

# 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.

---

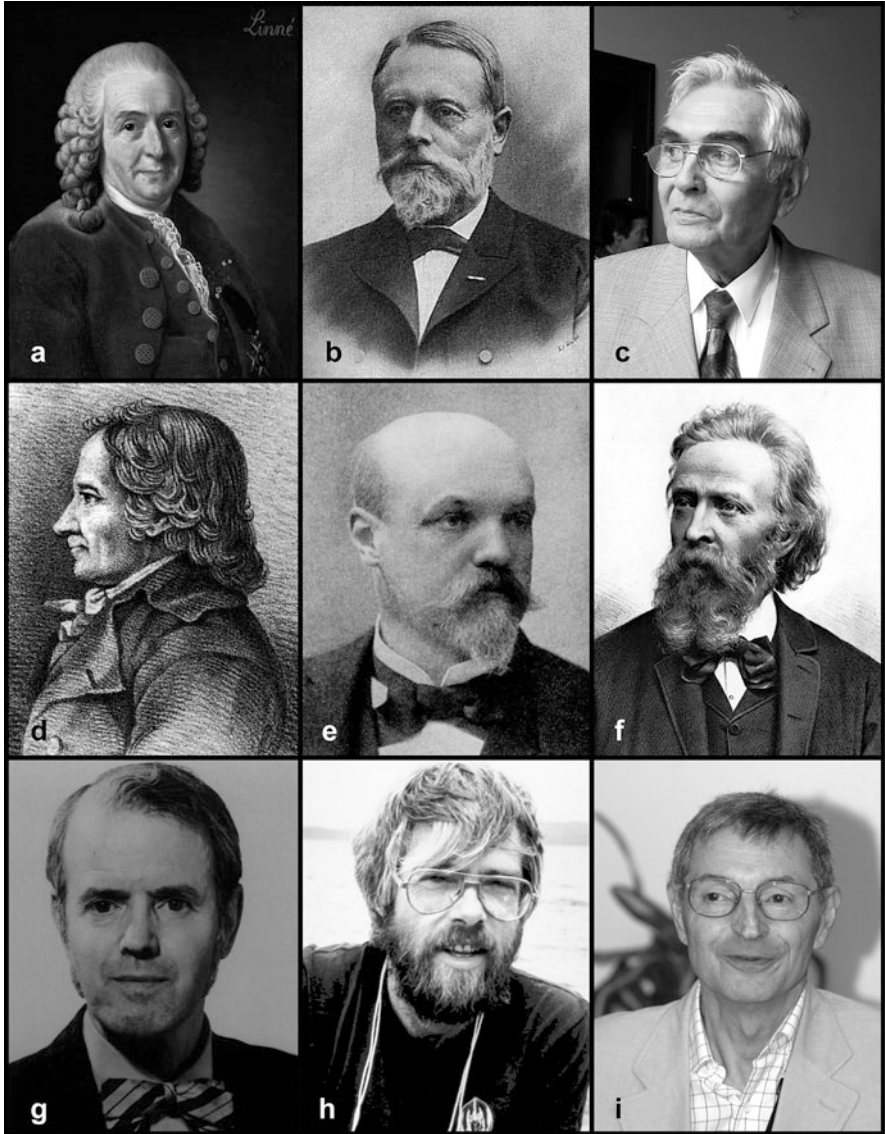
K. A. Hadfield (✉)

Water Research Group, Unit for Environmental Sciences and Management, North-West University, Potchefstroom, South Africa

e-mail: [kerry.malherbe@nwu.ac.za](mailto:kerry.malherbe@nwu.ac.za)

© Springer Nature Switzerland AG 2019

N. J. Smit et al. (eds.), *Parasitic Crustacea*, Zoological Monographs 3,  
[https://doi.org/10.1007/978-3-030-17385-2\\_2](https://doi.org/10.1007/978-3-030-17385-2_2)



**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 Lernaecidae 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 Thaumtopsyllidae 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 Abrisidae Karanovic, 2008
Family Anchimolgidae Humes & Boxshall, 1996
Family Anomoclausidae 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 Intramolidae Marchenkov & Boxshall, 1995
Family Iveidae Tung, Cheng, Lin, Ho, Kuo, Yu & Su, 2014
Family Jasmineiricolidae Boxshall, O'Reilly, Sikorski & Summerfield, 2015
Family Kellieriidae 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 Makrostromtidae 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 Phyllicolidae Delamare Debutteville & 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 Siphonostomatoidea 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 Hyponeoidea Heegaard, 1962
Family Kroyeriidae Kabata, 1979

(continued)

**Table 2.1** (continued)

Family Lernaepodidae Milne-Edwards, 1840
Family Lernanthropidae Kabata, 1979
Family Megapontiidae Heptner, 1968
Family Micropontiidae Gooding, 1957
Family Nanaspidae 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 Rataniiidae 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 Petraridae 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 Akentronida Häfele, 1911

(continued)

**Table 2.1** (continued)

Family Akentrogonida incertae sedis
Family Chthamalphilidae 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 Lernaediscidae 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 Anelasmataidae Gruvel, 1905
Family Koleolepadidae Hiro, 1933
Family Rhizolepadidae Zevina, 1980
Suborder Lepadomorpha Pilsbry, 1916
Family Poecilasmataidae Annandale, 1909
Order Sessilia Lamarck, 1818
Suborder Balanomomorpha 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 Kossmann, 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.

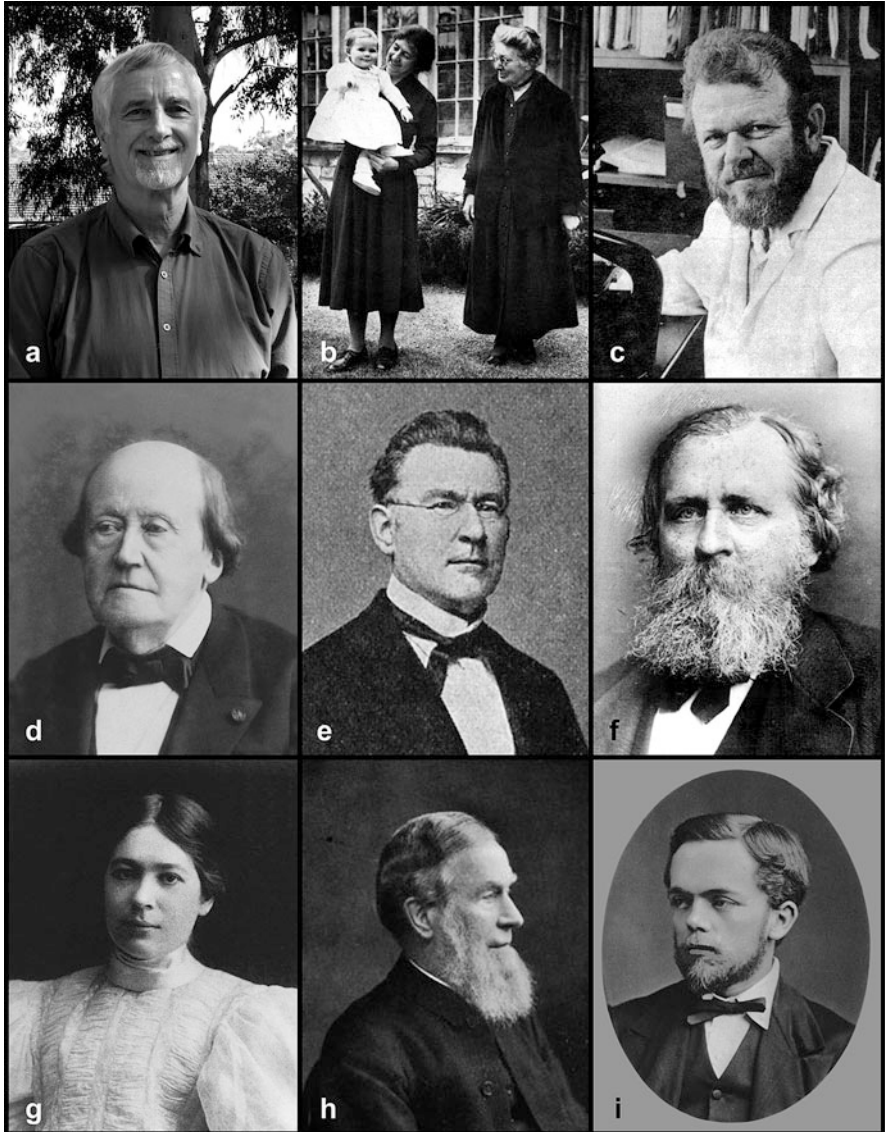
George “Richard” Harbison (Fig. 2.1h) noted that although other researchers had mentioned the parasitic mode of life, little research had been done on the life histories and host specificities of the parasitic amphipods. Using SCUBA to collect live material, Harbison and colleagues were able to observe 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 Cymothoidea (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 cirrolanid species *Cartetolana integra* (Miers, 1884) (an obligate associate of cirrionids; see Bruce 1986a); the cirrolanid *Neocirrolana 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 Cymothoidea, 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, Jørgen 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).

