

COPEPOD EVOLUTION

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To Kathleen
and
to Roberta,
Abigail, Keir, Natalie and Amy

COPEPOD EVOLUTION

By
RONY HUYS
and
GEOFFREY A. BOXSHALL

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PREFACE

Students of copepods have traditionally belonged to one of five more or less separate interest groups, i.e. the marine plankton, the freshwater plankton, sediment inhabiting forms, parasites of fishes and associates of invertebrate hosts. Each of these subject areas has remained rather isolated from the others, with little exchange of ideas. The series of International Conferences on Copepoda, now organised under the auspices of the World Association of Copepodologists, has made significant progress in breaking down barriers between the interest groups but studies of copepod systematics in particular have been hindered because these ecological categories do not correspond to taxonomic boundaries. For example, some orders, such as the Cyclopoida, contain representatives belonging to all five. In our opinion a systematic overview that provides order to the immense diversity of copepods is long overdue and we hope that it will greatly facilitate communication between the ecologically based interest groups. The primary aim of this volume is to provide a detailed examination of the phylogenetic relationships between the orders of copepods and, therefore, a reassessment of the major evolutionary trends within the Copepoda. The evolutionary perspective will provide a strong base for comparative biological studies as well as a robust framework for future taxonomic studies.

The need for a new evolutionary overview is enhanced by the discovery of many new and unusual copepods in the last two decades. In particular, the exploration of deep-sea hydrothermal vents and cold seeps, and of anchialine habitats has resulted in the discovery of several new families and the establishment of a new order, the Platycopioidea. In addition, an increasing volume of taxonomic work on the deep-sea meiobenthic community, on groundwater forms, and on associates of marine invertebrate hosts has resulted in the creation of numerous new families.

We have not relied on the literature. Instead we have attempted to examine specimens of the most primitive representatives of all orders and describe them by a consistent set of techniques (see Appendix 2). We have also used a consistent nomenclature for the body, the appendages and their component parts. This was necessary in order to facilitate comparison of different types of copepods, and to enable the identification of homologies between parts of the body, the limbs and their setation elements.

In the light of our decision to reexamine and verify every character for every order we became heavily dependent upon the collections of the great museums of the world and their curators, and upon the immense generosity of our fellow copepod specialists the world over. Without their help this project would never have been completed. It is a pleasure to record our gratitude to the following colleagues who lent us material from the collections in their care or from their personal collections: Gazim Abdelhalim (University of Khartoum), Maria Paloma Alvarez (Universidade de São Paulo), Philippe Bodin (Université de Bretagne Occidentale), Ruth Böttger-Schnack (Universität Kiel), Thomas Bowman (Smithsonian Institution), Marit Christiansen (Zoologisk Museum, University of Oslo), August Coomans (Rijksuniversiteit Gent), Roger Cressey (Smithsonian Institution), Danielle Defaye (Muséum National d'Histoire Naturelle), Gregory Deets (University of California, Long Beach), Harold Feinberg (American Museum of Natural History), Frank Ferrari (Smithsonian Oceanographic Sorting Center), Audun Fosshagen (University of Bergen), Mike Gee (Plymouth Marine Laboratory), Mark Grygier (University of the Ryukyus, Japan), Richard Hamond (Holt, Norfolk, U.K.), Gerd Hartmann (Universität Hamburg), Hans-Volkmar Herbst (Krefeld, Germany), Ju-shey Ho (University of California, Long Beach), Arthur Humes (Boston University), Thomas Iliffe (Texas A & M University), Helmut Kunz (Bischmisheim, Germany), Sybille Maas (Rijksuniversiteit Gent), Claude Monriot (Muséum National d'Histoire Naturelle), Susumu Ohtsuka (Hiroshima University), Roy Olerød (Naturhistorisk Riksmuseet, Stockholm), Dirk Platvoet (Instituut voor Taxonomische Zoölogie, Amsterdam), Paula Rothman (Smithsonian Institution), Raymond Rouch (Laboratoire Souterrain du CNRS, Moulis), Michel Segonzac (IFREMER, Brest), Chang-tai Shih (Canadian Museum of Nature, Ottawa), Jan Stock (Instituut voor Taxonomische Zoölogie, Amsterdam), Willem Vervoort (Rijksmuseum van Natuurlijke Historie, Leiden), Endre Willassen (Bergen Museum), Kris Willems (Rijksuniversiteit Gent), Torben Wolff (Zoologisk Museum, Copenhagen), Karel Wouters (Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels) and Wolfgang Zeidler (South Australian Museum, Adelaide). In many cases specimens

were given to us and we note here our intention to deposit this donated material in the collections of The Natural History Museum, (BM(NH)), so that others can have easy access to it in future.

