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Parasitic Crustacea

State of Knowledge and Future Trends

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Illustration of two stage 3 praniza larvae of the gnathiid isopod *Gnathia trimaculata* Coetzee, Smit, Grutter & Davies, 2009 parasitising blacktip reef sharks from the Great Barrier Reef, Australia (Illustration by Suanne Bosch)

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Editors

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About the Editors

Nico J. Smit is a Professor in Ecology and Director of Research of the Unit for Environmental Sciences and Management at North-West University, Potchefstroom Campus, South Africa. Nico's research focuses on the biodiversity, taxonomy and ecology of parasitic Crustacea and blood protozoa of marine and freshwater fishes and he has authored and co-authored more than 135 scientific papers and two edited books on these and other related topics. To date 15 PhD and 28 MSc students have graduated under his supervision. Nico has contributed to the management of national and international academic societies as president of the Parasitological Society of Southern Africa (PARSA), president of the South African Society of Aquatic Scientists (SASAqS) and committee member of the International Symposium on Fish Parasites (ISFP). Recently he has been the first South African aquatic parasitologist to be rated by the South African National Research Foundation (NRF) as an internationally acclaimed scientist.

Niel L. Bruce is an extraordinary Professor in Zoology at North-West University, Potchefstroom Campus, South Africa and a Research Associate of the Queensland Museum in Brisbane, Australia. He is a world expert on the taxonomy of marine isopod crustaceans, including the parasitic families. Niel has written more than 186 scientific papers, numerous reports, popular articles, five monographs and three edited books. He has worked at the Smithsonian Institution, Australian Museum, Zoological Museum in Copenhagen as Curator of Crustacea, National Institute of Water and Atmospheric Research in New Zealand as head of the Marine Invertebrate Biodiversity and Collections programs. Most recently Niel was Senior Curator at the Museum of Tropical Queensland. Niel's research continues to focus on the taxonomy, systematics, biogeography and biodiversity of tropical marine isopods, both free-living and parasitic forms. He has described or redescribed more than 500 species, 50 new genera and four new families of marine isopod. The other primary research focus, through graduate students, has been revisions of fish parasitic isopods of Southern Africa and Australia and Cirolanidae of Indonesia.

Kerry A. Hadfield is a Senior Lecturer in Zoology at North-West University, Potchefstroom Campus, South Africa and a committee member of the Parasitological Society of Southern Africa (PARSA). Dr. Hadfield received her doctoral degree from the University of Johannesburg where she revised several genera and species of cymothoid isopods from South Africa. Her focus has been predominantly on marine parasitic isopods of the families Cymothoidae and Gnathiidae but is now expanding to include most parasitic crustaceans. She is also one of the taxonomic editors for the World Register of Marine Species (WoRMS) and the World List of Marine Freshwater and Terrestrial Isopod Crustaceans. Kerry has published more than 20 papers describing one new genus of Isopoda and 15 new species (mostly from Africa).

Chapter 1
Introduction to Parasitic Crustacea: State of Knowledge and Future Trends

Nico J. Smit, Niel L. Bruce, and Kerry A. Hadfield

Abstract Parasitic crustaceans are globally considered to be some of the most successful and diverse parasites. They are ubiquitous in the aquatic environment and are known to occur on a wide range of vertebrate and invertebrate hosts. However, despite their common occurrence and large numbers, a book dedicated exclusively to these parasites has not been published. The book presented here provides detailed information on the major parasitic Crustacea groups, including those from Amphipoda, Ascothoracida, Branchiura, Cirripedia, Copepoda, Isopoda, Ostracoda, Pentastomida and Tantulocarida. Each chapter discusses the different aspects of the biology of these parasites, allowing for a better understanding of how the parasitic Crustacea function and for direct comparisons between different parasitic crustacean groups. In this book the authors review the history of discovery of the parasitic Crustacea; their biodiversity and taxonomy; their adaptations and types of crustacean symbiotic associations; their life cycle and life history strategies; their effects on their hosts; their role as vectors, hypersymbionts and hyperparasites and their molecular contribution (parasitic barnacles only), as well as their ecological significance. In addition to reviewing all of the relevant literature, new and unpublished data are included in all of the chapters. Altogether, this book highlights the morphological and ecological attributes that have made the parasitic Crustacea successful and aims to inspire and encourage current and future research into this ecological and economical important field of study.

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1.1 Introduction

The parasitic life strategy is so successful that currently there are more parasite species than free-living species worldwide. Parasitic species can be found in all the major groups of animals and plants ranging from unicellular organisms to arthropods and vertebrates. The different types of parasitism range from facultative, where the parasite usually is free living and may feed only occasionally on a host, to highly specialised obligate parasitism where the parasite undergoes total morphological transformation and is completely reliant on the host for survival. One group of parasites that highlights the full range of evolutionary adaptations to the parasitic lifestyle is the Crustacea.

Crustaceans are one of the most diverse metazoan phyla on Earth, demonstrating a remarkable variety of lifestyles, and a wide range of crustacean groups have entered into parasitic relationships with invertebrate and vertebrate hosts. Parasitism has evolved independently multiple times and across several groups in the Crustacea. Morphological adaptations to this lifestyle include reduction of setae, reduction or loss of appendages through fusion of body segments and, in many, development of a worm-like body. Approximate estimations of species numbers are impossible given the large number of potential hosts yet to be examined, but thousands are already known. Within the parasitic Crustacea, the Copepoda are the most diverse group in terms of morphology, species numbers and host utilisation, and their hosts include almost all other metazoan phyla. The Branchiura are exclusively parasitic, infecting marine and freshwater fish. The Ascothoracida are marine parasites of various echinoderms and cnidarians, occurring from the intertidal to the deep sea. Parasitic Cirripedia include all Rhizocephala, which parasitise other Crustacea, and some Thoracica, with *Rhizolepas* Day, 1939 species infecting polychaetes and one species of *Anelasma* Darwin, 1852 parasitising dogfish. The Tantulocarida is related to the Thecostraca; all are parasites of marine crustacean hosts. Pentastomids parasitise the respiratory passages of marine, freshwater and terrestrial vertebrates. One family of ostracods, Entocytheridae, is parasitic on the gills of freshwater decapod crustaceans. Among the Isopoda, the Cymothoida includes all the parasitic families; the Cymothooidea are predominantly parasites of fish, while the Bopyroidea and Cryptoniscoidea exclusively parasitise other crustaceans. The Cyamidae, ectoparasites of whales, are among only a few truly parasitic groups of Amphipoda.

Throughout the centuries, parasitic crustaceans have been studied on many levels, from the basic morphology and taxonomy to their complex biology and recently to cellular and molecular level. Thousands of research papers have been published on all aspects of their biology and as a group have featured in chapters within a wide range of books. These include basic parasitology textbooks such as Bush et al. (2001) and Goater et al. (2014), as well as more specialised text on marine parasitology (Rohde 2005) and fish parasitology (Woo 2006; Woo and Buchmann 2012). However, no single book exists that is completely devoted to this unique group of organisms. The aim of this book is to compile a single authoritative work by experts in the field, dealing with all the various aspects of the biology of parasitic Crustacea, so providing a concise summary of existing knowledge complemented with new information from the authors' own research. This will make it a one-stop knowledge hub for all researchers, lecturers, students and practitioners interested in parasitic Crustacea.