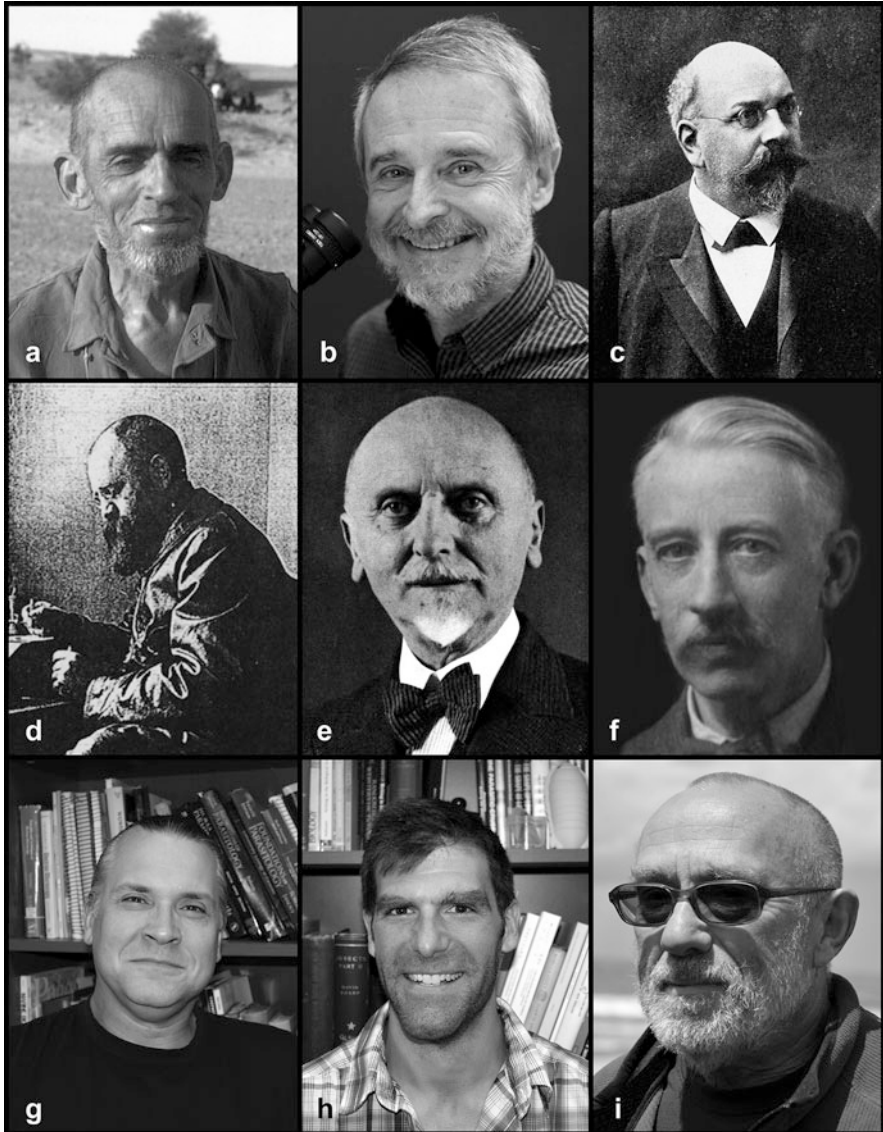
Another noteworthy contributor was the French naturalist, Théodore André Monod (Fig. 2.3a), a genuine polymath with many different interests. He was also a leading expert on the Sahara and published more than 1200 publications in his 98 years. Of those publications, more than 50 were on isopods. Taking 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





**Fig. 2.3** (a) Théodore André Monod, (b) Niel Lucien Bruce, (c) Alfred Mathieu Giard, (d) Jules Bonnier, (e) Hugo Frederik Nierstrasz, (f) Geraldo Abraham Brender à Brandis, (g) Christopher B. Boyko, (h) Jason D. Williams, (i) John C. Markham. Images (a) and (c) © Wikipedia Commons public domain; image (d) from [sm-wimereux.univ-lille1.fr/accueil/historique/index.php](http://sm-wimereux.univ-lille1.fr/accueil/historique/index.php); image (e) from Jordan (1938); image (f) © Streekarchief Gooi en Vechtstreek/gooienvechtstorie.nl

Table 2.1). The Bopyroidea has three families: Bopyridae, Entoniscidae and Ionidae. The Cryptoniscoidea has nine accepted families: Asconiscidae, Cabiropidae, Crinoniscidae, Cryptoniscidae, Cyproniscidae, Dajidae, Entophilidae,

Hemioniscidae and Podaconidae. *Proteolepas bivincta* Darwin, 1854 (from the family Crinoniscidae), was originally thought to be a parasitic barnacle; however, in 1993 William Anderson Newman noted how Darwin had misidentified the isopod's broken attachment limbs as first antennae of the barnacle cyprid.

The second group are the isopods that are temporarily or permanently parasitic on fish. These isopods belong to the superfamily Cymothooidea and include six partly or wholly parasitic families (as well as “micropredators”). They are the families Anuropidae, Aegidae, Barybrotidae, Corallanidae, Cymothoidae, Gnathiidae and Tridentellidae (see Table 2.1).

Dajidae parasitise other crustaceans, usually decapods (Bush et al. 2001; Rohde 2005), and the Entoniscidae are internal parasites that live in the haemocoel of their crab hosts. Some members of the superfamily Cryptoniscoidea are cryptic parasites and hyperparasites of other crustaceans. Cyproniscids and cabiropsids are parasitic on free-living isopods and Podaconidae are parasites of amphipods. In the Cryptoniscidae, genera such as *Danalia* Giard, 1887, and *Liriopsis* Schultze in Müller, 1859, are hyperparasitic on rhizocephalan cirripedes, which parasitise crustaceans such as the false king crab (Peresan and Roccatagliata 2005). Limited information is available on the monogeneric family Tridentellidae, but the mouthparts appear to be well adapted for rasping and piercing into fish host tissues (Bruce 1984). Barybrotidae is a monotypic genus, with the only known species *Barybrotus indus* Schioedte & Meinert, 1879 recorded from the gills of the devil ray *Mobula mobular* (Bonnaterre, 1788) (previously *Mobula diabolus*) (see Moreira and Sadowsky 1978). The Aegidae and Corallanidae are temporary parasites as they often leave the host after their blood meal, but more frequently, these isopods have been classed as free-living micropredators (Brusca 1983; Bruce 1993, 2004, 2009). The three more well-known groups are discussed below in more detail.

### 2.3.1 Bopyridae

Members of this family are parasitic on other crustaceans, especially crabs and shrimps. To date, there are 10 subfamilies, 167 genera, 607 species and 12 subspecies. These parasitic isopods are usually found within the branchial chamber of their hosts causing a noticeable protuberance, but there are several species that attach to the host's abdomen. The first described bopyrid was *Bopyrus squillarum* Latreille, 1802 from the Baltic prawn. This species inhabits the gill chamber of *Palaemon adspersus* Rathke, 1837.