We are also grateful to Rick Brusca (San Diego Natural History Museum), Ju-shey Ho (University of California, Long Beach), Gordon Paterson (BM(NH)) and Richard Thomas (BM(NH)) for their advice and assistance with using the PAUP programs. We would like to record our special thanks for the generous assistance given by Sheila Halsey (BM(NH)), in the preparation of reference lists, figure legends, organizing material, proof reading and in many other ways. Her help has ensured a more rapid progress towards publication.

We are also pleased to acknowledge the considerable help we have received in the preparation of material for study. Mrs Rita Van Driessche in Gent and Alan Warren and the staff of the Electron Microscopy Unit at the Natural History Museum in London provided valuable assistance with Scanning Electron Microscopy. We would also like to thank David Cooper for preparing the histological sections. Part of this work was carried out under Research Grant 2.0009.81 of the Belgian Fund for Collective Fundamental Research and EEC Science Grant ST2*0443. For their continuing support and for the provision of laboratory and other facilities we are grateful to Professor Carlo Heip (Delta Institute for Hydrobiological Research, Yerseke), Professor August Coomans (Rijksuniversiteit Gent), and to successive Keepers of Zoology, John Peake and Colin Curds, and the Head of Crustacea, Roger Lincoln, at The Natural History Museum, London.

Lastly we both would like to acknowledge the encouragement and understanding we have received from our respective families. They have shared with us the conception, gestation and, finally, the birth of this book. We would not have succeeded without them and it is only fitting that we should dedicate this volume to them.

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Chapter 1

INTRODUCTION TO THE COPEPODS

1.1 COPEPOD HABITATS

Copepods are aquatic crustaceans, the diminutive relatives of the crabs and shrimps. In terms of their size, diversity and abundance they can be regarded as the insects of the seas. Over 10,000 species are currently known but, since the true diversity of the benthic harpacticoids and of the poecilostomatoid and siphonostomatoid associates of marine invertebrates, has yet to be revealed, this number could easily double by the middle of the twenty first century. 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 (figure 1.1). They also have an immense vertical range occurring from depths of 9995-10002 metres in the Philippine Trench (Wolff, 1960) to an altitude of 5540 metres up in the Himalayan mountains (Löffler, 1968). This vertical range represents about three quarters of the maximum possible range on the Earth's surface, from the deepest point in the Marianas Trench to the peak of Mount Everest (about 20,372 metres).

Marine Plankton: The sheer abundance of copepods in marine plankton secures for them a vital role in the marine economy. Sir Alister Hardy (1970) estimated that the copepods are the most numerous metazoan animals in the world, even outnumbering the insects which have more species but fewer individuals and the nematodes, both of which have had some claim to this position of preeminence. Hardy's estimate is based primarily on the planktonic copepods that inhabit the oceans of the world. The entire oceanic realm, which covers about 71 per cent of the world's surface to an average depth of about 3700 metres, provides an immense volume of water (1347 million cubic kilometres) all of which is home to free-swimming copepods. They are found from the ocean surface to the bottom of the hadal trenches and occur in densities ranging from 70,000 per cubic metre in the shallow waters of the North Sea, down to 100 per cubic metre at depths of 4,000 metres in the North Atlantic and up to 1.5 million per cubic metre in mating swarms in coral reef environments (Hamner & Carleton, 1979). Some species exploit the ephemeral habitat at the ice-water interface of polar and subpolar ice and can reach densities of 12,500 individuals per square metre during the algal blooms of the late spring (Kern & Carey, 1983).

Freshwater Plankton: Copepods are also abundant in freshwater planktonic communities. Members of the families Cyclopidae in the Cyclopoida, Canthocamptidae in the Harpacticoida, and Diaptomidae in the Calanoida are particularly successful in all kinds of freshwater habitats, from the saline lakes in the Antarctic Vestfold Hills (Burton & Hamond, 1981) to the high altitude lakes on the southern slopes of the Himalayan mountains (Löffler, 1968). Occasionally representatives of other families are dominant, such as the temorid *Epischura baikalensis* Sars which comprises up to 96 per cent of the animal plankton of Lake Baikal.

Marine Sediments: Copepods also live in marine sediments, inhabiting the microscopic spaces between the sediment particles. In this meiofaunal community they are typically second in abundance only to nematodes. Meiofaunal copepods tend to become more abundant as the particle size of the sediment increases and in coarse sands they often outnumber the nematodes (Hicks & Coull, 1983). They are found in all sediment types from mud to sand and at all depths from the intertidal zone to the deepest oceanic ooze. The density changes with sediment type and with depth. Typical densities in shallow water ecosystems (down to about 100 metres) are in the order of 200 to 300 individuals per 10 square centimetres of sediment surface but they range from 0