1.2 Chapter Synopsis

Following this introductory chapter, Chap. 2 presents the history of discovery for the different groups of parasitic Crustacea and their major historical influences. It introduces the different taxonomic groups and provides a synopsis of the discovery and growth of the knowledge for each taxon. The knowledge development in each group is reviewed, from the first parasite discovered to other key historical highlights in both the taxonomic and ecological areas that influenced the group up to the present. This serves as a preview to the host-parasite interactions that are covered in the subsequent chapters. Those specific researchers who added significant contributions to our knowledge of the parasitic Crustacea are also introduced (i.e. a "who's who" depicting leading parasitologists in this field). This review of the crustacean parasites provides a basic background to these abundant organisms, contributes to a better understanding of their unique niche in the aquatic environment and identifies the gaps of knowledge for these groups.

In Chap. 3, the authors reviewed the current understanding of the classification, systematics and global diversity (e.g. species richness patterns, patterns of host utilisation) of each of the parasitic Crustacea groups, highlighting areas of uncertainty or controversy that are in need of further research. Tabulated data on the taxa, species richness and hosts for the parasitic Crustacea groups were provided. Evidence of parasites from the fossil record, and the timing of origin of parasitic clades, were reviewed to provide insights into the history of coevolution between crustacean parasites and their hosts in order to set the scene for the following chapter.

The different life strategies and types of crustacean symbiotic associations, with examples, are discussed in Chap. 4. Most crustacean parasites are in some kind of association with other species: epibiosis, inquilinism, commensalism, mutualism, parasitism and eusociality. All six of these categories are discussed with examples. Regarding parasites, this can range from temporary to highly specialised permanent parasitism where the parasite undergoes total morphological adaptation, becoming metabolically completely reliant on the host for its survival. Parasitism is subdivided into ectoparasites, mesoparasites, endoparasites, parasitic castrators, parasitoidism and sponge hotels, the latter to accommodate the complex crustacean association with sponges. The chapter concludes with remarks on the global distribution of Branchiura, of which all the species are parasites of fish and amphibian tadpoles.

Parasites are said to only do two things: feed and reproduce. In Chap. 5, the authors focused on the way the parasitic Crustacea reproduce. These reproduction strategies can cause severe problems in aquaculture, aquariums and in our important food items around the world. Ironically, if their reproductive strategy is too successful, both the hosts and the parasites die. These life strategies have not received their warranted attention, and little is known about reproduction in many groups of crustaceans. In this chapter, the known reproductive strategies are distinguished, described and attributed to each crustacean group. Crustaceans have developed fascinating "tricks" in their strategies to take advantage of their hosts' behaviour, reproduction or vulnerabilities; environmental conditions; seasons; and a myriad of other factors to accomplish the impossible: find the right host in incredibly vast emptiness. Four new life cycles are suggested in the chapter: complex rebrooding, micro-male, mesoparasite and prey-predator transfer. Additionally, four new life cycle behaviours (nursery hiding, mid-moult stage, positive precursor, negative precursor) and four strategies (opossum attack, double parasitism, duplex arrangement, simple rebrooding) are named.

Chapter 6 discusses the effects parasitic Crustacea have on their respective hosts and aims at providing a holistic view of the direct impact of these parasites on ecological and economically important hosts. The pathological effects of a parasitic crustacean at the individual host level are relatively well understood; however, how they infect the physiological, immunological and reproductive status of hosts is much less studied. Quantifying these effects is difficult due to the poorly understood interactions between parasite, host and environmental determinants. Furthermore, the information of these parasitic Crustacea on the population and community levels is also scanty. The effects of sea lice on salmonids are probably the most understood and documented as these parasites cause a large economic impact on farmed salmon, resulting in a better understanding and control of this parasite. Unfortunately, this is not the case for other parasites where there is still much to be discovered if given the proper attention and funding.

Parasitic Crustacea also play an important role as definitive, intermediate and paratenic hosts, as well as vectors themselves. Chapter 7 presents this very interesting and seldom documented phenomenon. Several copepods are considered to be mechanical vectors or alternative hosts of a number of viral diseases between fishes. Ergasilids parasitic on the gill filaments of fishes can support the replication of shrimp viruses and likely act as viral vectors. Some branchiurans are thought to serve as mechanical vectors of several viruses to fishes, as well as acting as intermediate hosts for fish nematodes. Barnacles on the carapace and gill filaments of crabs can also support shrimp viruses. Several species of gnathiid isopods likely act as definitive hosts and vectors of fish blood parasites of the genus *Haemogregarina* Danilewsky, 1885; they may also transmit some fish viruses and may be paratenic or intermediate hosts for nematode larvae. Cymothoid isopods may transmit lymphocystis virus to fishes. It is likely that there are many more unpublished records of parasitic Crustacea vector associations, and areas of research are identified for future studies.

Parasitic crustaceans have also been reported to host their own symbionts. Chapter 8 deals with the reported records of hypersymbionts and hyperparasites on or in parasitic Crustacea. Microsporidians, peritrich ciliates, udonellids, tantulocarids and parasitic isopods have been found on parasitic copepods, isopods, branchiurans and barnacles. Information on peritrichs on Branchiura and Copepoda are noted, including unpublished data from the author. The monogenean group of udonellids are parasitic on copepods, and sometimes branchiurans, which occur on the skin of their host fish. Tantulocaridans have been reported from siphonostomatoid copepods. Parasitic isopods from the family Cabiropidae are hyperparasites of other parasitic isopods from the family Bopyridae, while other isopods from the family Cryptoniscidae are hyperparasitic on rhizocephalan barnacles. The effects of these hypersymbionts and hyperparasites on their respective hosts are also discussed, as well as biological control for sea lice and bopyrid isopods.

Molecular advances in the study of parasitic Crustacea are crucial for the understanding of their systematics, taxonomy and, even in some cases, life cycle elucidation. In Chap. 9, the authors present the phylogenetic position of Mycetomorpha within the Rhizocephala (parasitic barnacles) as a case study of how molecular-based phylogeny can serve to clarify morphological evolution and remove apparent homoplasies within the parasitic Crustacea. In Crustacea, phylogenetic analysis of parasitic forms has often been met with severe obstacles, both with respect to identifying their closest free-living relatives and with respect to intrinsic analysis of the parasitic species themselves. The reason for this is the paucity and sometimes almost total absence of characters that can be compared both between the parasites and their free-living forms and among the parasites themselves, as their very mode of life mostly entails various degrees of simplification in body morphology. With respect to the parasitic barnacles (Rhizocephala), the situation is much more critical because the parasites offer few, if any, traits that can reasonably be compared with other cirripedes and only few, very generalised traits for comparison between themselves. Until recently, rhizocephalan taxonomy relied exclusively on morphological larval characters, and only with DNA methods was it able to be confirmed that rhizocephalans are cirripedes and nested them within the taxon as the sister group to Thoracica. Additionally, recent hypotheses on family level relationships in Akentrogonida, based on larval structure and the sexual system, were largely confirmed, showing morphological characters can be powerful partners to molecular data in elucidating rhizocephalan phylogeny.

The book concludes with the ecological significance of the parasitic crustaceans discussed in Chap. 10. Crustaceans constitute the aquatic representatives of the most diverse animal phylum on the planet. The ecological “role” and significance of the free-living representatives have been well documented. For example, crustaceans comprise the majority of the zooplankton that function as primary consumers in aquatic food webs. Most work on the myriad parasitic crustaceans has focused on species that have become problematic for aquaculture. Much less is known about the ecological significance of the myriad parasitic forms. This stems largely from the fact that most parasitologists receive little if any training in ecology, and most aquatic ecologists receive little or no training in parasitology. Parasitic crustaceans can both transmit disease-causing organisms and create wounds that facilitate secondary infection, lower blood haematocrit levels and alter host immune function and metabolism, host movement patterns, feeding behaviour and interactions with other organisms. In high numbers, they can contribute directly to the death of the host and, in sublethal numbers, can be an indirect cause of death as well as reducing host growth and fecundity. Many crustacean parasites are themselves food for other organisms, sometimes including their own hosts. Any one of these can have consequences at the population level for the parasites and the hosts, as well as knock-on effects at the community level. This chapter reviews what is currently known about the ecology of parasitic crustaceans and highlights relevant literature in parasitology and aquatic ecology to chart the course of future study in this field.