French zoologists, Alfred Mathieu Giard (Fig. 2.3c) and Jules Bonnier (Fig. 2.3d), described 70 epicaridean isopod species together (38 of which were bopyrids). Bonnier proceeded to describe another 31 bopyrid species thereafter, although only six remain valid today. Bonnier started his zoological career after meeting Giard and was his student for nearly 30 years. In his 1900 review of the bopyrids, Bonnier named a species after Giard, *Bopyrina giardi* Bonnier, 1900, but it has since been synonymised with *Bopyrina ocellata* (Czerniavsky, 1868).

Furthermore, the infectious protozoan parasite genus *Giardia* Künstler, 1882, was named in honour of Giard for providing the first description of *Giardia lamblia* (Lambl, 1859) Kofoid & Christiansen, 1915. Sadly, both men passed away in 1908, Giard on his 62nd birthday and Bonnier at 49 years of age from a brain disease he contracted while on a trip in 1904.

Another duo that published 36 genera and 146 nominal isopod species together are Hugo Frederik Nierstrasz (Fig. 2.3e) and Geraldo Abraham Brender à Brandis (90 still valid) (Fig. 2.3f). Of these, 23 genera and 80 species are still valid bopyrid taxa. Nierstrasz was a Dutch zoologist who summarised the isopod knowledge at that time in his contributions to the *Siboga* Expedition (1923–1941), which took place from March 1899 to February 1900 in the Indonesian Archipelago (Nierstrasz and Brender à Brandis 1923; Nierstrasz 1931). Brender à Brandis was a Dutch artist, and it can reasonably be inferred that he was the illustrator for the bopyrid drawings in these joint publications.

Christopher B. Boyko (Fig. 2.3g) (with more than 100 publications) is one of the world leading bopyrid specialists publishing in the present era. Boyko and Jason D. Williams (Fig. 2.3h) (both American researchers) have made valuable contributions on these isopods including a review of the global diversity of the epicarideans (Williams and Boyko 2012). This publication provided a thorough overview of the bopyrids and cryptoniscoids including phylogeny and historic patterns, human-related issues, feeding biology and impacts on the hosts as well as biogeography and biodiversity of these isopods. Furthermore, these authors have detailed the methods for detection, collection and preservation of epicaridean parasitic isopods (Boyko and Williams 2016) and presented a new classification based on a molecular phylogenetic analysis (Boyko et al. 2013).

John C. Markham (Fig. 2.3i) has made substantial contributions to bopyrid knowledge describing 29 genera and 95 species of bopyrids. Other noteworthy publications include the evolution and zoogeography of the bopyrids (Markham 1986), revision of bopyrids from the north-western Atlantic Ocean (Markham 1988), Thailand (Markham 1985) as well as from Hong Kong and southern China (Markham 1982). Jianmei An (Fig. 2.4a) has also provided many valuable contributions on bopyrids. Many of these papers include reviews of the different genera, especially from China, as well as the description of new species (36 species) (An et al. 2009, 2015a, b).

### 2.3.2 Cymothoidae

Cymothoid isopods are obligate parasites of both marine and freshwater fishes that show high variability and consequently have often been misidentified (Smit et al. 2014). These isopods are ectoparasites, found in all oceans but with the greatest diversity in tropical and subtropical waters, feeding on fish host blood or haemolymph and possibly muscle tissue and mucus. There are 369 known cymothoid species in 43 genera. As previously mentioned, the first described parasitic isopods were *Aega psora*, *Anilocra physodes*, *Cymothoa oestrum* and *C. scopulorum*, of which the last three species are valid



**Fig. 2.4** (a) Jianmei An, (b) Vernon Everett Thatcher (on the right), (c) Jean-Paul Trilles, (d) Richard C. Brusca, (e) Ernest H. Williams Jr, (f) Lucy Bunkley-Williams, (g) Nico J. Smit, (h) Kerry A. Hadfield, (i) Gary Poore. Image (b) from Boeger (2011)

cymothoid isopods. The first illustrations of a cymothoid, however, appeared many years later (Desmarest 1825).

Cymothoid research has often been confined to a particular geographical region where a practicing taxonomist was based or where research vessels were sampled.

An example is Vernon Everett Thatcher (Fig. 2.4b), who published on cymothoids from a previously neglected area, South America freshwaters (Thatcher 1991, 2000). Thatcher described 15 new species from the region and produced papers on the mouthpart and pleopod morphology, comparing the morphology of the marine and freshwater cymothoids in some instances (Thatcher 1995, 1997).

Jean-Paul Trilles (Fig. 2.4c), a French parasitologist, has made notable contributions to the Cymothoidae, including many redescriptions and comprehensive taxonomic synonymies. One of the most significant publications on cymothoids is his *Prodromus*, an extensive catalogue of the cymothoids that provided an invaluable resource for subsequent workers on this family (Trilles 1994). Several other publications were on museum holdings as well as the description of new cymothoid species (see Trilles 1972, 1977, 2008).

The invertebrate zoologist, Richard C. Brusca (Fig. 2.4d), published the first modern review and influential monograph of the Cymothoidae of the Eastern Pacific (Brusca 1981). This monograph included information on cymothoid morphology, taxonomy, history, zoogeography, phylogeny and the first hypothesis of the evolution of these parasites. It was published in the cladistic phylogeny era of Crustacea, and provided the foundation for all future work in this field, where it is still the point of comparison for all modern phylogenies. Brusca has published over 160 articles and 13 books including the largest-selling text on invertebrate zoology *Invertebrates*, co-authored with his brother Gary Brusca. Some of his other noteworthy works include field guides of isopods from Costa Rica (Brusca and Iverson 1985) and the phylogenetic analysis and classification of isopods (Brusca and Wilson 1991).

Ernest (Bert) H. Williams Jr (Fig. 2.4e) and Lucy Bunkley-Williams (Fig. 2.4f) (a husband and wife team from Puerto Rico) have made significant contributions to knowledge of the Cymothoidae from the Caribbean, Japan and Thailand. This couple described 27 new species, corrected many errors in literature, and provided several noteworthy ecological notes for these isopods (Williams et al. 1982; Williams and Bunkley Williams 1986, 2000; Bunkley-Williams and Williams 1998). Other contributors to the biodiversity and taxonomy of cymothoids include V. V. Avdeev (a Russian researcher) who described 15 cymothoid species, Pieter Bleeker (a Dutch medical doctor, ichthyologist and herpetologist) who described 13 species, and N. Krishna Pillai (an Indian carcinologist) who described nine cymothoid species.

Recently, Nico J. Smit (Fig. 2.4g), Niel L. Bruce (Fig. 2.3b) and Kerry A. Hadfield (Fig. 2.4h) reviewed the global diversity of the cymothoids (Smit et al. 2014). Within this review, they included historic, biogeographic, systematic, taxonomic, reproductive and ecological information for these isopods. These three authors have also completed a number of taxonomic revisions of several genera from southern Africa (Hadfield et al. 2010, 2013, 2014, 2015; Hadfield and Smit 2017), including the description of several new species. Trilles (1994) mentioned there was a lack of information from the Southern Hemisphere, and specifically South Africa and South America, and these papers aimed at addressing this knowledge gap. Furthermore, these authors produced a publication on revising poorly known type material to minimise potential future misidentifications within one of the more complicated genera, *Ceratothoa* Dana, 1852 (Hadfield et al. 2016).

