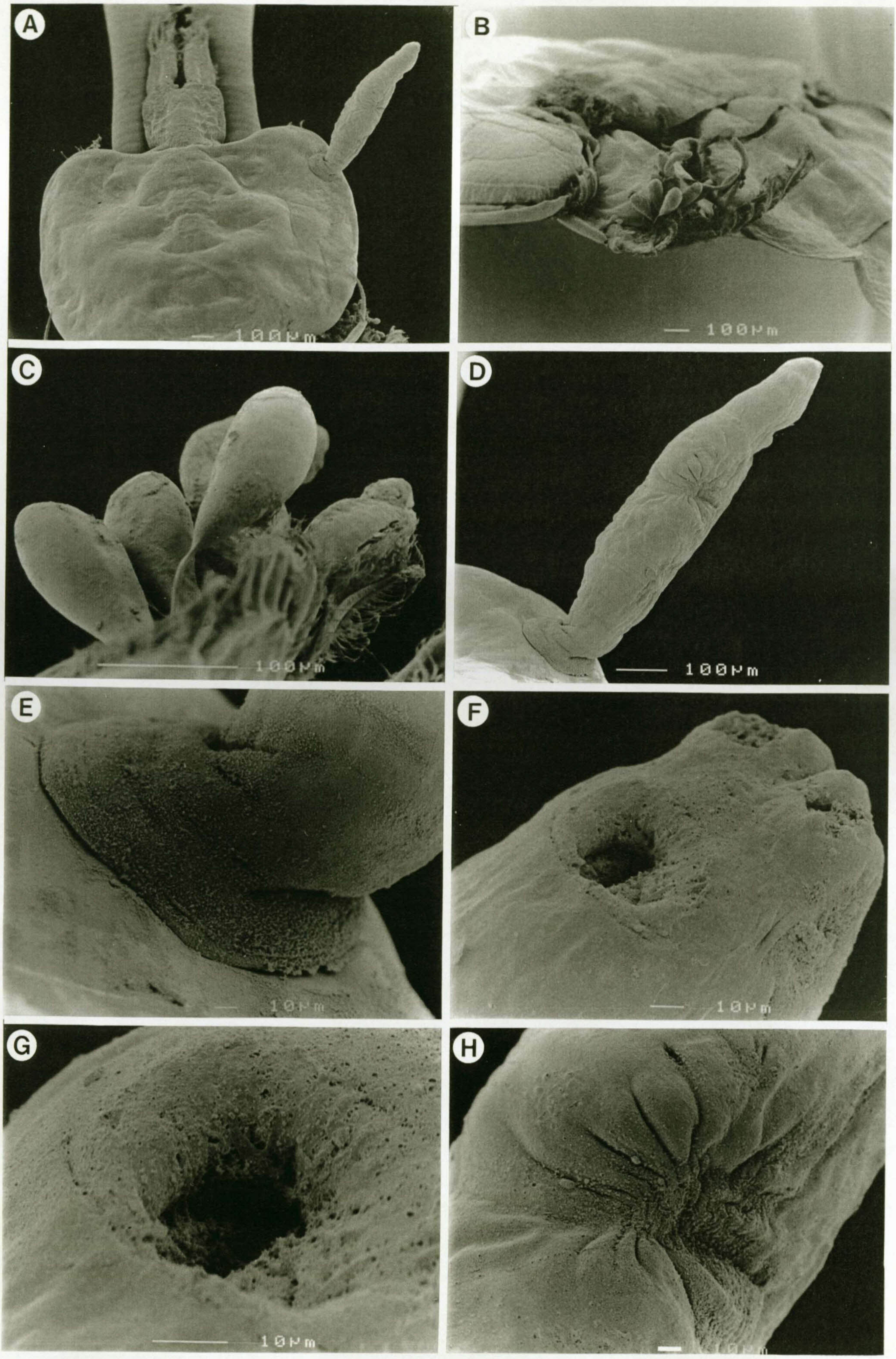
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Figure 6.3

Scanning electron micrographs of *Udonella caligorum* Johnston, 1835 occurring on the copepod host *Caligus engraulidis* Barnard, 1948, collected from the Lake St Lucia System in KwaZulu-Natal, South Africa.