1.3 Concluding Remarks

In conclusion, the authors and editors hope that on reading this book, the crustacean parasitologists will come away inspired by the contributions their work can make to the science of aquatic ecology, and aquatic ecologists should come away with an appreciation for the important role crustacean parasites play in the ecological systems.

Acknowledgements All the chapters of this book have been peer-reviewed by experts in the various fields of parasitic Crustacea, and the editors would hereby like to thank the nine anonymous reviewers for their time and constructive comments on each of the chapters. The editors would also like to thank Lars Koerner, Editor of Animal Sciences at Springer for initiating this project and his patience with us throughout the compilation of the book. Finally, we also like to thank Abinay Subramaniam, Project Coordinator (Books) for Springer Nature, for her assistance in preparing the final version of this book.

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Chapter 2
History of Discovery of Parasitic Crustacea

Kerry A. Hadfield

Abstract Parasitic Crustacea have been present in scientific literature since Linnaeus introduced the first classification system (binomial nomenclature). Crustaceans are considered to be the most morphologically diverse arthropods, with currently 19 parasitic orders known to science. This chapter reviews the history of discovery for each of the major parasitic Crustacea groups, highlighting some of the key developments that have influenced our current understanding of these parasites. Each taxonomic group is briefly introduced, followed by a synopsis on some of the outstanding contributions within that group. Knowledge development is followed, from the first parasites discovered to other historical highlights that influenced the groups up to this point. Other important discoveries (both taxonomic and ecological) are also noted, serving as a preview to the host-parasite interactions covered in the subsequent chapters. Additionally, several researchers who have added significant contributions to our knowledge of the parasitic Crustacea (specifically in taxonomy and discovery) are introduced, along with photographs of a select few. This historical review of the crustacean parasites provides a background to these diverse and abundant organisms and will contribute to a better understanding of their unique niche in the aquatic environment.

2.1 Introduction

Parasitic crustaceans were already represented at the introduction of binomial nomenclature by the Swedish taxonomist, Carl Linnaeus (Fig. 2.1a) (1758), including, amongst others, four species of fish parasitic isopods. In the more than two and a half centuries that followed, a great number of crustacean parasites were described, and while some parasitic crustacean groups, such as the copepods and isopods, are fairly well researched, limited information is available for the lesser known and less studied groups, such as the thoracicans and tantulocaridans.

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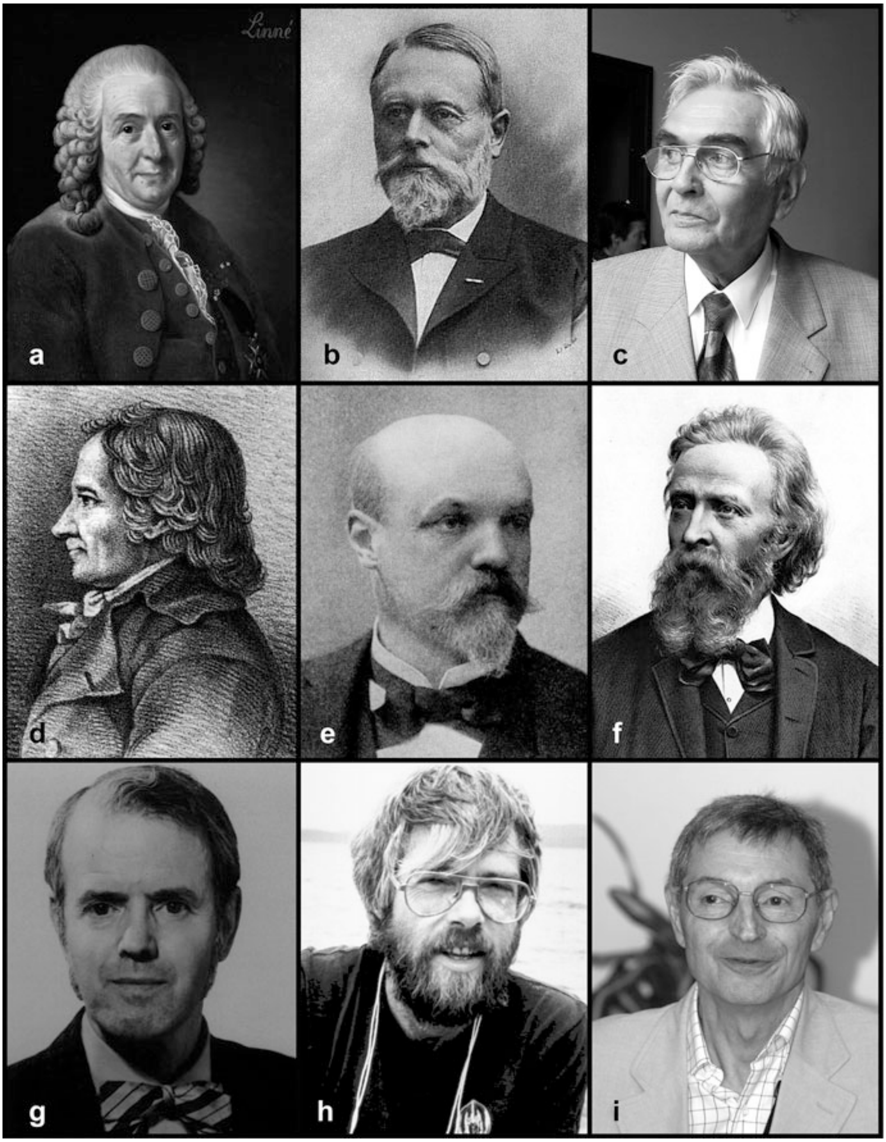

Fig. 2.1 (**a**) Carl Linnaeus, (**b**) Christian Frederik Lütken, (**c**) Hans-Eckhard Gruner, (**d**) Johan Christian Fabricius, (**e**) Carl Erik Alexander Bovallius, (**f**) Carl Friedrich Wilhelm Claus, (**g**) Thomas Elliot Bowman, (**h**) George "Richard" Harbison, (**i**) Philippe Laval. Image (**a**) oil on canvas by Alexander Roslin, © Wikipedia Commons public domain; image (**b**) © The Royal Library; image (**c**) from Coleman (2007); image (**d**) preface of Hope (1845); image (**e**) © Wikipedia Commons public domain; image (**f**) from Grobben (1899); image (**g**) from Ferrari (1996); image (**h**) courtesy of Woods Hole Oceanographic Institution Archives

Historically, crustacean collections were held in private collections or university museums. Collections from oceans were restricted to the intertidal regions or ship based, and for obvious reasons discovery lagged behind terrestrial discovery. The age of great ocean expeditions that fed into fish parasite knowledge included amongst others the US Exploring Expedition (several ships, 1838–1842), the *Galathea* Expedition (Danish, 1845–1847) and the *Siboga* Expedition (Dutch, 1899–1900). As scientific research developed, state (national) museums were founded as the major repositories for all natural history collections, such as the British Museum (founded in 1753 and the first national public museum in the world), the Muséum national d'histoire naturelle (1793) and in the New World, the US National Museum (1846), to name just three. As technology improved, scientists were able to use new techniques to not only collect parasites (such as SCUBA diving) but also to view them (such as scanning electron microscopy [SEM] and differential interference contrast [DIC] microscopy). Currently, the use of molecular biology techniques for parasites is on the rise. These techniques can assist with parasite identification and characterisation, as well as provide other useful information on the parasite origin and evolution (amongst other things).