### 2.3.3 *Gnathiidae*

Gnathiids differ from the other isopods in having only five functional pairs of legs, and only their larval stages are parasitic. The first recognisable drawing of a gnathiid was made by a Dutch zoologist, Slabber (1769), who drew a larval form and was uncertain as to which family the strange isopod belonged. The first adult male, *Gnathia maxillaris* (Montagu, 1804) (described as *Cancer maxillaris*), was described a few decades later by Montagu, who then went on to describe the first gnathiid larva found feeding on a fish host (Montagu 1804, 1813). Due to the unique appearance of this isopod, Leach (1814) established a new genus, *Gnathia* Leach, 1814. However, there was plenty of confusion regarding the appearance of three very different life forms (the adults, the swollen praniza larvae and the smaller zuphea larvae), which led researchers to believe that they were separate species (Risso 1816; Bate 1858). It was by accident that Hesse (1864) established the link between the different forms while keeping a praniza in water to sketch when it moulted into an adult. Forty years later, the first life cycle of a gnathiid, *Gnathia maxillaris*, was described by Smith (1904). This was the first account of the different life stages and development of these isopods, and Smith was able to observe that the adult stages do not feed.

There are currently 226 gnathiid species, in 12 different genera. Australian researchers, Brian Cohen and Gary Poore (Fig. 2.4i), described 30 of these species as part of a thorough review of gnathiid phylogeny and biogeography (Cohen and Poore 1994). Ten years later, Nico Smit (Fig. 2.4g) and Angela Davies-Russell (Fig. 2.5a) assembled a complete review of these gnathiid isopods summarising all of the morphology, life stages, behaviour and pathology up to this point (Smit and Davies 2004). These two authors also confirmed that gnathiids can act as vectors of fish blood parasites such as *Haemogregarina bigemina* Laveran & Mesnil, 1901 (see Chap. 7; Davies and Smit 2001).

Brian Kensley (Fig. 2.5b, g), posthumously, along with Marilyn Schotte (Fig. 2.5g) and Gary Poore (Figs. 2.4i and 2.5g), published descriptions of 12 new gnathiid species from the Indian Ocean (Kensley et al. 2009). Kensley (a zoologist born in South Africa) was a researcher at the Smithsonian National Museum of Natural History, specialising in systematics of isopods (and decapods), and has at least 20 species named after him. He published more than 150 crustacean-related articles in his lifetime as well as several field guides, including a guide to the Caribbean (Kensley and Schotte 1989) and South African (Kensley 1978) marine isopods and had many collaborations with other isopodologists (Fig. 2.5g).

Recent research on gnathiids from Japan has been published by Yuzo Ota and Katsuhiko Tanaka (from Japan), and Jörundur Svavarsson (from Iceland) worked on gnathiid ecology and taxonomy as well as deep-sea isopods. Several other ecological studies have also been completed on these small parasitic isopods. Their role in cleaning symbiosis has been studied by Lexa Grutter (Australia) (see Grutter 1996, 2003) as well as molecular studies to link juveniles to their adult counterparts and so identify the species (Grutter et al. 2000). Most of the current publications on gnathiid



**Fig. 2.5** (a) Angela Davies-Russell, (b) Brian Kensley, (c) Henry de Lacaze-Duthiers, (d) Hans Olof Brattström, (e) Mark Joseph Grygier, (f) Jens Thorvald Høeg, (g) isopod experts: Marilyn Schotte, Niel Bruce, Gary Poore, Wendy Moore (Brusca), Richard (Rick) Brusca and Brian Kensley (taken in 1997). Image (b) from Schotte (2005); image (c) © Wikipedia Commons public domain; image (d) obtained from Hans G. Hansson at [www.bemon.lovén.gu.se/petymol.b.html](http://www.bemon.lovén.gu.se/petymol.b.html); image (g) © Richard Brusca

ecology and behaviour (especially on coral reefs) are being investigated by Paul Sikkell (from Arkansas State University, USA) and colleagues (see Chap. 10). This research team is focusing on the role of these parasites in the marine food webs, their habitat associations, and their effect on the host fishes.

## 2.4 Ascothoracida

Superclass Multicrustacea Regier, Shultz, Zwick, Hussey, Ball, Wetzer, Martin & Cunningham, 2010

Subclass Thecostraca Gruvel, 1905

Infraclass Ascothoracida Lacaze-Duthiers, 1880

Ascothoracids are marine ecto- and meso-parasites, occurring in shallow intertidal habitats as well as the deep sea. They are diverse in morphology, biology and host range, and both the juvenile and adults are parasitic on echinoderms (excluding regular urchins and sea cucumbers) and cnidarians (e.g. corals, gorgonians, zoanthids) (Grygier and Høeg 2005). Ascothoracida is one of the three infraclasses of Thecostraca and Kentrogonida (see Table 2.1) and has approximately 107 known species in 6 families and 23 genera (Ahyong et al. 2011).

The French biologist, Henry de Lacaze-Duthiers (Fig. 2.5c) (who was an assistant to Henri Milne Edwards), described the first ascothoracid species as *Laura gerardiae* Lacaze-Duthiers, 1865. This species parasitises the gold coral, *Savalia savaglia* (Bertoloni, 1819), from Tunisia and Algeria (Lacaze-Duthiers 1865, 1883).

Although the first described, *Laura gerardiae* is not the most studied ascothoracid species. *Ulophysema oeresundense* Brattström, 1936, described by the Swedish zoologist Hans Olof Brattström (Fig. 2.5d), is one of the best researched ascothoracids. Brattström, who founded the journal *Sarsia* (named after the Norwegian natural scientists M. Sars and G.O. Sars), became an expert in ascothoracids following his PhD thesis research on echinoderms. He described the genus *Ulophysema* Brattström, 1936, and named five ascothoracid species. Furthermore, Brattström provided detailed reviews of the ecology, life cycle, morphology and larval development of *U. oeresundense* (Brattström 1936, 1947, 1948a, b). Shortly thereafter, Melander (1950) completed studies on the chromosomes of *U. oeresundense*, and the species was used in numerous reviews and comparisons with other species. As this parasite is found enclosed in different organs of irregular sea urchins (most often in the genital glands or perivisceral cavity), the ultrastructure of its integument was also studied by Bresciani and Jespersen (1985).

In 1976, Vladimir Lvovich Wagin produced a valuable monograph on the Ascothoracida (in Russian), including documentation of all the information known on these parasites up to that point (Wagin 1976). Most of the information gathered was from Russian articles that were largely inaccessible to the western world at that time. Only nine genera were listed in the infraclass in the 1970s; thereafter, research on the group was focused on taxonomy, with majority of the new genera and species



being described in the 1980s. However, since 2000, only one new ascothoracid species has been recorded, *Gorgonolaureus helenae* Kolbasov, 2004.

Most of the earlier studies on ascothoracids were primarily taxonomic and morphologically based; however, information regarding their ecology and life stages was also available in several publications. The adult stages of these parasites are striking and have distinguishing characteristics for easier species identification; however, the larval forms often need to be reared into adults in a laboratory before they can be identified. Studies on the larval stages became important, especially with the use of a scanning electron microscope (SEM) as utilised by Itô and Grygier (1990) on *Baccalaureus falsiramus* (Itô and Grygier 1990). Later Grygier (1992) reported on rearing larvae and their development, and most recently, Kolbasov et al. (2008a) thoroughly studied the external morphology of the first and second a-cyprid larvae.

In the last few years, research on these ascothoracid parasites has slowed down; however, there are still key players continuing in this field. Mark Joseph Grygier (Fig. 2.5e), an American based in Japan, is currently one of the world's leading experts on Ascothoracida and one of the most prolific authors on this group. Grygier has described 10 new ascothoracid genera as well as 51 new species (almost half of the known species in the infraclass). Grygier (1981) reviewed the sperm of *Dendrogaster* Knipovich, 1890, and determined that it was the most primitive sperm discovered in Crustacea (Grygier 1981). Two years later, he separated the crinoid-infecting *Waginella* Grygier, 1983, from *Synagoga* Norman, 1888, which disrupted the subordinal classification suggested by Wagin, which was based on the phylum of the host (Grygier 1983). The classification of the Ascothoracida was then updated by Grygier (1987), who divided the group into two orders and six families. A few years later Grygier (1996) completed a rare demographic study on a deep-sea parasite *Parascothorax synagogooides* Wagin, 1964, parasitising the brittlestar *Ophiophthalmus normani* (Lyman, 1879) (see Grygier 1991), and in 1996, he published a comprehensive account of the Ascothoracida (Grygier 1996).