A. Filamentous egg case

B. Basal disc of egg case

C. Cluster of egg cases and newly hatched udonellids

D. Young worm busy hatching

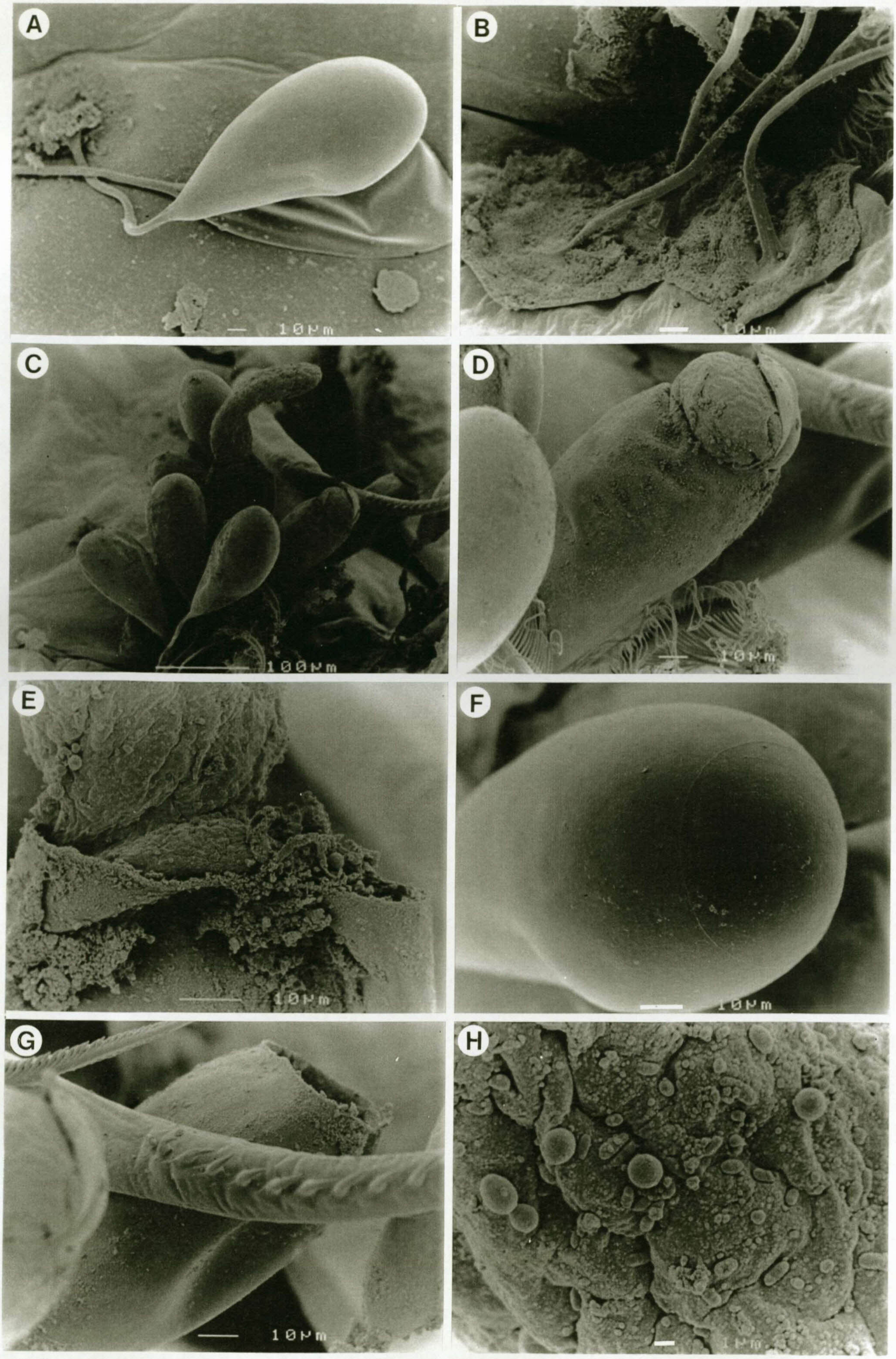
E. Posterior sucker visible on newly hatched udonellid