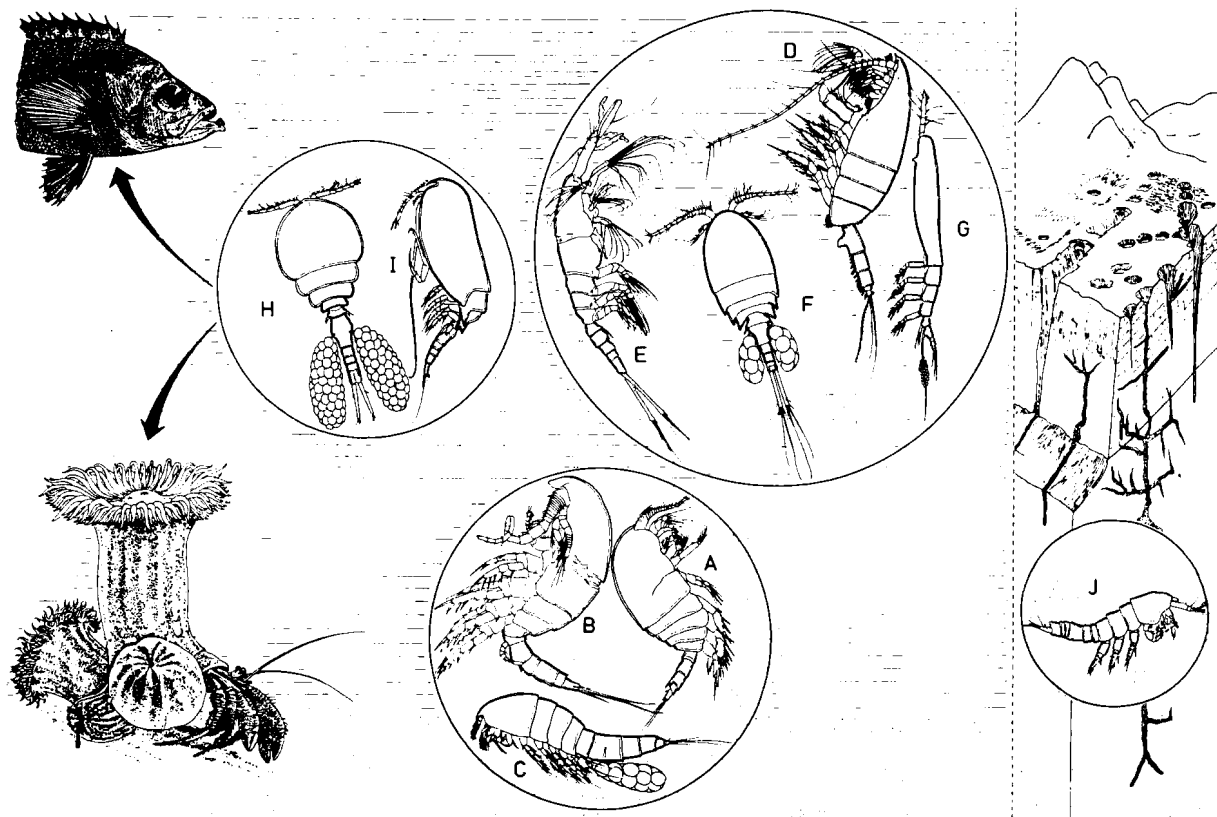


Figure 1.1. Copepod habitats: a schematic representation of the primary habitat of each of the ten copepod orders. A. Platycopioida. B. Misophrioida. C. Harpacticoida. D. Calanoida. E. Mormonilloida. F. Cyclopoida. G. Monstrilloida. H. Poecilostomatoida. I. Siphonostomatoida. J. Gelyelloida. [A-C, benthic; D-G, planktonic; H and I, associated; J, groundwater.]

to over 6,000. Numbers decline with depth and in deep-sea sediments typical densities are 20 to 30 individuals per 10 square centimetres of sediment surface, with a range from 1 to over 400. Meiofaunal specialists usually work with small cores of sediment, hence they calculate densities for columns of sediment beneath a surface area of 10 square centimetres. Typical densities per square metre of surface in shallow waters become 200,000 to 300,000, with a maximum of over 6 million.

Plant Associates: In the marine environment copepods are commonly found on intertidal and subtidal algae and even on some flowering plants, such as the sea grasses (Bell et al., 1984). Some inhabit the sediment and detritus trapped in the interstices of the complex, ramifying holdfast of the alga but many are true phytal copepods and are highly specialised for life on the surface of the fronds. Under reduced silt-clay or detrital loads the dominant and most ubiquitous meiofaunal taxa on marine algae are the harpacticoid copepods. Some harpacticoids belonging to the family Darcythompsoniidae are exclusively associated with the microflora of decaying mangrove leaves (Por, 1984a).