Current research on the Ascothoracida focuses on the phylogenetic relationships within the group and in relation to the other Thecostraca taxa. Jens Thorvald Høeg (Fig. 2.5f), a professor at the University of Copenhagen, and colleagues recently studied the evolution of parasitic Thecostraca and supported Ascothoracida as a monophyletic taxon with high confidence. The taxon sampling in this infraclass is still limited according to Pérez-Losada et al. (2009) and the classification could once again change after more research. Other studies have included the evolution of morphology and ecology of the Thecostraca (Høeg et al. 2009) and support that Ascothoracida and Cirripedia are the sister groups to Facetotecta (Pérez-Losada et al. 2009).

## 2.5 Cirripedia

Superclass Multicrustacea Regier, Shultz, Zwick, Hussey, Ball, Wetzer, Martin & Cunningham, 2010

Subclass Thecostraca Gruvel, 1905

Infraclass Cirripedia Burmeister, 1834

Barnacles are amongst the most economically important marine crustaceans, renowned for fouling ship hulls and marine structures. They are sessile as adults, with motile larval stages, and in intertidal rocky shores form the recognisable “barnacle zone”. Barnacles are known to be both parasites and commensals (occurring in sponges as well as on corals, whales, etc.) and can act as castrating parasites of crabs (family Sacculinidae).

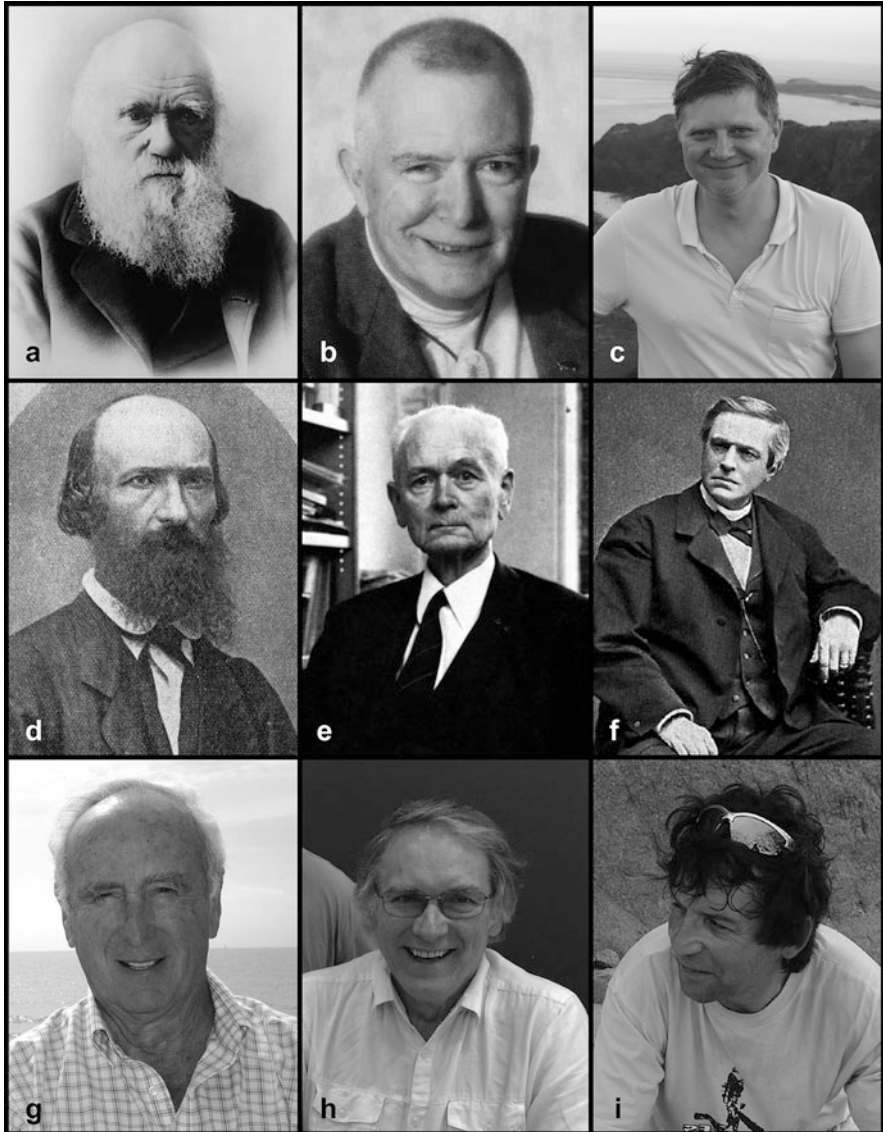
### 2.5.1 *Acrothoracica*

This superorder of barnacles is only partially parasitic. These tiny barnacles, called burrowing barnacles, burrow into calcareous substrates such as mollusc and thoracican barnacle shells. Within the family Trypetesidae, there are two genera, *Tomlinsonia* Turquier, 1985 (with two known species), and *Trypetesa* Norman, 1903 (five known species), which are found exclusively inhabiting the shells of hermit crabs (Williams et al. 2011).

*Trypetesa lampas* (Hancock, 1849) was the first burrowing barnacle described, with Hancock discovering it in the shells of gastropods that were inhabited by hermit crabs (Hancock 1849). Charles Darwin (Fig. 2.6a) noticed it was very similar to *Cryptophialus* Darwin, 1854 but placed into *Alcippe* Hancock, 1849 (now *Trypetesa* Norman, 1903) (see Darwin 1854). In 1872, Noll placed both *Alcippe* and *Cryptophialus* into Darwin’s order Abdominalia. In 1905, Gruvel realised that the cirri on the terminal body segments thought to be abdominal appendages (hence the order’s name) was in fact from the thorax, so the order was changed to Acrothoracica. Around the same time, Norman (1903) changed the genus name from *Alcippe* to *Trypetesa*, as the former name was preoccupied (homonym) by birds in the family Pellorneidae.

Jack Tomlinson (Fig. 2.6b), who was recognised as one of the world authorities of this group, revised the burrowing barnacles known at that time, including information on all of the different systems, taxonomy and ecology (Tomlinson 1969, 1987). More recently there have been many studies on the larvae as well as phylogeny and systematics of this group by Gregory Kolbasov (Fig. 2.6c) and colleagues (Kolbasov 2002, 2009; Kolbasov et al. 2014), as well as the phylogenetic relationships of the different barnacle orders (Lin et al. 2016). However, the data on the ecology of these barnacles, especially on the Trypetesidae, are scanty.

In 2011, the first publication of egg predation by a burrowing barnacle was recorded (Williams et al. 2011). *Trypetesa lampas*, removed from ovigerous female hosts, were found to contain hermit crab eggs, chorions, as well as yolk in their gut. There is still uncertainty surrounding how these barnacles feed, but this research documented how they can have significant negative effects on hermit crab reproduction. Other studies have showed blue-green algae-like particles in the gut of *Trypetesa lampas* (see Kamens 1981), and it may be that barnacles in male hermit crabs filter feed on particles from the water, whereas barnacles in females feed on the hermit crab eggs (Williams et al. 2011). Murphy and Williams (2013) verified this



**Fig. 2.6** (a) Charles Darwin, (b) Jack T. Tomlinson, (c) Gregory Kolbasov, (d) Johann Friedrich Theodor (Fritz) Müller, (e) Hilbrand Boschma, (f) Sven Ludvig Lovén, (g) William Anderson Newman, (h) Geoffrey Allan Boxshall, (i) Rony Huys. Images (a), (d), (e) and (f) © Wikipedia Commons public domain; image (b) from public obituary at [www.oakdaleleader.com/obituaries/jack-tomlinson](http://www.oakdaleleader.com/obituaries/jack-tomlinson)

study and suggested that the more accurate term for these barnacles may be “transient parasites” as they can be harmful in some cases but cause no harmful impact in other cases. Larsen et al. (2016) added that the barnacles do not rely on the egg

predation to any substantial degree and found much of the data they collected on prevalence, load, reproductive cycles, and host relationships differed from previous studies. This highlighted the fact that there is still a lot of work to be done on these barnacles before we fully understand their ecology.