F. Operculum visible on egg case

G. Empty egg case

H. Bacteria and fungi attached to udonellid

Scale-bar: C - 100µm. A, B, D, E, F & G - 10µm. H - 1µm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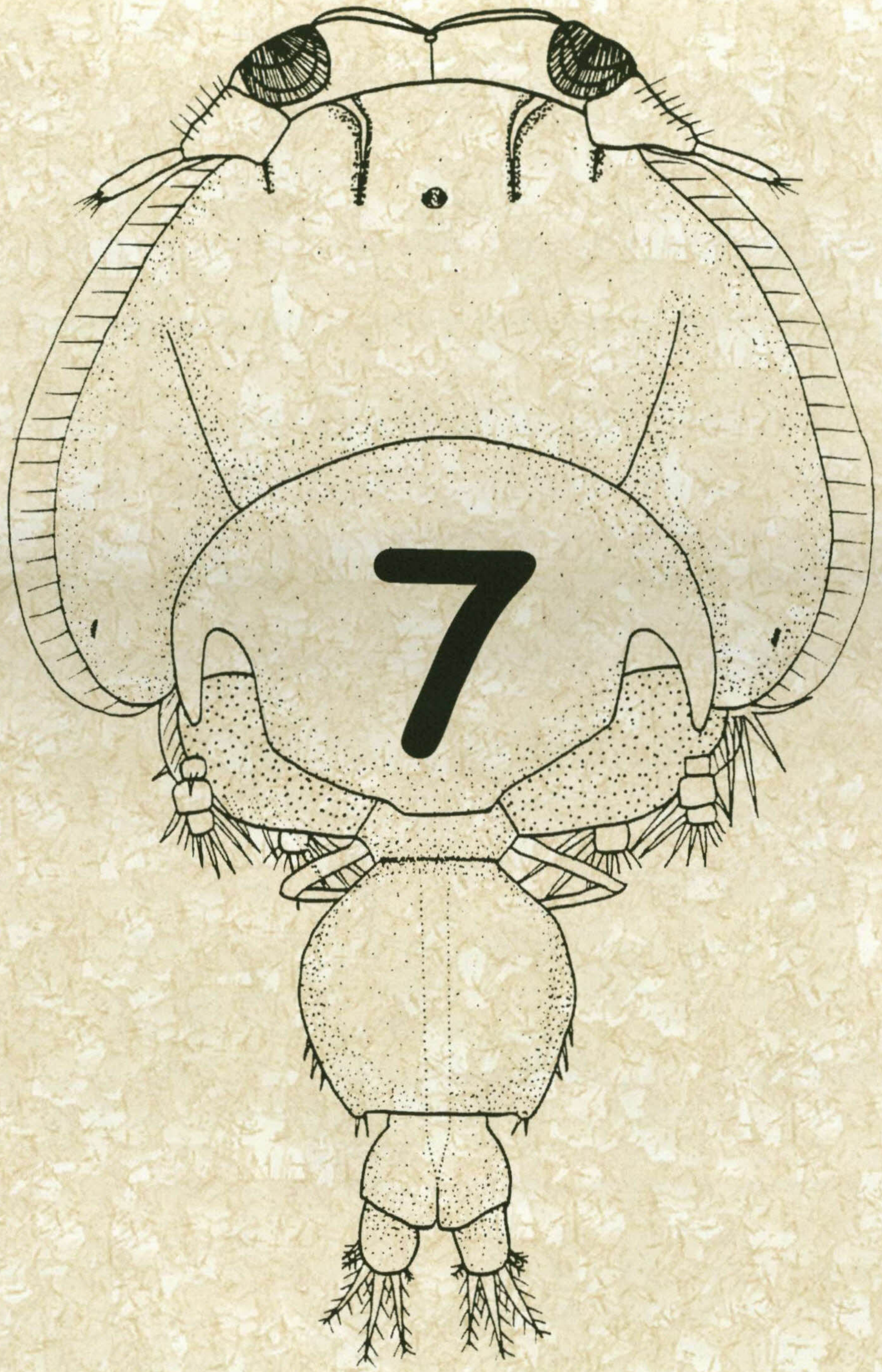
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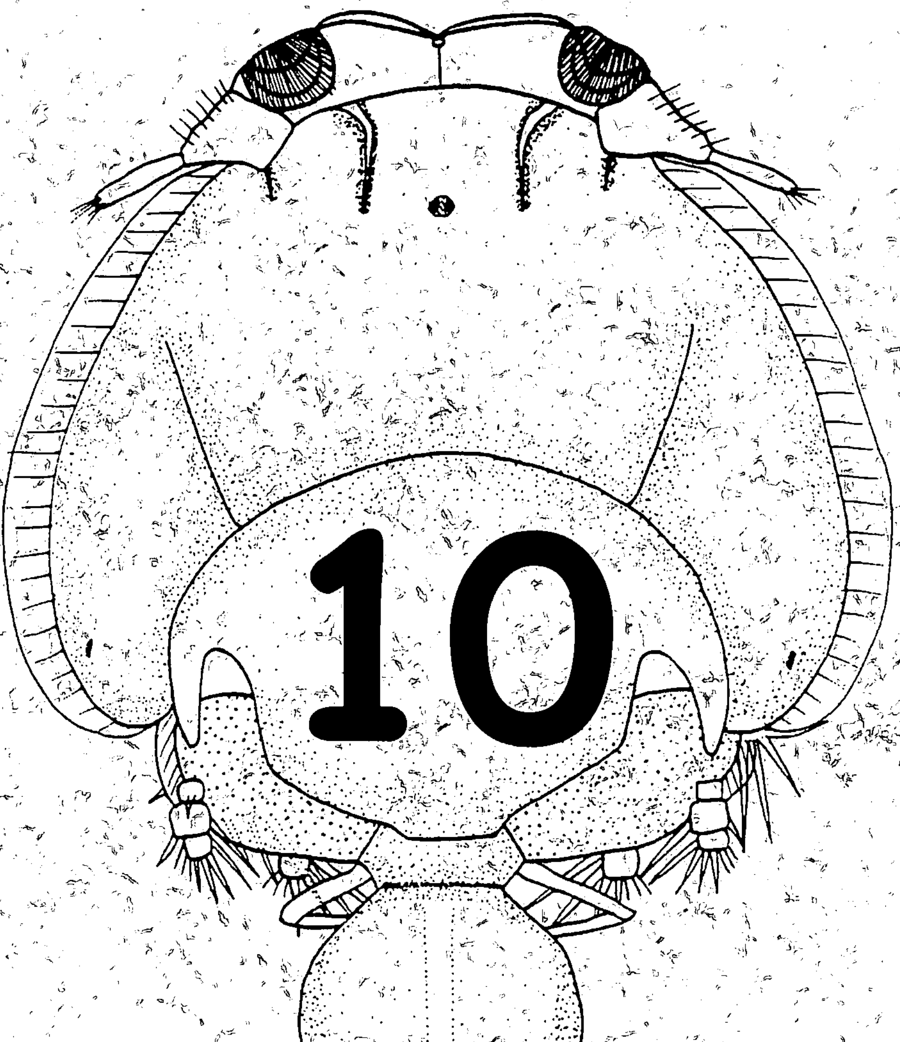
OPSOMMING