Cryptic Habitats: Other habitats exploited by free living copepods are damp terrestrial situations. Reid (1986) surveyed many of these cryptic habitats. In the organic soil of wet campo marsh in tropical South America Reid found densities ranging from 1,000 to 178,000 per square metre. In the soil of a sedge meadow in the Canadian tundra Bliss et al. (1973) found mean densities of over 6500 copepods per square metre. Copepods are particularly abundant in forest litter, even at high altitude. Sphagnum bogs and terrestrial mosses are also favoured habitats for copepods. They often colonise water tanks in farm and other buildings and are frequently taken in drinking water. A thriving population of freshwater cyclopoids inhabits the water tanks on the roof of the Natural History Museum in London. Copepods have been reported from even more bizarre habitats, such as the pools between the leaves of bromeliads in tropical rainforests. *Phyllognathopus*

viguierei (Maupas) is commonly found in the liquid retained at the bases of leaves of pineapples in Botanic Gardens (Lowndes, 1931) and in supermarkets in the U.S.A. The cyclopoid *Cryptocyclops anninae* Lowndes was first collected from water contained in empty coconut shells (Lowndes, 1928). Yeatman (1983) also surveyed unusual microhabitats in some South Pacific Islands and reported copepods from taro leaf axils, tree holes, crab burrows and discarded car tyres. They even occur in hot springs, where they are active at water temperatures between 38 and 58°C (Itô & Burton, 1980).

Subterranean Habitats: They live in groundwater and can regularly be caught in springs, wells and pools in caves. The small order Gelyelloida, comprising just two species, occurs only in subterranean waters in the karstic systems of Switzerland and France. Gelyelloids have been recovered from filtration of subterranean water from boreholes 60 metres below ground level. Two harpacticoid families, the Parastenocarididae and Chappuisiidae, are specialised groundwater inhabitants. Parastenocaridids are widely distributed in groundwater throughout Eurasia, Africa and the Americas. They can occur in oceanic islands, such as the Canary Islands, but are absent from New Zealand. The Chappuisiidae comprises only two species, both found only in groundwaters accompanying the Danube, Elbe, Rhine and Weser rivers and their tributaries, in Central Europe. The cyclopoid family Cyclopidae contains many specialised subterranean species. Lescher-Moutoué (1974a,b) reviewed the taxonomy and biology of the subterranean cyclopids in southern France and recorded forty-one species and subspecies in this region alone.

Deep-sea Vents and Anchialine Caves: In the last two decades much emphasis has been placed on the investigation of the fauna of two particular habitats, anchialine caves and deep-sea hydrothermal vents and cold seeps. These habitats have revealed many interesting new forms of copepods. The study of anchialine caves has relied primarily on SCUBA diving techniques and has produced many of the most primitive known copepods in the orders Platycopioida, Calanoida and Misophrioida. Access to the fauna of deep-sea vents and cold seeps has been provided mainly by submersibles. Here, many primitive associated copepods belonging to the orders Siphonostomatoida and Poecilostomatoida have been found.

Animal Associates: The abundance and diversity of the free-living forms is only part of the amazing success of the copepods. Nearly half of all known species live in symbiotic relationships with other organisms. They are known to have been living in close association with other phyla at least since the Lower Cretaceous. Copepods parasitise virtually every phylum of animals from sponges and coelenterates to vertebrates including mammals, and they enter into a variety of commensal or other associations with a similar range of hosts (Table 1). Those parasitic on fishes and those living in symbiotic associations with marine invertebrates have been reviewed recently by Kabata (1981) and Gotto (1979) respectively. Most are external parasites, living on the body surface of their hosts but many have colonised more sheltered microhabitats, including the gills, nostrils, mouth and lateral line canals of fishes, the baleen plates of whales, the mantle cavity and gills of molluscs, the brood pouches and gill chambers of other crustaceans, the genital bursa of ophiuroid echinoderms, and the internal canal systems of sponges and coelenterates. Some have even become endoparasites, burrowing into the musculature of their hosts, living within the body cavity, or inhabiting the digestive tract.

Parasitic copepods can occur in very large numbers. Humes (1973) found 17,294 individuals of the siphonostomatoid *Collocherides astroboae* Stock on two shallow-water basket stars in Madagascar. Infestations of over 13,400 individuals of *Ergasilus sieboldi* Nordmann have been reported from the gills of a single host fish (Abdelhalim, 1990). Even restricted microhabitats on a host can carry a substantial population; up to 39 individuals of *Bomolochus confusus* Stock were found in the nostrils of a single cod caught in the North Sea (Boxshall, 1974a). Parasitic and associated copepods occur at all depths, from the intertidal zone to the deep sea, and have been reported in large numbers on the invertebrates of the hydrothermal vent and cold seep communities (Humes, 1988). Humes (1990) found 15,284 females and 8 males of *Stygiopontius quadrispinosus* Humes in a jar containing 210 ml of flocculent material collected from a massive sulphide deposit and a colony of vestimentiferan worms at a depth of 3250 metres on the Gorda Ridge. Parasitic and

associated copepods are predominantly marine although a few parasitise freshwater molluscs, fishes and, rarely, amphibians.