## 2.5.2 *Rhizocephala*

This order contains the obligate parasites and was first discovered by Cavolini (1787) but only grouped together as Rhizocephala by the German zoologist, Johann Friedrich Theodor (Fritz) Müller (Fig. 2.6d) in 1862 (Müller 1862). They are endoparasites of other crustaceans, especially decapods. Currently there are 2 orders, 11 families, 41 genera and 288 species known. The adult females have lost most of the traits usually associated with Crustacea and are also known to influence the morphology and biology of their hosts which sets them apart from other groups. These adult female parasitic barnacles consist of an “externa” (an external sac-like body for reproduction) and an “interna” (a root-like body inside the host for nutrient uptake), with the male inside the female externa, joined by a small stalk (Høeg 1995; Høeg and Lützen 1995). Many rhizocephalans are known to cause parasitic sterilisation or castration of their crustacean hosts. Depending on the species, these parasites can lower reproductive outputs, cause eggs to die within a few days or completely inhibit gonad processes required for reproduction (Høeg 1995). Along with the degeneration of the gonads, rhizocephalans can also cause feminisation of male hosts. This may include testes converting to ovaries, changes in the overall shape and size of the hosts and possibly even changing the behaviour of the host (Høeg 1995).

Rhizocephalans are divided into two orders: Akentrogonida and Kentrogonida (see Table 2.1). Whereas all kentrogonids exhibit similar characteristics (including the presence of the specialised female post-settlement stage, the kentrogon, as well as the equivalent male stage, the trichogon), all of the akentrogonids do not have similar characteristics other than the absence of the kentrogon (Walker 2001). Within the Kentrogonida is the family Sacculinidae, which is one of the more renowned groups of parasites due to their ability to cause parasitic sterilisation in crabs. The genus *Sacculina* Thompson, 1836, holds the majority of the rhizocephalan species with approximately 129 known species. The first described species was *Sacculina carcini* Thompson, 1836, making it one of the most studied barnacle parasites.

Hilbrand Boschma (Fig. 2.6e), a former director of the Rijksmuseum van Natuurlijke Historie (Naturalis), Leiden, Netherlands, had a particular interest in rhizocephalans. Boschma (and colleagues) described half of the currently recognised rhizocephalan species (2 families, 8 genera and 144 species). Most of these species are in the genus *Sacculina*, with 98 of the 128 known species named by Boschma. Some of his more substantial publications were on rhizocephalans from the North

Atlantic (Boschma 1928), from the British Museum collections (Boschma 1933), as well as notes and new species from Sacculinidae (Boschma 1937, 1950, 1955).

Jens Thorvald Høeg (Fig. 2.5f) has also added numerous contributions on the ecology of these parasites. In 1991, Høeg reviewed the sexual system of the rhizocephalans and a year later added ultrastructure information regarding their morphology (Høeg 1992). He also completed taxonomic and phylogenetic studies with colleagues round the same time (Høeg and Rybakov 1992; Høeg and Lützen 1993), as well as revised the biology and life cycle of these barnacles (Høeg 1995).

Other contributors to this group include Olga Korn and colleagues, from the Russian Academy of Sciences, Moscow, who have published several papers on the larval development and ecology of the rhizocephalans (Kas'yanov et al. 1997; Korn et al. 2000; Kashenko et al. 2002) as well as reproductive studies on several species (Korn 1985, 1989; Korn et al. 2004). Bo Øksnebjerg, in his review of the Mediterranean and Black Sea rhizocephalans, provided a thorough summary of available information on the biology, ecology, biogeography and taxonomy of these parasites, including information for each of the 25 species known from the region at that time (Øksnebjerg 2000). Henrik Glenner, from the University of Bergen, has published many papers on barnacles and related crustacean groups too, most relating to the evolution and phylogenetic relationships of the parasitic barnacles (Glenner and Hebsgaard 2006; Glenner et al. 2010).

As rhizocephalans affect the reproductive systems of their hosts, it was proposed that these parasites could possibly aid in biological control of invasive host species. Murphy and Goggin (2000) analysed the genetic discrimination of sacculinid parasites to determine if they could control invasive European green crabs that have had a negative effect on the softshell clam fisheries in North America. Unfortunately, the parasite is not host specific, and it could spread if it were introduced as a control agent (Murphy and Goggin 2000). This was put to the test by Goddard et al. (2005). Four native North American crab species were infected with the European green crab's natural parasite, *Sacculina carcini* Thompson, 1836. Although the parasite preferred the green crab, there were still a significant number of native crabs infected (all without producing a reproductive sac) which would result in the loss of many indigenous species.

Using both molecular and morphological techniques in classifying these parasitic barnacles has recently resulted in some interesting findings. A new genus, *Polyascus* Glenner, Lützen & Takahashi, 2003, was described after analyses on ten *Sacculina* species showed three asexually reproducing species formed a monophyletic clade and failed to support a monophyletic *Sacculina* clade (Glenner et al. 2003). Furthermore, in a different study using both techniques again, three species of *Sacculina* were found on a single host in a single locality for the first time (Tsuchida et al. 2006). Recent information on the phylogeny (using morphological characters and molecular data), from Høeg and Glenner and colleagues, can be seen in Chap. 9.

### 2.5.3 *Thoracica*

Thoracican barnacles are what most people would recognise as a barnacle. They are acorn or stalked (goose-neck) barnacles, and almost 1000 species are known worldwide. Many are symbionts on corals and sponges, with others associated with molluscs, sea snakes, turtles, whales and crustaceans (Ross and Newman 1967). Whale and turtle barnacles, which live on the skin of several whale and turtle species, appear to be parasitic but do not absorb nutrients from the hosts themselves and are considered commensals (Frick et al. 2011). Only two genera were originally thought to be parasitic, namely, the monotypic genus *Anelasma* Darwin, 1851, comprising *Anelasma squalicola* (Lovén, 1844), and *Rhizolepas* Day, 1939 (with two species, *R. annelidicola* Day, 1939, and *R. gurjanovae* Zevina, 1968). However, after recent publications, more genera have been recognised as parasitic.

*Anelasma squalicola* parasitises deep-water lantern sharks of the family Etmopteridae (Long and Waggoner 1993). Although this species was described many decades ago, it has rarely been studied. It was first noted by Gunnerus (1763) on the velvet belly lantern shark, *Etmopterus spinax* (Linnaeus, 1758), but he did not name or adequately describe it. This paper was largely overlooked by researchers, and only a decade later did the Swedish marine zoologist Sven Ludvig Lovén (Fig. 2.6f) (1844) formally describe it as “*Alepas squalicola*”. Shortly thereafter, Charles Darwin (Fig. 2.6a) realised in his monographic review of barnacles (Darwin 1851) that the species was in the wrong genus and assigned it to his new genus, *Anelasma*. Recently, the feeding strategy of this species was analysed to determine if the barnacle is purely parasitic or is still capable of using suspension feeding to obtain nutrition (Ommundsen et al. 2016). The authors concluded that the barnacle uses the host exclusively as a food source using a *de novo* evolved feeding mechanism. Other noteworthy publications on *A. squalicola* include the phylogenetic analysis of these barnacles (Rees et al. 2014), as well as studies that it causes retarded growth in the shark reproductive organs (Yano and Musick 2000).

The other thoracican barnacle genus, *Rhizolepas*, parasitises polychaetes. The first species of the genus was *R. annelidicola* originally described from South Africa by John Hemsworth Day on the scale-worm, *Laetmonice producta* Grube, 1876. It does not have an open mouth or anus, oral appendages or digestive diverticula and undoubtedly obtains its food from the host via its extensive root system (Day 1939).