Caligus Müller, 1785 is kaligid kopepode wat eksklusief op mariene visgashere gevind word. Hierdie genus word deur meer as 200 spesies wereldwyd verteenwoordig en is ook die grootste genus van parasitiese kopepode. 'n Totaal van 39 spesies van *Caligus* parasiete is van die kus van Afrika beskryf en 26 van hierdie spesies word aan die Suid-Afrikaanse kuslyn gevind. Gedurende navorsings opnames uitgevoer vanaf 1992 tot 1998 in die St Lucia Meer sowel as van 1997 tot 1999 by die De Hoop Natuurreservaat en Jeffreysbaai is kaligid kopepode van die genus *Caligus* versamel. Hierdie parasiete was op die liggaamsoppervlak en kieue van 'n verskeidenheid estuariene en intergety visspesies gevind. Vier verskillende spesies, naamlik *Caligus acanthopagri* Lin, Ho & Chen, 1994, *C. confusus* Pillai, 1961, *C. engraulidis* Barnard, 1948 en *C. mortis* Kensley, 1970 was vanaf mariene gashere versamel. Die eersgenoemde drie spesies was in die St Lucia Meer, KwaZulu-Natal, aan die ooskus van Suid-Afrika versamel en *C. mortis* was by die De Hoop Natuurreservaat en Jeffreysbaai aan die suidkus van Suid-Afrika versamel. In hierdie studie word die mannetjies van *C. engraulidis* en *C. mortis* vir die eerste keer beskryf. Na aanleiding van verdere navorsing is 'n baie interessante hipersimbiont vanaf die kaligids gevind. Sessiele siliofore was op beide *C. acanthopagri* en *C. engraulidis* aangetref. Dit verteenwoordig die eerste rekord van hierdie simbiont van Suid-Afrika. Die hipersimbiont *Udonella caligorum* Johnston, 1835 was op die kaligid gasheer *C. engraulidis* gevind. Hierdie wurm is 'n verteenwoordiger van die klas Monogenea en het 'n gekompliseerde geskiedenis. Sedert dit in 1835 beskryf was, is dit in verskillende taksa en families geplaas. Filogeneties en morfologiese analises plaas hierdie wurm as 'n verteenwoordiger van die subklas Polyonchoinea saam met die Gyrodactylidae. Hierdie hipersimbionte voed nie op die kopepode nie en het dus geen negatiewe effek op hul gashere nie.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APPENDIX 1