Table 1. Copepods as associates of Metazoan phyla

	Calanoida	Harpacticoida	Monstrilloida	Cyclopoida	Poecilostomatoida	Siphonostomatoida
Porifera	—	+	—	+	+	+
Cnidaria	+	+	—	+	+	+
Platyhelminthes	—	+	—	—	+	—
Nemertea	—	—	—	—	+	—
Sipunculida	—	—	—	—	+	—
Vestimentifera	—	—	—	—	—	+
Echiura	—	—	—	—	+	—
Annelida	—	+	+	—	+	+
Mollusca	—	+	+	+	+	+
Arthropoda	—	+	—	—	+	+
Phoronida	—	—	—	—	+	—
Bryozoa	—	+	—	—	—	—
Brachiopoda	—	—	—	—	+	—
Echinodermata	—	+	—	+	+	+
Hemichordata	—	—	—	+	+	—
Chordata						
Urochordata	—	+	—	+	+	+
Vertebrata						
Chondrichthyes	—	—	—	—	+	+
Osteichthyes	—	+	—	+	+	+
Amphibia	—	—	—	+	—	—
Mammalia	—	+	—	—	—	+

In the majority of parasitic copepods it is the adults that are parasitic but the monstrilloids have naupliar stages that are endoparasites of polychaete worms and gastropod molluscs. The adults are free-living but non-feeding members of the marine plankton. The aberrant cyclopoid family Thespesiopsyllidae also has parasitic nauplii and free adults, but the nauplii inhabit the stomach of brittlestars in this case. The siphonostomatoid family Pennellidae exhibits, at least in some genera, a two host life cycle. Larval development through the copepodid stages to maturity occurs on the first host, which may be either a pelagic mollusc (as in *Cardiodectes* Wilson) or a fish (as in *Lernaeocera* de Blainville). After mating on the intermediate host the adult females locate and attach to a final host, on which egg production takes place. These pennellids often exhibit a profound metamorphosis during which the adult female changes shape and increases dramatically in size prior to commencing egg production.

1.2 THE IMPORTANCE OF COPEPODS

Ecological Importance: It would be extremely difficult to overstate the importance of copepods to the marine economy. The abundant calanoid and cyclopoid copepods of the plankton form the first vital link in the food chain that leads from the minute algal cells of the phytoplankton up to the large fishes and mammals. These phytoplankton-feeding copepods are by far the most important primary consumers in marine planktonic communities and, as such, form the base of virtually all pelagic food chains. Copepods are so abundant that even their faecal pellets, which are produced at rates of up to 200 per individual per day, represent an ecologically important energy source for detritus feeders. The flux of faecal pellets to the ocean floor may have a significant impact on nutrient cycling and sedimentation rates.

Most commercially exploited fishes, in temperate waters at least, feed directly on copepods during their larval development and some, such as the herring, continue to feed on copepods as adults. It is not only pelagic fishes that utilise copepods as an important food source. Harpacticoid copepods are the predominant meiofaunal element in the diets of flatfishes and salmonids, which are target species for a rapidly expanding mariculture industry in Europe and North America. Harpacticoids have a high nutritional value and the various life cycle stages of the copepod are intermediate in size between rotifers and brineshrimp nauplii (which are commonly used as live fish food) and, as such, bridge a gap in the size spectrum of available food. These copepods may have an essential role to play in the future development of fish farming (Gee, 1989).

Copepod Pests: Copepods can be important as pest species. The salmon louse *Lepeophtheirus salmonis* Krøyer, for example, can cause devastating economic losses to salmon farmers. These lice breed rapidly in the salmon cages and can kill the fish directly by their feeding activity or indirectly by causing skin lesions that allow microbial diseases to become established. Other copepods are commercially important because they adversely affect the condition of the fish. Kabata (1958) found that heavy infestation by the gill parasite *Lernaeocera* caused a weight loss of up to 28.9 per cent in haddock, *Melanogrammus aeglefinus* (Linn.), caught off Scotland. Mann (1952) reported similar losses caused by the same parasite on other gadid hosts. It has been calculated that weight losses of this magnitude would amount to about two million pounds lost on the total Scottish haddock catch for a given year (Sinderman, 1970). Parasites of commercially important shellfishes, such as *Mytilicola intestinalis* Steuer (European mytilicoliasis) and *M. orientalis* Mori (oriental mytilicoliasis) which parasitise mussels, were also thought to cause considerable loss of weight in infested hosts (Mann, 1951) and thereby reduce their market value but recent work (Gresty, 1990) suggests that the mussel, *Mytilus edulis* Linn. can sustain high infection levels of *M. intestinalis* without suffering any significant adverse effects. Large copepod parasites that live embedded in the flesh of their fish hosts, such as *Sphyrion lumpi* Krøyer, reduce the marketability of the fish by causing problems during filleting. Release of blood from large, engorged females of the endoparasitic philichthyid *Sarcotaces* Olsson also disrupts filleting of its host fish as it stains the flesh.