In 1969, Arnold Ross and William Anderson Newman (Fig. 2.6g) detailed information on a coral-eating barnacle, *Hoekia monticulariae* (Gray, 1831) from a then monotypic genus (with updated information in Ross and Newman 1995). This species was found to feed on coral tissue and differs from *Anelasma* and *Rhizolepas* in having modified the basic feeding mechanism rather than using a separate absorptive process (root system), making it the only sessile barnacle to be wholly parasitic (Ross and Newman 1969, 1995; Frick et al. 2011). There seems to be host specificity in this group of parasites as only *Hydnophora* Fischer von Waldheim, 1807, corals are infected (Ross and Newman 2000).

Another barnacle recently recognised as parasitic is *Koleolepas avis* (Hiro, 1931). This species, from the monotypic family Koleolepadidae, feeds actively on the sea anemone's tentacles (Yusa and Yamato 1999). It lives with these anemones (usually from the genus *Calliactis* Verrill, 1869) that are attached to the gastropod shells inhabited by hermit crabs (usually from the genus *Dardanus* Paulson, 1875) (Yusa et al. 2001; Hosie 2014).

The Microlepadidae are also known to live on diademateid echinoids (sea urchins). First described in 1907, *Microlepas diadema* Hoek, 1907, was studied after Paulus Peronius Cato Hoek observed a specimen on the end of a club-shaped spine on the hat-pin sea urchin in Indonesia (Hoek 1907). No other species were described until 1991 when Mark Grygier (Fig. 2.5e) and William Anderson Newman (Fig. 2.6g) added another genus and two new species to this group of parasites (Grygier and Newman 1991). Although their method of feeding has not been thoroughly studied, these barnacles cause detrimental effects to their host. Grignard and Jangoux (1994) concluded that the barnacles inhibited the growth of the urchin spine upon which it attaches. The thoracopods are not used for filter-feeding, and it is unlikely that they scavenge, so it is possible that much of their food is obtained from host tissue (Grygier and Newman 1991).

Lastly, the symbiotic genus *Octolasmis* Gray, 1825 is reported to cause damage to its decapod hosts (such as the blue crab *Callinectes sapidus* Rathbun, 1896). The first species, *Octolasmis warwicki* Gray, 1825, was described in 1825 by John Edward Gray. These parasites are found in large numbers and infect the gill chambers where they are attached to the lamellae of their host (Voris et al. 2000). Due to the high number of parasites, the gas exchange of the hosts can also be affected, with heavily infested hosts dying in extreme cases (Gannon and Wheatly 1992).

## 2.6 Tantulocarida

Superclass Multicrustacea Regier, Shultz, Zwick, Hussey, Ball, Wetzer, Martin & Cunningham, 2010

Subclass Tantulocarida Boxshall & Lincoln, 1983

Tantulocaridans are micro-crustaceans that infest several marine crustacean hosts including amphipods, copepods, cumaceans, isopods, ostracods and tanaids as ectoparasitic larvae (Boxshall and Vader 1993). They are often found attached to the external surfaces of these hosts and can occur in all depths and temperatures in the marine waters. These minute parasites are the smallest of the parasitic Crustacea with size ranges between 80 and 400  $\mu\text{m}$  (Kolbasov et al. 2008b).

Although originally discovered by Jules Bonnier (Fig. 2.3d) in 1903, these parasites were misidentified for many years (as copepods and isopods). In 1975, Becker described a new parasitic crustacean genus infesting copepods off the coast of Peru. This parasite, *Basipodella harpacticola* Becker, 1975, was incorrectly placed into the subclass Copepoda. In 1980, *Deoterthron* Bradford & Hewitt,

1980, was discovered parasitising ostracods in New Zealand (Bradford and Hewitt 1980). Bradford and Hewitt (1980) noticed that the two genera were closely related but considered them to belong with the Cirripedia rather than the Copepoda. Grygier (1983) noted that although he agreed these species belonged in the then “Maxillopoda” (now Oligostraca and Multicrustacea), they did not fit in either the Copepoda or Cirripedia. In resolving this uncertainty, Geoffrey Allan Boxshall (Fig. 2.6h) and Roger J. Lincoln (1983) proposed a new class, Tantulocarida, with the two genera *Basipodella* Becker, 1975 and *Deoterthron*, distinct but of similar rank to the Cirripedia and Copepoda.

Although this group of tiny parasites gained attention from 1975, Boxshall and Lincoln (1987) studied the description of a parasite named *Cumoniscus kruppi* Bonnier, 1903 (originally classified as an epicaridean isopod) which they then added to the Tantulocarida making it the first described tantulocaridan species. This species was unable to be classified to family level due to the lack of information on other life stages; however, Huys et al. (1993) rectified this after discovering a tantalus larva on a small male cumacean (the only species to be found on a cumacean up to that point).

Following the formation of this new class, many new tantulocaridan genera and species have been described. Many genera are monotypic, and this subclass has 5 families (see Table 2.1), 23 genera and 36 known species (Ahyong et al. 2011) although, due to their tiny size, many more are thought to occur but have not been discovered yet. Geoffrey Allan Boxshall (Fig. 2.6h) has made a noteworthy contribution to this tantulocaridan taxonomy, being involved in the description of three families, three genera and ten species.

Boxshall and Rony Huys (Fig. 2.6i) have published on various aspects of the dual life cycle (Boxshall and Lincoln 1987; Huys 1991; Huys et al. 1993), with Gregory Kolbasov (Fig. 2.6c) and colleagues adding information on the external morphology of the different life stages (Kolbasov et al. 2008b). Recent studies focus more on the phylogeny of the group and suggest that the Deoterthridae and Basipodellidae are possibly paraphyletic or polyphyletic which could change the number of families in the future (Kolbasov et al. 2008b; Savchenko and Kolbasov 2009; Petrunina et al. 2013). However, more studies are still required in all aspects of this group as there are still many unknowns (most likely due to their small size).

## 2.7 Copepoda

Superclass Multicrustacea Regier, Shultz, Zwick, Hussey, Ball, Wetzer, Martin & Cunningham, 2010

Subclass Copepoda Milne-Edwards, 1840

Copepods (“oar-footed”) are one of the most abundant crustacean taxa, so named after the pair of swimming legs that move together like the oars on a sculling ship. They are known to be free-living, symbiotic (or “associates”) and parasitic. Those



that are parasitic are known to infect a large range of hosts (almost every phylum), from sponges and echinoderms to fish and mammals. Parasitic copepods are usually found on the external surfaces of their hosts, often sheltered in microhabitats such as the gills, nostrils, mantle cavities and genital folds, but there are some that are endoparasites, occurring in the muscles, digestive tracts and body cavities of their hosts (Huys and Boxshall 1991).