NAVRAE / ENQUIRIES Mev M S Liebenberg

TELEFOON / TELEPHONE (021) 483 3584

FAKS / FAX (021) 483 4158

VERWYSING / REFERENCE ANO 2/17

DATUM / DATE 10 Februarie 1997

PROVINCIAL ADMINISTRATION: WESTERN CAPE

Cape Nature Conservation

PROVINSIALE ADMINISTRASIE: WES-KAAP

Kaapse Natuurbewaring

Departement Dierkunde/Entomologie
Fakulteit Natuurwetenskappe
Universiteit van die Oranje-Vrystaat
Posbus 339
BLOEMFONTEIN
9300

Geagte Mnr N Smit

PERMIT NO. 2/1997: PERMIT VIR VERSAMELING VAN GETYPOEL VISSE EN GESELEKTEERDE INTERGETY INVERTEBRATA VIR PARASIET STUDIES

1. Ingevolge artikel 73 van die Ordonnansie op Natuur- en Omgewingsbewaring, 1974 (Ordonnansie 19 van 1974) word magtiging aan u verleen vir die versameling van getypoelvisse en geselekteerde intergety invertebrata vir navorsingsdoeleindes aan die De Hoop Natuurreservaat kus.

2. Die voorwaardes van hierdie permit is as volg:

2.1 Nie meer as 20 individue per spesie mag versamel word nie.

2.2 Alle ander organismes wat nie vir die projek benodig word nie, moet onmiddelik en onbeseerd in die water teruggeplaas word.

2.3 'n Volledige versalg t.o.v. die navorsing en versameling van organismes moet binne 'n redelike tyd na afloop van die ekskursie aan hierdie kantoor voorsien word.

2.4 Hierdie permit is geldig vanaf 28 Maart 1997 tot 30 April 1997.

Die uwe

DIREKTEUR: NATUURBEWARING

ENQUIRIES NAVRAE Grietha Liebenberg
TELEPHONE TELEFOON (021) 483 3584
FAX FAKS (021) 483 4158
REFERENCE VERWYSING ANO 2/17
DATE DATUM 16 Maart 1998

APPENDIX 2

PROVINCIAL ADMINISTRATION: WESTERN CAPE
Cape Nature Conservation

PROVINSIALE REGERING: WES-KAAP
Kaapse Natuurbewaring

Hoof Direktoraat Natuur & Omgewingsbewaring
Private Bag/Privaatsak 9086
27 MAR 1998
CAPE TOWN/KAAPSTAD
Chief Directorate Nature & Environmental Conservation

Prof JG van As & Medewerkers
Universiteit van die Oranje-Vrystaat
Departement Dierkunde/Entomologie
Fakulteit Natuurwetenskappe
Posbus 339
BLOEMFONTEIN
9300

Geagte Prof van As & Medewerkers

PERMIT NO. 2/1998: PERMIT VIR VERSAMELING VAN GETYPOEL VISSE EN GESELEKTEERDE INTERGETY INVERTEBRATA VIR PARASIET STUDIES

1. Ingevolge artikel 73 van die Ordonnansie op Natuur- en Omgewingsbewaring, 1974 (Ordonnansie 19 van 1974) word magtiging aan u en u medewerkers verleen vir die versameling van getypoel visse en geselekteerde intergety invertebrata vir navorsingsdoeleindes aan die De Hoop Natuurreservaat kus.

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2.4 Hierdie permit is geldig vanaf 27 Maart 1998 tot 30 April 1998.