The aim of this chapter is to reflect on the history of discovery for each of the major parasitic groups within Crustacea, showing that research on particular parasites increased with the presence of an individual or research group actively interested in that specific parasite group. It is envisaged that understanding the past research will indicate the gaps in our knowledge within these groups and contribute to identifying where research should focus in the future. The chapter focused primarily on the taxonomic and systematic discovery of parasitic crustaceans, along with notes on selected contributors to our knowledge of parasitic Crustacea. It should be noted that the chapter is not intended to be a checklist and does not refer to every researcher who has worked on the parasitic Crustacea.

2.2 Amphipoda

Superclass Multicrustacea Regier, Shultz, Zwick, Hussey, Ball, Wetzer, Martin & Cunningham, 2010
Class Malacostraca Latreille, 1802
Subclass Eumalacostraca Grobben, 1892
Superorder Peracarida Calman, 1904
Order Amphipoda Latreille, 1816

The status of any amphipod as a "true parasite" is often questioned, as there is no evidence that any have harmful effects upon their hosts. Amphipods associated with other animals are frequently referred to as commensals (i.e. members of Leucothoidae are typically found associated with sessile invertebrates such as sponges, utilising the current produced by the sponge to feed). Only a few groups of amphipods are recognised as parasitic: Cyamidae ("whale lice"), Hyperiidea and Trischizostomidae (see Table 2.1).

Table 2.1 Classification, up to family level, of the parasitic Crustacea according to the World Register of Marine Species (WoRMS) (2018)

Phylum Arthropoda Siebold & Stannius 1845
Subphylum Crustacea Brünnich, 1772
Superclass Multicrustacea Regier, Shultz, Zwick, Hussey, Ball, Wetzer, Martin & Cunningham, 2010
Class Hexanauplia Oakley, Wolfe, Lindgren & Zaharof, 2013
Subclass Copepoda Milne-Edwards, 1840
Infraclass Neocopepoda Huys & Boxshall, 1991
Superorder Podoplea Giesbrecht, 1882
Order Cyclopoida Burmeister, 1834
Family Archinotodelphyidae Lang, 1949
Family Ascidicolidae Thorell, 1859
Family Botryllophilidae Sars G.O., 1921
Family Buproridae Thorell, 1859
Family Chitonophilidae Avdeev & Sirenko, 1991
Family Chordeumiidae Boxshall, 1988
Family Cucumaricolidae Bouligand & Delamare Deboutteville, 1959
Family Cyclopettidae Martínez Arbizu, 2000
Family Cyclopidae Rafinesque, 1815
Family Cyclopinidae Sars G.O., 1913
Family Cyclopoida incertae sedis
Family Enterognathidae Illg & Dudley, 1980
Family Enteropsidae Thorell, 1859
Family Fratiidae Ho, Conradi & López-González, 1998
Family Giselinidae Martínez Arbizu, 2000
Family Hemicyclopinidae Martínez Arbizu, 2001
Family Lernaeidae Cobbold, 1879
Family Mantridae Leigh-Sharpe, 1934
Family Micrallectidae Huys, 2001
Family Notodelphyidae Dana, 1853
Family Oithonidae Dana, 1853
Family Ozmanidae Ho & Thatcher, 1989
Family Psammocyclopinidae Martínez Arbizu, 2001
Family Pterinopsyllidae Sars G.O., 1913
Family Schminkepinellidae Martínez Arbizu, 2006
Family Smirnovipinidae Martínez Arbizu, 1997
Family Speleoithonidae Rocha & Iliffe, 1991
Family Thaumatopsyllidae Sars G.O., 1913
Order Harpacticoida Sars M., 1903
Family Balaenophilidae Sars G.O., 1910
Family Tisbidae Stebbing, 1910
Order Monstrilloida Sars G.O., 1901
Family Monstrillidae Dana, 1849
Order Poecilostomatoida Thorell, 1859

(continued)

Table 2.1 (continued)

	Family Abrsiidae Karanovic, 2008
	Family Anchimolgidae Humes & Boxshall, 1996
	Family Anomoclausiidae Gotto, 1964
	Family Antheacheridae Sars M., 1870
	Family Anthessiidae Humes, 1986
	Family Bomolochidae Claus, 1875
	Family Bradophilidae Marchenkov, 2002
	Family Catiniidae Bocquet & Stock, 1957
	Family Chondracanthidae Milne-Edwards, 1840
	Family Clausidiidae Embleton, 1901
	Family Clausiidae Giesbrecht, 1895
	Family Corallovexiidae Stock, 1975
	Family Corycaeidae Dana, 1852
	Family Echiurophilidae Delamare-Deboutteville & Nunes-Ruivo, 1955
	Family Entobiidae Ho, 1984
	Family Erebonasteridae Humes, 1987
	Family Ergasilidae Burmeister, 1835
	Family Eunicicolidae Sars G.O., 1918
	Family Gadilicolidae Boxshall & O'Reilly, 2015
	Family Gastrodelphyidae List, 1889
	Family Herpyllobiidae Hansen, 1892
	Family Intramolgidae Marchenkov & Boxshall, 1995
	Family Iveidae Tung, Cheng, Lin, Ho, Kuo, Yu & Su, 2014
	Family Jasmineiricolidae Boxshall, O'Reilly, Sikorski & Summerfield, 2015
	Family Kelleriidae Humes & Boxshall, 1996
	Family Lamippidae Joliet, 1882
	Family Leaniricolidae Huys, 2016
	Family Lichomolgidae Kossmann, 1877
	Family Lubbockiidae Huys & Böttger-Schnack, 1997
	Family Macrochironidae Humes & Boxshall, 1996
	Family Makrostrotidae Huys, Fatih, Ohtsuka & Llewellyn-Hughes, 2012
	Family Mesoglicolidae Zulueta, 1911
	Family Myicolidae Yamaguti, 1936
	Family Mytilicolidae Bocquet & Stock, 1957
	Family Nereicolidae Claus, 1875
	Family Octopicolidae Humes & Boxshall, 1996
	Family Oncaeidae Giesbrecht, 1893
	Family Paralubbockiidae Boxshall & Huys, 1989
	Family Philichthyidae Vogt, 1877
	Family Philoblennidae Izawa, 1976
	Family Phyllodicolidae Delamare Deboutteville & Laubier, 1961
	Family Pionodesmotidae Bonnier, 1898
	Family Poecilostomatoida incertae sedis

(continued)

Table 2.1 (continued)