The harpacticoid copepods *Amenophia orientalis* Ho & Hong and *Parathalestris infestus* Ho & Hong are pests of Wakame, the brown seaweed that is cultivated widely in Korea and Japan as a food crop. These copepods make galls and pinholes in the fronds of the seaweed and reduce its commercial value (Ho & Hong, 1988).

Copepods as Disease Vectors: Copepods are also important as vectors of some human parasites, the most important of these being the guineaworm, *Dracunculus medinensis* Linn., known as the fiery serpent in biblical times. Certain species of freshwater copepods, mainly belonging to the genera *Mesocyclops* Sars and *Thermocyclops* Kiefer, are infested with the larval stages of this nematode in parts of equatorial Africa and the Indian subcontinent. If swallowed in drinking water the guineaworm larva can develop to maturity inside the human body and can cause temporary or permanent disablement, or death. Other human parasites, such as the fish tapeworm *Diphyllobothrium latum* (Linn.), also require a copepod intermediate host in order to complete their life cycles. Freshwater copepods ingest the free swimming coracidium larva of the tapeworm which develops into a proceroid larva. The second intermediate host, a freshwater fish, swallows the infected copepod and the proceroid larva develops into a plerocercoid larva inside the fish. This larva is infective to man and completes its life cycle if eaten in raw or undercooked fish.

Copepods in Biological Control: Some freshwater copepods are the intermediate hosts for *Coelomomyces* Keilin fungus which parasitises larval mosquitoes and can cause high mortalities (Whisler et al., 1974, 1975). The introduction into mosquito breeding sites of infected copepods containing active planonts in the haemocoel, may provide an effective biological control technique for malarial mosquitoes (Toohey et al., 1982). Similarly other copepods, including species of *Mesocyclops*, act as the intermediate host of a sporozoan parasite of mosquitoes that is under investigation as a possible agent of biological control.