Liebenberg
waarnemende **DIREKTEUR**

KAAPSE NATUURBEWARING

ADDENDUM TOT PERMIT NO. 2/1998

PROJEKLEIERS :

Prof. J. G. Van As D.*Sc. PU CHO*
Prof. L. Basson *PhD. RAU*

MEDEWERKERS:

Dr. L.L. van As *PhD. UOVS*
N.J. Smit *Msc. UOVS*
K.W. Christison *BSc.Hons. UOVS*
H. Botes Bsc. *Hons. OUVS*
N.J. Grobler Bsc. *Hons. OUVS*

[signature]

waarnemende DIREKTEUR

Hoof Direktoraat Natuur & Omgewingsbewaring
Private Bag/Privaatsak 9086
27 MAR 1998
CAPE TOWN/KAAPSTAD
Chief Directorate Nature & Environmental Conservation

ENQUIRIES NAVRAE Grietha Liebenberg

TELEPHONE TELEFOON (021) 483 3584

FAX FAKS (021) 483 4158

REFERENCE VERWYSING ANO 2/17

DATE DATUM 19 Maart 1999

APPENDIX 3

PROVINCIAL ADMINISTRATION: WESTERN CAPE
Cape Nature Conservation

PROVINSIALE REGERING: WES-KAAP
Kaapse Natuurbewaring

Prof. JG van As en Medewerkers
Universiteit van die Oranje-Vrystaat
Department Dierkunde/Entomologie
Fakulteit Natuurwetenskappe
Posbus 339
BLOEMFONTEIN
9300

Geagte Prof. van As & Medewerkers

PERMIT NO. 1/99: PERMIT VIR VERSAMELING VAN GETYPOEL VISSE EN GESELEKTEERDE INTERGETY INVERTEBRATA VIR PARASIET STUDIES

1. Ingevolge artikel 73 van die Ordonnansie op Natuur- en Omgewingsbewaring, 1974 (Ordonnansie 19 van 1974) word magtiging aan u en u medewerkers verleen vir die versameling van getypoel visse en geselekteerde intergety invertebrata vir navorsingsdoeleindes aan die De Hoop Natuurreservaat kus.

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2.3 'n Volledige verslag t.o.v. die navorsing en versameling van organismes moet binne 'n redelike tyd na afloop van die ekskursie aan hierdie kantoor voorsien word.

2.4 Hierdie permit is geldig vanaf 19 Maart 1999 tot 3o April 1999.

DIREKTEUR

UTILITAS BUILDING 1 DORP STREET
PRIVATE BAG X9086 CAPE TOWN 9000

UTILITASGEBOU DORPSTRAAT 1
PRIVAATSAK X9086 KAAPSTAD 8000

KAAPSE NATUURBEWARING

ADDENDUM TOT PERMIT NR. 1/1999

PROJEKLEIERS:

Prof. JG van As D.Sc. PU CHO
Prof L Basson PhD RAU

BESOEKENDE WETENSKAPLIKE:

Prof. I Dykova (Czech Republic)

NAVORSERS/MEDEWERKERS:

Dr. LL van As PhD UOVS
NJ Smit Msc UOVS
KW Christison Msc UOVS
H Botes Bsc Hons UOVS
NJ Grobler Bsc Hons UOVS
CC Reed Bsc Hons UOVS
C Jansen van Resnburg Bsc Hons UOVS
G Visagie - Tegnikus