Family Polyankyliidae Ho & Kim I.H., 1997
Family Praxillinicolidae Huys, 2016
Family Pseudanthessiidae Humes & Stock, 1972
Family Rhynchomolgidae Humes & Stock, 1972
Family Sabelliphilidae Gurney, 1927
Family Saccopsidae Lützen, 1964
Family Sapphirinidae Thorell, 1859
Family Serpulidicolidae Stock, 1979
Family Shiinoidae Cressey, 1975
Family Spiophanicolidae Ho, 1984
Family Splanchnotrophidae Norman & Scott T., 1906
Family Strepidae Cheng, Liu & Dai, 2016
Family Synapticolidae Humes & Boxshall, 1996
Family Synaptiphilidae Bocquet & Stock, 1957
Family Taeniacanthidae Wilson C.B., 1911
Family Telsidae Ho, 1967
Family Thamnomolgidae Humes & Boxshall, 1996
Family Urocopiidae Humes & Stock, 1972
Family Vahiniidae Humes, 1967
Family Ventriculinidae Leigh-Sharpe, 1934
Family Xarifiidae Humes, 1960
Family Xenocoelomatidae Bresciani & Lutzen, 1966
Order Siphonostomatoida Thorell, 1859
Family Archidactylinidae Izawa, 1996
Family Artotrogidae Brady, 1880
Family Asterocheridae Giesbrecht, 1899
Family Brychiopontiidae Humes, 1974
Family Caligidae Burmeister, 1835
Family Calverocheridae Stock, 1968
Family Cancerillidae Giesbrecht, 1897
Family Codobidae Boxshall & Ohtsuka, 2001
Family Coralliomyzontidae Humes & Stock, 1991
Family Dichelesthiidae Milne-Edwards, 1840
Family Dichelinidae Boxshall & Ohtsuka, 2001
Family Dinopontiidae Murnane, 1967
Family Dirivultidae Humes & Dojiri, 1980
Family Dissonidae Kurtz, 1924
Family Ecbathyriontidae Humes, 1987
Family Entomolepididae Brady, 1899
Family Eudactylinidae Wilson C.B., 1932
Family Hatschekiidae Kabata, 1979
Family Hyponeoidae Heegaard, 1962
Family Kroyeriidae Kabata, 1979

(continued)

Table 2.1 (continued)

Family Lernaeopodidae Milne-Edwards, 1840
Family Lernanthropidae Kabata, 1979
Family Megapontiidae Heptner, 1968
Family Micropontiidae Gooding, 1957
Family Nanaspididae Humes & Cressey, 1959
Family Nicothoidae Dana, 1852
Family Pandaridae Milne-Edwards, 1840
Family Pennellidae Burmeister, 1835
Family Pontoeciellidae Giesbrecht, 1895
Family Pseudocycnidae Wilson C.B., 1922
Family Pseudohatschekiidae Tang, Izawa, Uyeno & Nagasawa, 2010
Family Rataniidae Giesbrecht, 1897
Family Scottomyzontidae Ivanenko, Ferrari & Smurov, 2001
Family Siphonostomatoida incertae sedis
Family Sphyriidae Wilson C.B., 1919
Family Sponginticolidae Topsent, 1928
Family Spongiocnizontidae Stock & Kleeton, 1964
Family Stellicomitidae Humes & Cressey, 1958
Family Tanypleuridae Kabata, 1969
Family Trebiidae Wilson C.B., 1905
Subclass Tantulocarida Boxshall & Lincoln, 1983
Family Basipodellidae Boxshall & Lincoln, 1983
Family Deoterthridae Boxshall & Lincoln, 1987
Family Doryphallophoridae Huys, 1991
Family Microdajidae Boxshall & Lincoln, 1987
Family Onceroxenidae Huys, 1991
Subclass Thecostraca Gruvel, 1905
Infraclass Ascothoracida Lacaze-Duthiers, 1880
Order Dendrogastrida Grygier, 1987
Family Ascothoracidae Grygier, 1987
Family Ctenosculidae Thiele, 1925
Family Dendrogastridae Gruvel, 1905
Order Laurida Grygier, 1987
Family Lauridae Gruvel, 1905
Family Petrarcidae Gruvel, 1905
Family Synagogidae Gruvel, 1905
Infraclass Cirripedia Burmeister, 1834
Superorder Acrothoracica Gruvel, 1905
Order Lithoglyptida Kolbasov, Newman & Hoeg, 2009
Family Lithoglyptidae Aurivillius, 1892
Family Trypetesidae Stebbing, 1910
Superorder Rhizocephala Müller, 1862
Order Akentrogonida Häfele, 1911

(continued)

Table 2.1 (continued)

Family Akentrogonida incertae sedis
Family Chthamalophilidae Bocquet-Védrine, 1961
Family Clistosaccidae Boschma, 1928
Family Duplorbidae Høeg & Rybakov, 1992
Family Mycetomorphidae Høeg & Rybakov, 1992
Family Polysaccidae Lützen & Takahashi, 1996
Family Thompsoniidae Høeg & Rybakov, 1992
Order Kentrogonida Delage, 1884
Family Lernaeodiscidae Boschma, 1928
Family Parthenopeidae Rybakov & Høeg, 2013
Family Peltogastridae Lilljeborg, 1860
Family Sacculinidae Lilljeborg, 1860
Superorder Thoracica Darwin, 1854
Order Lepadiformes Buckeridge & Newman, 2006
Suborder Heteralepadomorpha Newman, 1987
Family Anelasmatidae Gruvel, 1905
Family Koleolepadidae Hiro, 1933
Family Rhizolepadidae Zevina, 1980
Suborder Lepadomorpha Pilsbry, 1916
Family Poecilasmatidae Annandale, 1909
Order Sessilia Lamarck, 1818
Suborder Balanomorpha Pilsbry, 1916
Family Pyrgomatidae Gray, 1825
Infraclass Facetotecta Grygier, 1985
Class Malacostraca Latreille, 1802
Subclass Eumalacostraca Grobben, 1892
Superorder Peracarida Calman, 1904
Order Amphipoda Latreille, 1816
Superfamily Lysianassoidea Dana, 1849
Family Trischizostomatidae Lilljeborg, 1865
Suborder Hyperiidea Milne-Edwards, 1830
Infraorder Physocephalata Bowman & Gruner, 1973
Superfamily Phronimoidea Rafinesque, 1815
Family Dairellidae Bovallius, 1887
Family Hyperiidae Dana, 1852
Family Lestrigonidae Zeidler, 2004
Family Phronimidae Rafinesque, 1815
Superfamily Platysceloidea Spence Bate, 1862
Family Brachyscelidae Stephensen, 1923
Family Lycaeidae Claus, 1879
Family Oxycephalidae Dana, 1852
Superfamily Vibilioidea Dana, 1852
Family Vibiliidae Dana, 1852

(continued)

Table 2.1 (continued)

Infraorder Physosomata
Suborder Senticaudata Lowry & Myers, 2013
Infraorder Corophiida Leach, 1814 (sensu Lowry & Myers, 2013)
Superfamily Caprelloidea Leach, 1814
Family Cyamidae Rafinesque, 1815
Order Isopoda Latreille, 1817
Suborder Cymothoida Wägele, 1989
Superfamily Bopyroidea Rafinesque, 1815
Family Bopyridae Rafinesque, 1815
Family Entoniscidae Kossmann, 1881
Superfamily Cryptoniscoidea Kosmann, 1880
Family Cabiropidae Giard & Bonnier, 1887
Family Cryptoniscidae Kossmann, 1880
Family Cyproniscidae Bonnier, 1900
Family Dajidae Giard & Bonnier, 1887
Family Podasconidae Giard & Bonnier, 1895
Superfamily Cymothooidea Leach, 1814
Family Anuropidae Stebbing, 1893
Family Aegidae White, 1850
Family Barybrotidae Hansen, 1890
Family Corallanidae Hansen, 1890
Family Cymothoidae Leach, 1814
Family Gnathiidae Leach, 1814
Family Tridentellidae Bruce, 1984
Superclass Oligostraca Zrzavý, Hypša & Vlášková, 1998
Class Ichthyostraca Zrzavý, Hypša & Vlášková, 1998
Subclass Branchiura Thorell, 1864
Order Arguloida Yamaguti, 1963
Superfamily Arguloidea Yamaguti, 1963
Family Argulidae Leach, 1819
Subclass Pentastomida Diesing, 1836
Order Cephalobaenida Heymons, 1935
Family Cephalobaenidae Heymons, 1922
Order Porocephalida Heymons, 1935
Superfamily Linguatuloidea Haldeman, 1851
Family Linguatulidae Haldeman, 1851
Family Subtriquetridae Fain, 1961
Superfamily Porocephaloidea Sambon, 1922
Family Porocephalidae Sambon, 1922
Family Sebekidae Sambon, 1922
Order Raillietiellida Almeida & Christoffersen, 1999
Family Raillietiellidae Sambon, 1922
Order Reighardiida Almeida & Christoffersen, 1999