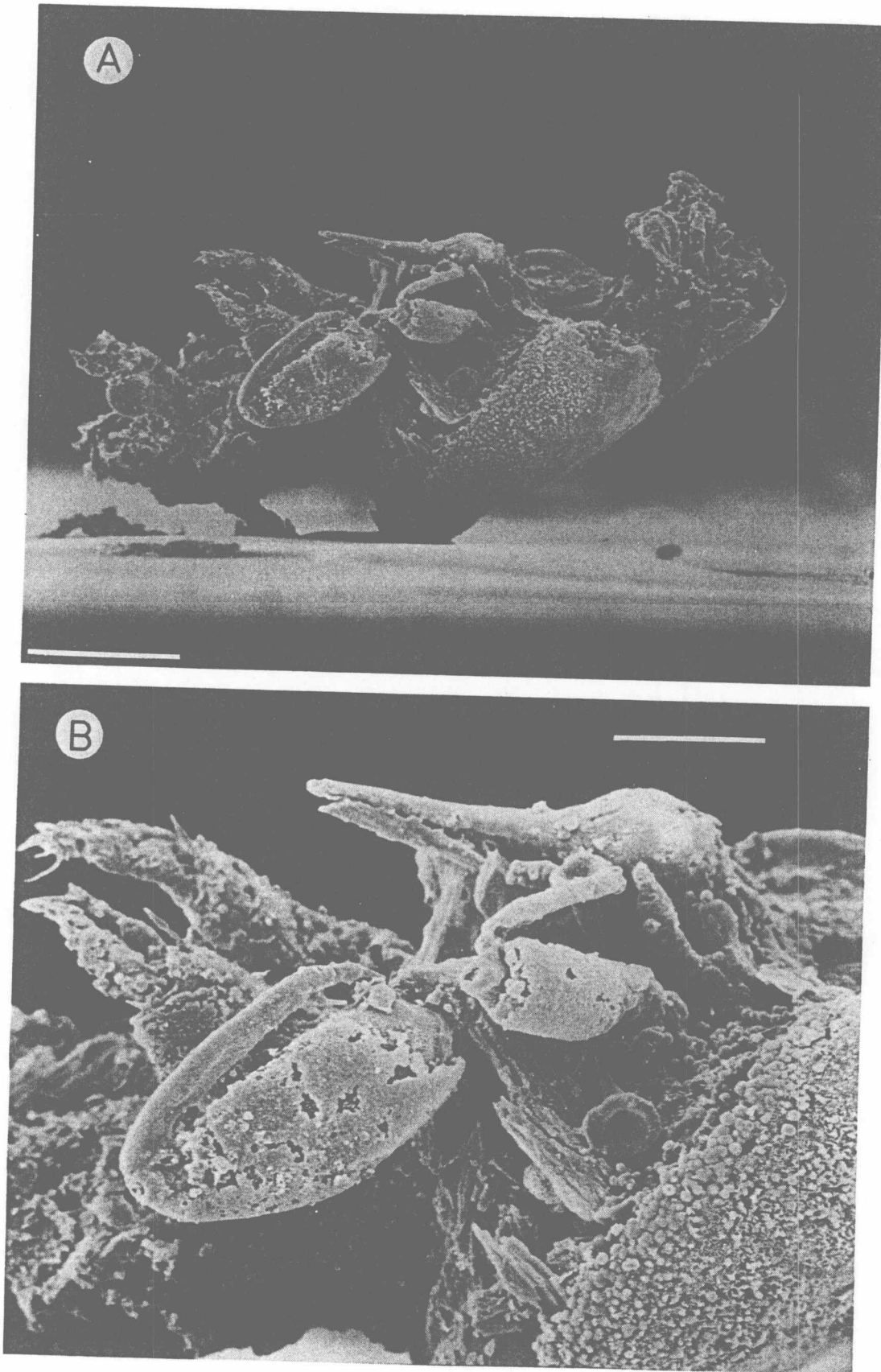


Figure 1.3.2. *Kabatarina pattersoni*, female. [A fossil parasitic copepod from the Lower Cretaceous.] **A.** Cephalothorax, lateral view. **B.** Mouthparts, lateral view. Scale bars A = 100 μ m, B = 50 μ m.

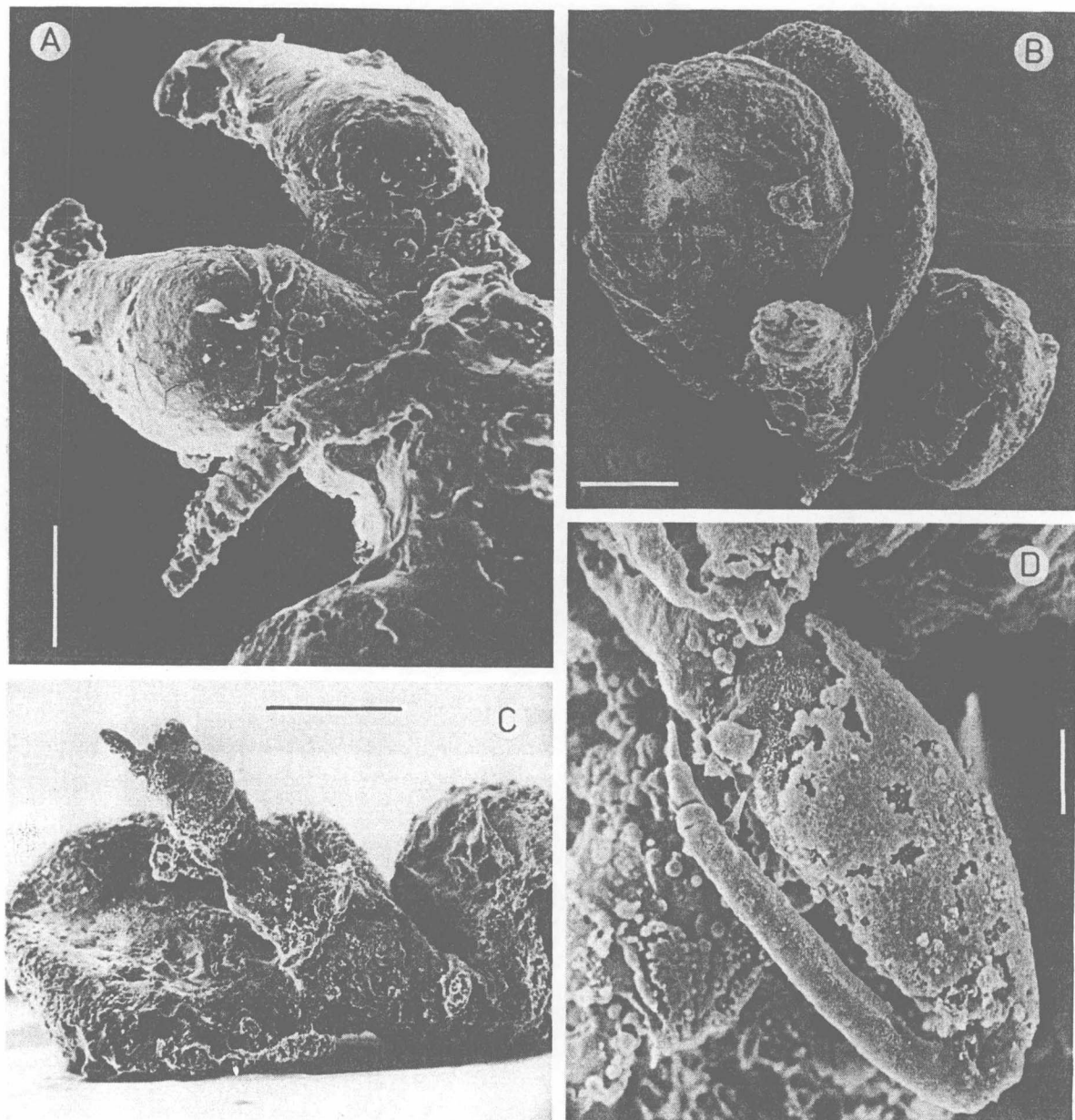


Figure 1.3.3. *Kabatarina pattersoni*, female. **A.** Antennae and proximal part of left antennule in situ, dorso-lateral view. **B.** Elytra of posterior pedigerous somites, posterior view. **C.** Urosome, ventral view. **D.** Maxilliped, ventro-lateral view. Scale bars A = 50 μ m, B-C = 100 μ m, D = 20 μ m.