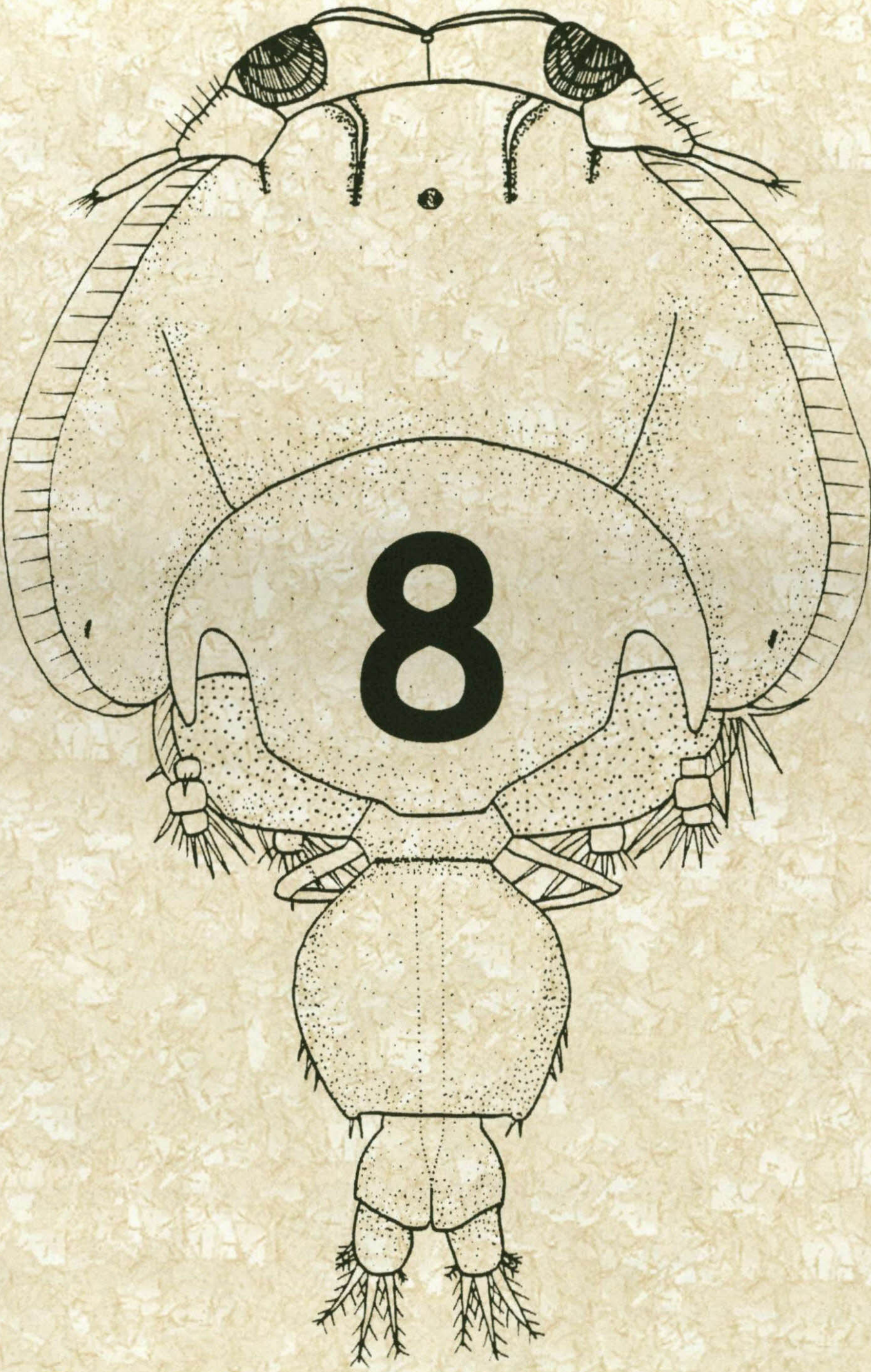
Hoof Direktoraat Natuur & Omgewingsbewaring
Private Bag/Privaatsak 9086
19 MAR 1999
CAPE TOWN/KAAPSTAD
Chief Directorate Nature & Environmental Conservation

DIREKTEUR

XYLANDER, W. 1988. Ultrastructural studies on Udonellidae: evidence for a postion within the Neodermata. *Fortschritte der Zoologie*, **36**: 51-57.

YAMAGUTI, S. 1963a. Parasitic Copepoda and Branchiura of fishes. *Interscience Publishers*. New York, 1104pp.