(continued)

Table 2.1 (continued)

Family Reighardiidae Heymons, 1926
Class Ostracoda Latreille, 1802
Subclass Myodocopa Sars, 1866
Order Myodocopida Sars, 1866
Suborder Myodocopina Sars, 1866
Superfamily Cypridinoidea Baird, 1850
Family Cypridinidae Baird, 1850

2.2.1 *Cyamidae*

The term "whale lice" is a misnomer as these are in fact crustaceans, with most cyamids being dorsoventrally flattened and unable to swim, relying on direct contact for transmission from one host to another. They have a rudimentary pleon with the posterior three pairs of legs enlarged and adapted to cling onto their host. Cyamids are known to attach to whales, dolphins and porpoises (Martínez et al. 2008), where they can be highly host specific, and more than one species can be found on one host at a time.

The first cyamid described was *Cyamus ceti* (Linnaeus, 1758) (originally as *Oniscus ceti* since the genus *Cyamus* was described by Latreille in 1796), and a number of new species were discovered in the 1800s. Christian Frederik Lütken (Fig. 2.1b) described seven new *Cyamus* species as well as the genus, *Platycyamus* Lütken, 1870, all of which were incorporated into the first cyamid monograph (Lütken 1873). Lütken, a Danish zoologist, worked on a number of aquatic groups including corals, jellyfish, crustaceans and annelids, but his passion lay with echinoderms and fishes, and thus only a few of his papers were dedicated to cyamids. Although cyamids were known in many parts of the world, between 1888 and 1931, no new cyamid species were described.

In 1967, Yuk-Maan Leung provided the first illustrated key for the cyamids along with a guide to the literature (Leung 1967). Leung also described the first life cycle of a cyamid (*Cyamus scammoni* Dall, 1872 on the grey whale) which provided valuable information on the reproductive behaviour of these parasites (Leung 1976). Around the same time, Hans-Eckhard Gruner (Fig. 2.1c) completed a comprehensive catalogue of the Cyamidae (Gruner 1975). Gruner contributed to the taxonomy of amphipods and isopods and was best known for his *Lehrbuch der Speziellen Zoologie* (Textbook on Special Zoology) published in 1980. A few years later, in 1999, Joel Martin and John Heyning provided an updated key and checklist for these parasites, which proved helpful in subsequent studies (Martin and Heyning 1999).

As cyamids are permanently attached to constantly moving cetaceans, in-depth studies on the parasites have been difficult; however, despite these challenges, many scientists have been able to report on their ecology. Juan Antonio Balbuena and Juan Antonio Raga published many papers on parasites of marine mammals and discussed the ecology and host relationships of whale lice on pilot whales (Balbuena and Raga 1991). Furthermore, Victoria Rowntree, an American whale researcher, has noted many behavioural aspects of these amphipods (on right whales in particular). Cyamids are known to aggregate in areas where there is the least amount of stress (out of the main water flow areas), such as the skin folds on the head, eyes, flippers, blowholes, lip margins, around barnacles and callosities (Leung 1970a, b; Rowntree 1996). The abundance of the cyamids on their host is inversely proportional to the host's swimming speed, with slower whales having several thousand on a single host and faster-swimming dolphins having fewer (Goater et al. 2014). The mouthparts of the cyamids are highly modified, with setae and short spines on the maxillae, maxillules and mandibles, for excavating and eating host skin. Rowntree (1996) confirmed that these ectoparasites eat whale skin containing pigments (seen in the intestines of the amphipods), and shortly thereafter Schell et al. (2000) confirmed this diet with the aid of stable carbon and nitrogen isotopes. More recently, Rowntree and colleagues have used genetic sequence variation in the whale lice of right whales in order to determine population histories (Kaliszewska et al. 2005).

Carl J. Pfeiffer, researcher of marine mammals, and his colleagues provided additional information on the anatomy of cyamids (marsupium, eggs, juveniles and cuticle) (Pfeiffer and Viers 1998), as well as on the ocular musculature (Levin and Pfeiffer 1999). Pfeiffer also completely revised the whale lice in a chapter dedicated to the crustaceans in the published book *Encyclopaedia of Marine Mammals* (Pfeiffer 2002).

Alan A. Myers and James K. Lowry, amphipod specialists from Ireland and Australia, respectively, also presented a new classification for the suborder Corophiidea (see Myers and Lowry 2003). However, most of the amphipod higher-level classification and phylogenetic relationships are still not agreed upon, with preliminary molecular work and the previously proposed relationships not being consistent (Väinölä et al. 2008). More recently, Myers and Lowry revised the amphipod classification, established a new suborder Senticaudata (including the Cyamidae), and introduced the level parvorder between infraorder and superfamily, a first for amphipod taxonomy (Lowry and Myers 2013). The family Cyamidae currently has 32 recorded species from six genera.

2.2.2 *Hyperiidea*

Parasitic amphipods, in the suborder Hyperiidea, have a large cephalothorax and eyes and are exclusively marine (mostly pelagic). These crustaceans live associated with other zooplankton where they may be parasitic or commensals on organisms such as jellyfish, ctenophores, molluscs and tunicates. The association of a hyperiid and gelatinous zooplankton is considered parasitic if the amphipod is within the tissue of the host for nutritional purposes (host tissue can be seen in the amphipod stomach contents after feeding) (de Lima and Valentin 2001).

The first three species of Hyperiidea were described in 1775. Johan Christian Fabricius (Fig. 2.1d) (a Danish zoologist) described two of these species, namely, *Cystisoma spinosum* (Fabricius, 1775) (*nomen dubium*) and *Scina crassicornis* (Fabricius, 1775). The third species, *Phronima sedentaria* (Forskål, 1775), was described by the Swedish researcher, Peter Forskål. Interestingly, both these men were students of Linnaeus at some point. Although these three species were the first named hyperiids, there was an earlier record in 1762 by H. Strøm of a hyperiid in association with a host, where *Hyperia medusarum* (Müller, 1776) was located inside a large jellyfish (Harbison et al. 1977).

Many of the early systematic monographs on these parasites were completed by the Swedish biologist Carl Erik Alexander Bovallius (1887a, b, c, 1889, 1890) (Fig. 2.1e) and the German zoologist Carl Friedrich Wilhelm Claus (1879a, b) (Fig. 2.1f). Thomas Elliot Bowman (an American carcinologist) (Fig. 2.1g) and Hans-Eckhard Gruner thoroughly reviewed the families and genera of Hyperiidea in 1973 (Bowman and Gruner 1973). This review became the foundation for all other systematic work on these amphipods. Not only did it focus on identifying the large collection of hyperiid Amphipoda sampled during the Dana Expedition (1928–1930), but it also included a detailed section on their morphology and ecology.