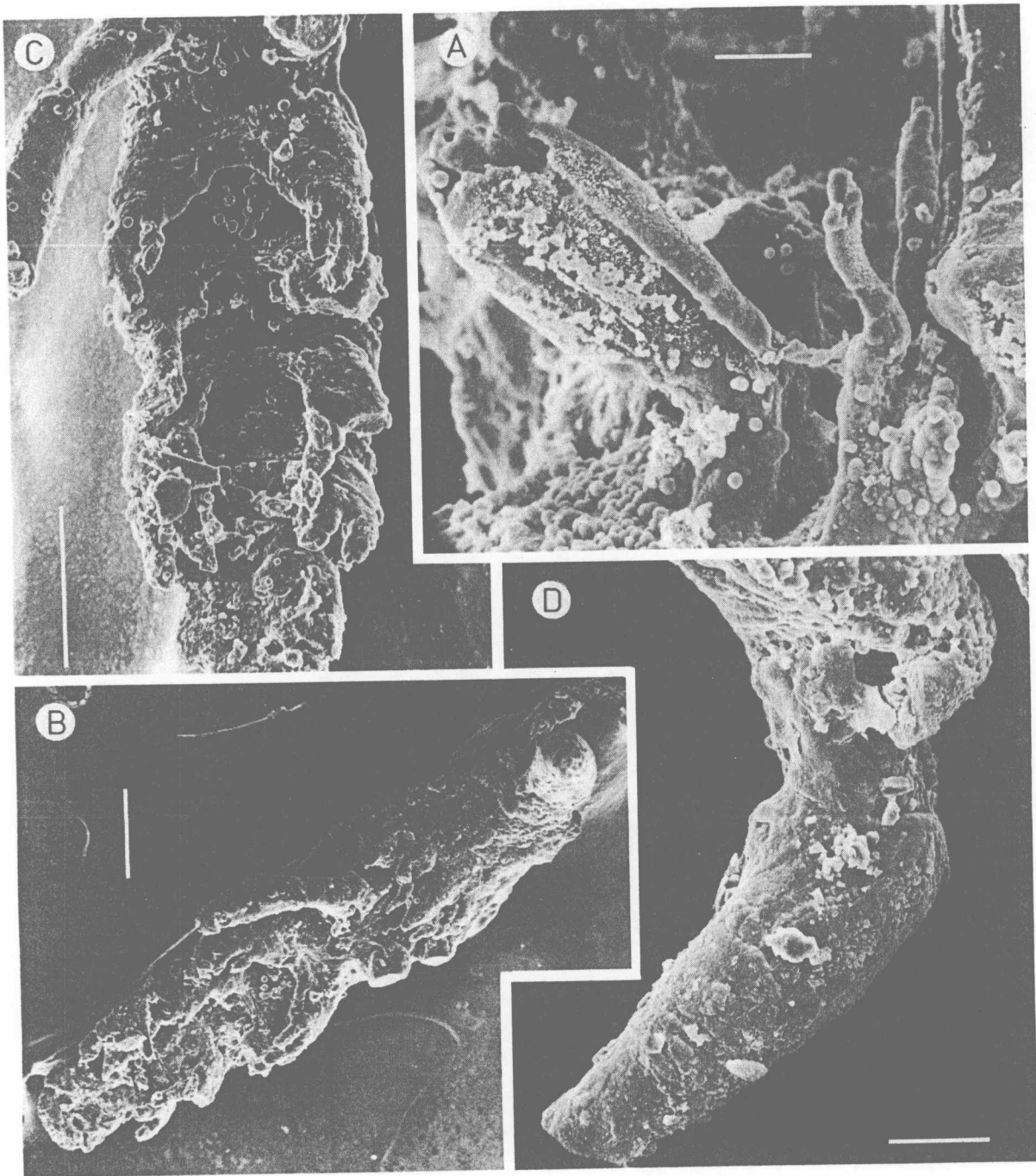


Figure 1.3.4. *Kabatarina pattersoni*. **A.** Female maxilla and maxillule, antero-ventral view. **B.** Male, ventral view. **C.** Male legs 1 to 4, ventral view. **D.** Male antenna, lateral view. Scale bars A = 30μm, B-C = 100μm, D = 40μm.