*Article not seen in original form.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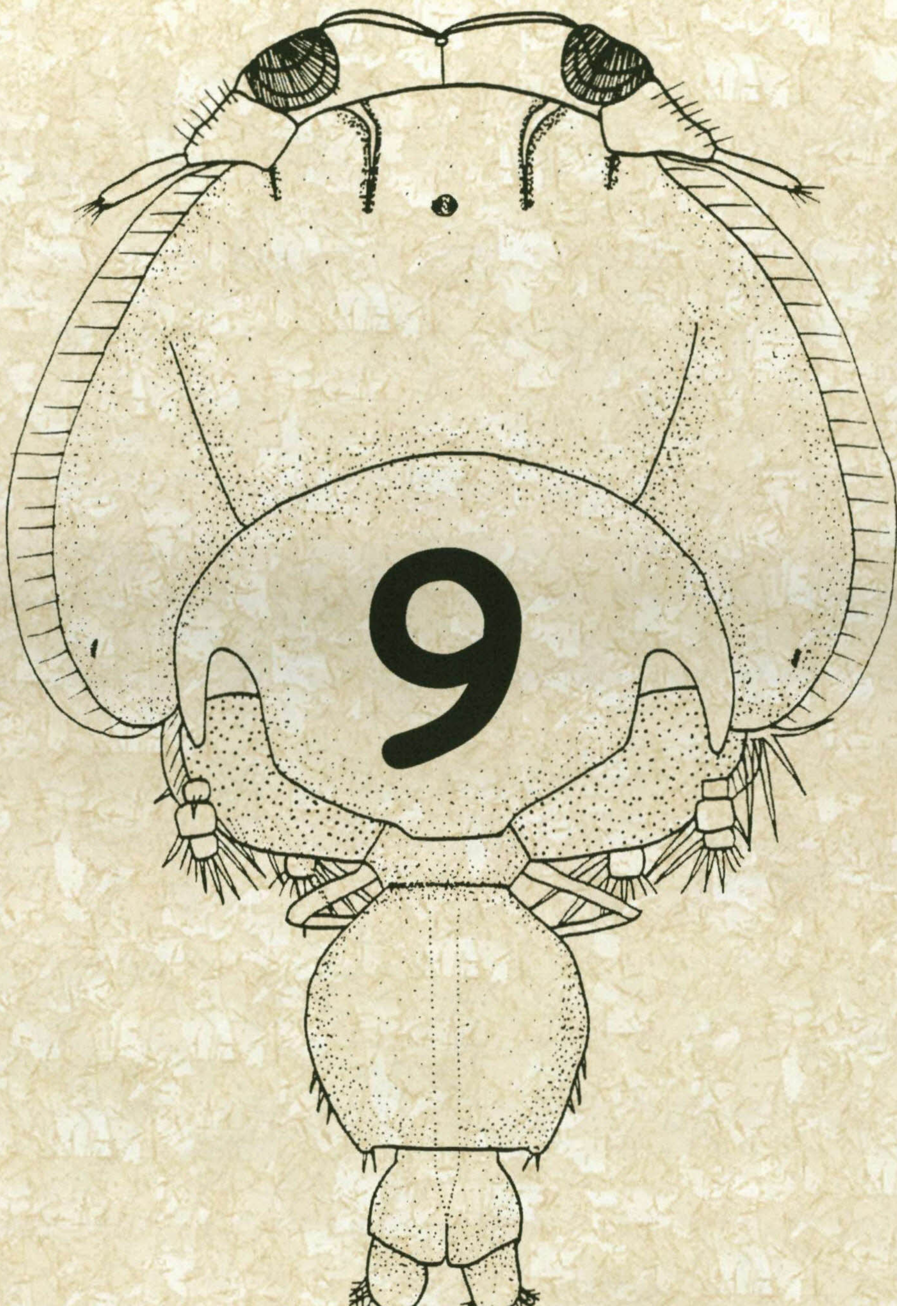
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ABSTRACT

Caligus Müller, 1785 are caligid copepods found almost exclusively on marine fish hosts. This genus is represented by more than 200 species in the oceans of the world and is the largest genus of parasitic copepods. A total of 39 species of *Caligus* parasites have been recorded off the coast of Africa, and 26 species are found along the South African coastline. Surveys carried out from 1992 to 1998 in Lake St Lucia and from 1997 to 1999 at De Hoop Nature Reserve and Jeffreys Bay along the coast of South Africa, revealed the presence of caligid copepods, of the genus *Caligus* Müller, 1785, occurring on the body surfaces and gills of many estuarine and intertidal fish species. Four different species were collected from marine hosts namely, *Caligus acanthopagri* Lin, Ho & Chen, 1994, *Caligus confusus* Pillai, 1961, *Caligus engraulidis* Barnard, 1948, and *Caligus mortis* Kensley, 1970. The first three species mentioned were collected in Lake St Lucia, KwaZulu-Natal, on the east coast of South Africa, and *C. mortis* were collected at De Hoop Nature Reserve and Jeffreys Bay on the south coast of South Africa. In the present study, males of *C. engraulidis* and *C. mortis* are described for the first time and is new to science. Further studies revealed that interesting hypersymbionts were found attached to the caligids. Sessiline ciliophorans were found on both *C. acanthopagri* and *C. engraulidis* and represents a first record for South Africa. *Udonella caligorum* Johnston, 1835 were found on the caligid host *C. engraulidis*. This monogenean worm have a complicated history, for it was placed in different taxa and families since it was first described in 1835. Phylogenetic analysis as well as morphological analysis places this worm firmly as a polyonchoinean monogenean alongside the Gyrodactylidae. These hypersymbionts do not feed on the copepods and have no detrimental effects on their hosts.