George "Richard" Harbison (Fig. 2.1h) noted that although other researchers had mentioned the parasitic mode of life, little research had been done on the life histories and host specificities of the parasitic amphipods. Using SCUBA to collect live material, Harbison and colleagues were able to observe a number of associations between the amphipods and their hosts that had never been noted before (Harbison et al. 1977; Madin and Harbison 1977). Many observations of living hyperiids were also made by Philippe Laval (from 1963 until he retired in 2004) (Fig. 2.1i). Laval was one of the first researchers to recognise that all hyperiids have a parasitic way of life (noted in his doctoral thesis in 1974), which was later confirmed by Harbison et al. (1977) and published (amongst others) an extensive paper on these parasites associated with gelatinous zooplankton (Laval 1980).

More recently, Wolfgang Zeidler (Fig. 2.2a), formerly working at the South Australian Museum, revised the taxonomy of the Hyperiidea (Zeidler 2003a, b, 2004a, b, 2006, 2009, 2012, 2015; Zeidler and De Broyer 2009). These extensive reviews included assessments of the systematic relationships between the genera as well as keys for the families, genera and species, drawings of the species and diagnoses for the different taxa. Hyperiidea has 283 accepted species and 76 genera of which Zeidler has described 12 families, 5 genera and 23 species.

2.2.3 *Trischizostomidae*

At present, there are 18 species of *Trischizostoma* Boeck, 1861, most of which are considered ectoparasites of fish species. These amphipods occur between 22 and 3655 m depth (Freire and Serejo 2004) and have specifically adapted styliform mouthparts and a modified gnathopod 1 for this parasitic way of life.

The first described *Trischizostoma* was *T. nicaeense* (Costa, 1853) (as *Guerina nicaeensis* Chevreux, 1905) from Nice, France. Elsie Wilkins Sexton (an English

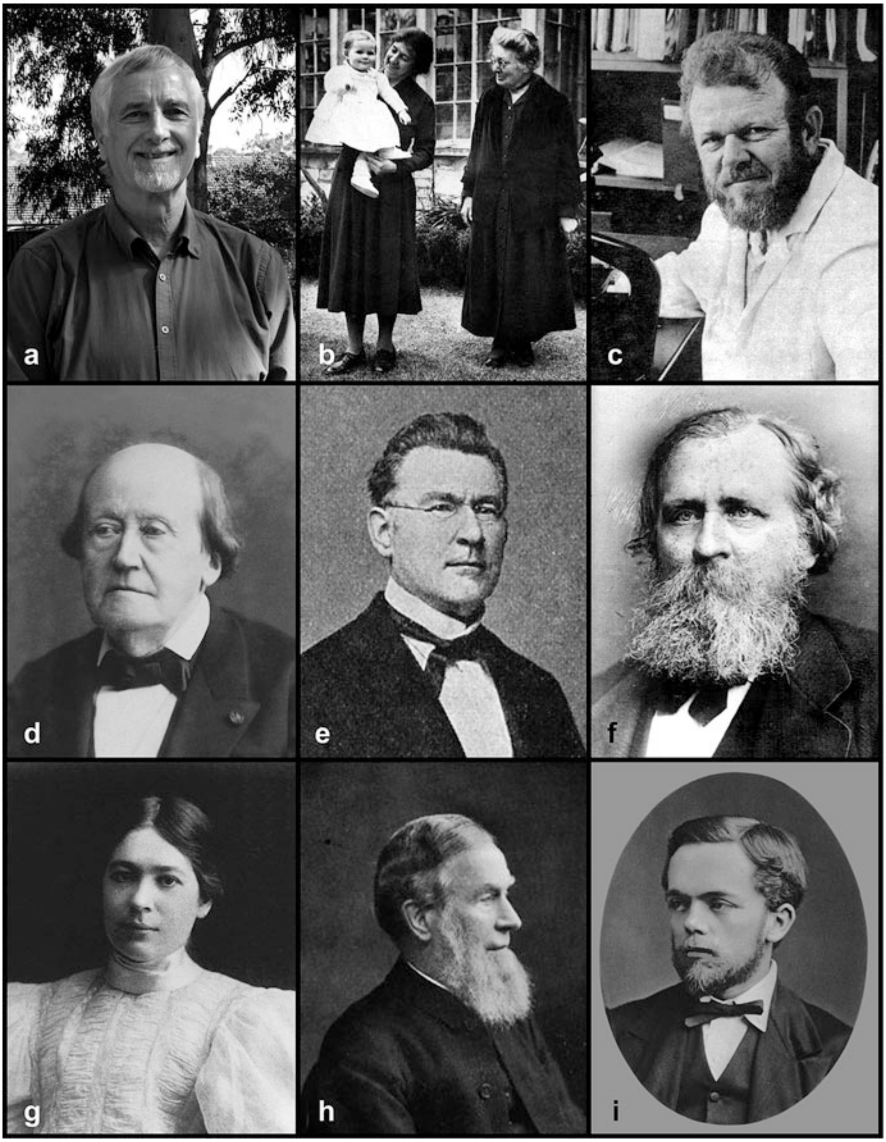

Fig. 2.2 (**a**) Wolfgang Zeidler, (**b**) Elsie Wilkins Sexton (on the right), (**c**) Jerry Laurens Barnard, (**d**) Henri Milne Edwards, (**e**) Jörgen Matthias Christian Schioedte, (**f**) Frederik Vilhelm August Meinert, (**g**) Harriet Richardson, (**h**) Thomas Roscoe Rede Stebbing, (**i**) Edward John Miers. Image (**b**) from Spooner (1960); image (**c**) from Thomas (1992); images (**d**), (**e**) and (**h**) © Wikipedia Commons public domain; image (**f**) from Truesdale (1993); image (**g**) from Damkaer (2000); image (**i**) from Gordon (1971)

zoologist) (Fig. 2.2b) published a review of the genus in 1908, highlighting the historical moments as well as including species descriptions and drawings of the species known at that time (Sexton 1908). Sexton's research into these amphipods helped to clarify the taxonomy of the genus. She had accurate and superior illustrations by the standard of the day and continued to work even after her 80th birthday.

In 1961, Jerry Laurens Barnard (Fig. 2.2c) described a new species of *Trischizostoma* and in doing so divided the genus into two groups: those with a large conspicuous rostrum, strongly styliform mouthparts and an entire telson and those with a smaller deflexed rostrum, much less styliform mouthparts and a telson cleft to the middle (Barnard 1961). Barnard was an outstanding amphipod taxonomist, primarily working on the Gammaridea. Years later, Vinogradov (1991) published a key for the genus in Russian. In 2004, Freire and Serejo (2004) provided a key to the Brazilian species and recorded the first *Trischizostoma* from the Southwest Atlantic Ocean. A recent publication by Winfield et al. (2017) added the first record from the north-east Pacific. The distribution of these two groups now is as follows: the "entire telson" group are known from the north-east and south-west Atlantic Ocean, the north-west and north-east Pacific Ocean and the Indo-Pacific, while the "notched telson" group are from the south-east Atlantic and south-west Indian Ocean (Winfield et al. 2017).

2.3 Isopoda

Superclass Multicrustacea Regier, Shultz, Zwick, Hussey, Ball, Wetzer, Martin & Cunningham, 2010
Class Malacostraca Latreille, 1802
Subclass Eumalacostraca Grobben, 1892
Superorder Peracarida Calman, 1904
Order Isopoda Latreille, 1817

Isopods were named in reference to the legs being of similar size and shape (see Bunkley-Williams and Williams 1994). There are 95 families of Isopoda, with approximately 10,300 isopod species worldwide (Ahyong et al. 2011), including the terrestrial taxa. Only seven families are known to be parasitic, and these all belong within the suborder Cymothoida (see Brandt and Poore 2003), and all parasitise either fish or crustaceans.

There are a few instances of isopods living symbiotically with other groups, but the trophic nature of the association remains unknown. Some examples include the cirolanid species *Cartetolana integra* (Miers, 1884) (an obligate associate of crinoids; see Bruce 1986a); the cirolanid *Neocirolana hermitensis* (Boone, 1918) (possibly a brood predator of hermit crabs; see Bruce 1994a); the sphaeromatids from *Xynosphaera* Bruce, 1994b (burrows into soft corals; see Bruce 1994b); and the relatively large sphaeromatid genus *Oxinasphaera* Bruce, 1997 (exclusively associated with marine sponges; see Lörz and Bruce 2008).

The oldest parasitic isopod has recently been determined by Nagler et al. (2017). A fossilised isopod reported to be 168 million years old appears to be "deeply nested" within the suborder Cymothoida, and most closely related to Gnathiidae. This is based on morphological characteristics such as the sucking-piercing mouthparts (seen in ectoparasitic isopods) and strongly curved dactyli (used to attach to their hosts).

However, the first isopods named were in 1758 by Carl Linnaeus (Fig. 2.1a) (also known as Carl von Linné after his ennoblement). The tenth edition of his publication *Systema Naturae* (1758) was designated as the starting point for binomial and zoological nomenclature by the International Congress of Zoology. That work included the description of seven isopod species, namely, *Aega psora* (Linnaeus, 1758), *Anilocra physodes* (Linnaeus, 1758), *Asellus aquaticus* (Linnaeus, 1758), *Cymothoa oestrum* (Linnaeus, 1758), *Cymothoa scopulorum* (Linnaeus, 1758), *Oniscus asellus* Linnaeus, 1758 and *Saduria entomon* (Linnaeus, 1758). Four of these species are parasitic: *Aega psora* and *Anilocra physodes* are external attaching parasites, while *Cymothoa oestrum* and *C. scopulorum* are found in the buccal cavity of various fish species. *Cymothoa* Fabricius, 1793, is recognised as the first unequivocally fish parasitic isopod genus.

The first significant contributor after Linnaeus was the English naturalist, William Elford Leach. Leach, who was one of the world's leading crustacean experts at that time and friend to both Cuvier and Lamarck (great naturalists of the time), established the parasitic families Cymothoidae and Gnathiidae. Furthermore, Leach also described 25 genera, eight of which are fish parasitic (six still valid), and 36 species between 1775 and 1818. Sadly, there is reportedly no known portrait of Leach (Harrison and Smith 2008). However, what is arguably the most memorable fact about Leach is his interesting play on the name Caroline/Carolina in nine acronymic isopod genera in 1818: *Anilocra* Leach, 1818; *Canolira* Leach, 1818; *Cirolana* Leach, 1818; *Conilera* Leach, 1818; *Livoneca* Leach, 1818, *Nelocira* Leach, 1818; *Nerocila* Leach, 1818; *Olencira* Leach, 1818; and *Rocinela* Leach, 1818. It is believed that this was in reference to Queen Caroline of Britain (estranged wife of the Prince of Wales) and was a repetitive insult to the woman who was described as an "unlovable adulteress" (see Bruce 1995). Around the same time these cymothoids were being discovered, Constantine Samuel Rafinesque (a French polymath) founded the family Bopyridae.

In 1840, Henri Milne Edwards (Fig. 2.2d) completed the first review of Crustacea from all over the world, including the description of 30 new cymothoid species. Some years later, Danish authors, Jörgen Matthias Christian Schioedte (Fig. 2.2e) and Frederik Vilhelm August Meinert (Fig. 2.2f), produced a series of outstanding monographs from 1879 to 1884 comprehensively revising (on a global scale) the families Aegidae and Cymothoidae (Schioedte and Meinert 1879, 1881, 1883, 1884). These detailed monographs became the foundation for future studies of these parasitic isopods and described an impressive 63 new species (49 of which are still valid).

The "first lady of isopods", Harriet Richardson (Searle) (Fig. 2.2g), was an American carcinologist. In her 22 years of publishing on isopods, she described 58 new genera and 268 new species of isopods, with her best-known work being *A monograph on the isopods of North America* (Richardson 1905). A number of these isopods were from the parasitic families Bopyridae (23 species) and Cymothoidae (22 species). At 40 years old (1914), Richardson gave birth to a handicapped son and spent much of her time thereafter caring for him and only occasionally publishing papers, with her last paper being published in 1926 (Damkaer 2002).

Around the same time, other isopod taxonomists were describing species from the Indo-West Pacific region. Reverend Thomas Roscoe Rede Stebbing (Fig. 2.2h) was a British zoologist, who focused on Crustacea (specifically isopods and amphipods) and described 77 new species of isopods in his 1873–1912 publications. His work included many new genera and reports of these crustaceans from little studied areas, particularly in the Indian Ocean, such as India and South Africa (Stebbing 1910a, b). Edward John Miers (Fig. 2.2i), also a British zoologist and the crustacean curator at the Natural History Museum in London, described 40 new isopod species from 1875 to 1905 mainly from the Indo-Pacific region including Malaysia, Australia, New Zealand and South America (Miers 1876, 1877, 1880).

Another noteworthy contributor was the French naturalist, Théodore André Monod (Fig. 2.3a), a genuine polymath with many different interests. He was also a leading expert on the Sahara and published more than 1200 publications in his 98 years. Of those publications, more than 50 were on isopods. Taking every opportunity to explore and conduct research around the world, he described 5 new genera and 60 new species of isopods and documented isopods from around the world including Australia, France and frequently from various parts of Africa. Monod made major contributions to some families, notably his monumental monograph of the Gnathiidae (Monod 1926) and his influential review of the Cirolanidae (Monod 1930), as well as the first reports on fish parasitic Isopoda from areas such as Vietnam (Monod 1934) and western Africa (Monod 1924, 1931).

The US carcinologist, Thomas Elliot Bowman (Fig. 2.1g), published 163 scientific papers and described 65 new isopod species. His primary interest lay with the isopods, but he also published several papers on copepods. He had a lively personality and a passion for his work that did not stop even after his retirement. Most of Bowman's publications were taxonomic, but he also worked on the ecology and biology of these crustaceans.

Perhaps the greatest contributor to isopod taxonomy in recent decades is the Australian taxonomist, Niel Lucien Bruce (Fig. 2.3b). Bruce has described or redescribed more than 600 species of isopod (381 new species, 56 new genera), covering many different environments and families, in particular the Aegidae, Cirolanidae, Corallanidae, Cymothoidae and Sphaeromatidae. He has more than 180 scientific papers, 6 monographs and 4 edited books and is one of the leading isopod experts on both the free-living and parasitic species. Although most of Bruce's work has focused on Australian species, many of his publications have revised generic concepts and nomenclature and have resolved some of the many problematic taxonomic issues within these families (Bruce 1986b, 1987a, b, c, 1990).

Within the suborder Cymothoida there are two distinct parasitic groups—those parasitising fishes and those parasitising crustaceans. The group parasitising crustaceans (infraorder Epicaridea) include the Bopyroidea and Cryptoniscoidea (see