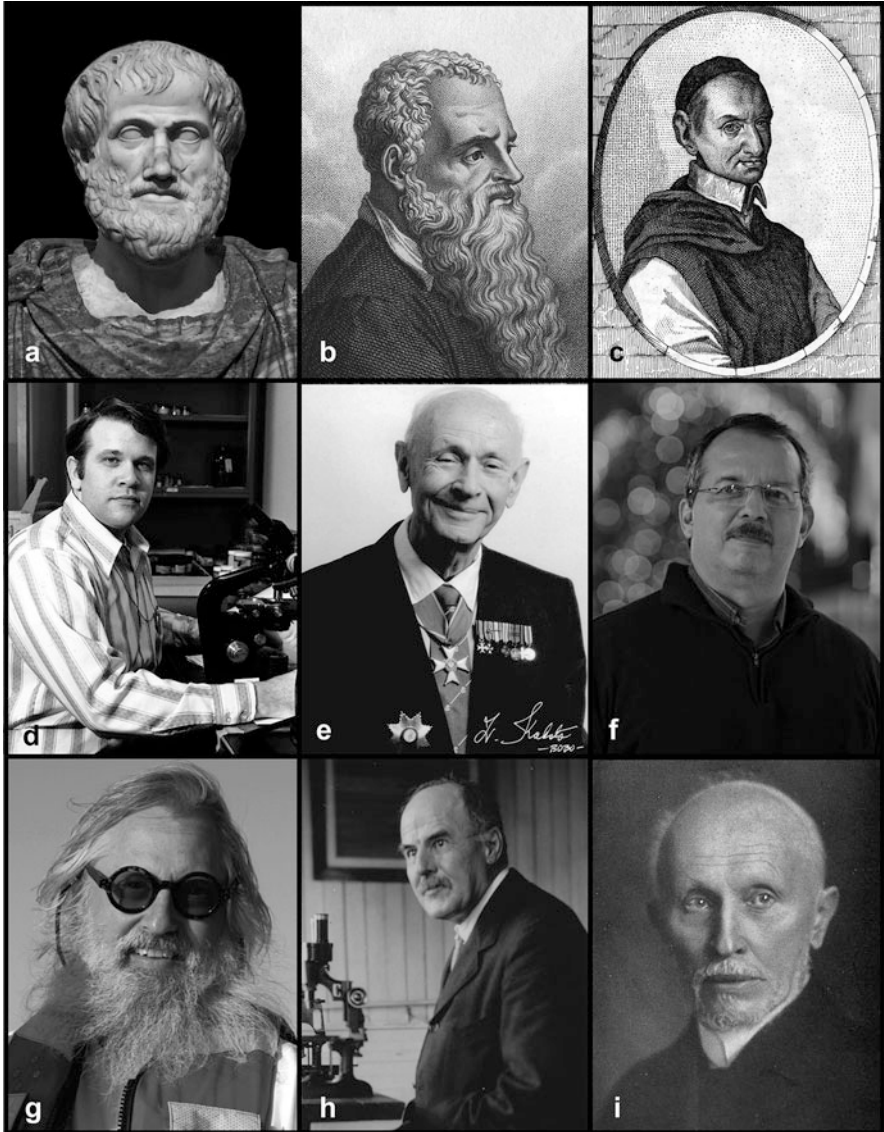
The Greek philosopher Aristotle (Fig. 2.7a) is considered to be the first person to take note of a copepod. In his book, *History of Animals* (350 BC), he mentions how the tuna and swordfish are infected with a parasite which was nicknamed the “gadfly”. It looked like a “grub” and was found next to the fins, resembling a scorpion in shape, and the size of a spider. Over the years, various researchers have pondered on what parasite is referred to in this text, possibly isopods or branchiurans; however, based on the descriptive traits given, it is believed to be a copepod (Damkaer 2002). Aristotle also mentioned “sea lice” found on the red mullet, devoid of blood and with a flat tail, and that most likely refers to branchiurans.

It was centuries later when the first drawing of a copepod appeared. Guillaume Rondelet (Fig. 2.7b) (a medical physician and zoologist) illustrated a fish parasite along with its tuna host, with the parasite attached near the pectoral fin (Rondelet 1554). The information confirmed Aristotle’s observations on the tuna, and two names were proposed: *Oestrus* (the marine “horsefly”) and *Asilus* (the marine “gadfly”). This particular species is believed to be the large and easily noticeable species, *Brachiella thynni* Cuvier, 1830 (see Kabata 1979).

In 1671, Paolo Silvio Boccone (Fig. 2.7c) noticed a copepod (which he referred to as a leech “sangsue”) from a swordfish that was “tormented by a flea”. It was apparently the size of a pea and attached firmly to the host (Boccone 1671). This most probably referred to the symbiotic barnacle known to occur on these hosts. Over the years, several other pedunculate barnacles have been recorded associated with copepods, but the copepods seem unaffected by the barnacles (Williams 1978; Benz 1984).

Although the free-living copepods were ranked with other crustaceans from an early stage, the parasitic forms appeared to be a lot more problematic. Many early scientists placed these parasites with molluscs or worms, and it was only in 1819 when Jacques Simon Amand Suriray recognised them as “caligids and neighbouring genera” and noticed the early development of young hatching from the egg “filaments” (Suriray 1819).

In what is undoubtedly the most extensive review of the early contributions to copepodology, *The Copepodologist’s Cabinet*, by David M. Damkaer (Fig. 2.7d), is a compilation of early copepod history and the 90 researchers whose work contributed to the advancement of copepod knowledge from 350 BC to 1832 (Damkaer 2002). It includes detailed information on the copepodologists, with historic portraits and illustrations, and a thorough history of discovery for the copepods. This was the first of a projected three volumes in the series, with the second detailing the research up to the nineteenth century (currently in production), with an overlap of the third publication which will include the Golden Age of Copepodology and conclude with research completed up to approximately 1950 (Damkaer 2002).



**Fig. 2.7** (a) Aristotle [marble portrait bust, Roman copy (second century BC) of a Greek original (c. 330 BC)], (b) Guillaume Rondelet, (c) Paolo Silvio Boccone, (d) David M Damkaer, (e) Zbigniew 'Bob' Kabata, (f) Eduardo Suárez-Morales, (g) George William Benz, (h) Charles Branch Wilson, (i) Johannes Thiele. Images (a), (c) and (i) © Wikipedia Commons public domain; image (b) from Mian et al. (2014); image (e) from Benz and Goater (2015); image (g) from Bullard (2016); image (h) from History of the Marine Biological Laboratory at <https://history.archives.mbl.edu/archives/topics/people/gallery>

Another significant contributor to copepod taxonomy was Zbigniew “Bob” Kabata (Fig. 2.7e). Kabata was a world-renowned fish parasitologist and one of the pioneers of research into fish parasitology and diseases. He was born in Poland, and his fascination with marine science began while working as a deckhand on a North Sea trawler out of Aberdeen. Kabata became internationally recognised as the world’s copepod expert with 159 publications (including his books *Parasitic Copepoda of British Fishes* and *Parasites and Diseases of Fish Cultured in the Tropics*) (Kabata 1979, 1985) describing 20 new genera and more than 100 new species. His work on this group has been acknowledged by other researchers in this field through patronymy of 22 taxa, the most memorable of which must be the copepod genus and species *Bobkabata kabatabobbus* Hogans & Benz, 1990.

Currently, two of the most recognised names in copepodology are Geoffrey Allan Boxshall (Fig. 2.6h) and Rony Huys (Fig. 2.6i) (British and Belgian zoologists respectively) from the Natural History Museum, London. Both researchers have made noteworthy contributions to other parasitic crustacean groups, but their copepod publications have formed the foundation for many of the subsequent studies in this group and have established themselves as world leading authorities on copepods (Huys and Boxshall 1991; Boxshall and Halsey 2004; Huys 2009). Boxshall has been involved in the naming of 338 taxa (of which 317 are still valid). Those copepod taxa that are in use include a new infraclass, a new order, 16 families, a subfamily, 67 genera and 231 species. Likewise, Huys has named 334 taxa of which 308 are still valid, including a new infraclass, a new order, 16 families and 2 subfamilies, 128 genera, 2 subgenera, 157 species and a subspecies. In fact, both of these copepodologists have named genera after each other in honour of their extraordinary work in this group of crustaceans, namely, *Boxshallia* Huys, 1988, and *Huysia* Jaume, Boxshall & Iliffe, 1998.

### 2.7.1 Cyclopoida

Cyclopoids have an abdomen that is narrower than the thorax, and the first antenna is of intermediate length (only half the length of the body). The first two cyclopoids were described by Carl Linnaeus (Fig. 2.1a), namely, *Cyclops quadricornis quadricornis* (Linnaeus, 1758) and *Lernaea cyprinacea* Linnaeus, 1758. *Cyclops* Müller, 1785, is one of the most common freshwater copepod genera with approximately 200 valid species. It belongs to the family Cyclopidae, which is the largest cyclopoid family with over 1100 valid species. Members of this family are predominantly free-living; however, several species are intermediate hosts for numerous pathogenic human and fish parasites such as Guinea worm (*Dracunculus medinensis* (Linnaeus, 1758)), as well as cestodes (tapeworms) and nematodes (round worms) (Piasecki et al. 2004). Recently, *Eucyclops bathanalicola* Boxshall & Strong, 2006 was described from Lake Tanganyika in a rare occurrence of a freshwater copepod parasitic on an invertebrate host (mantle cavity of *Bathania straeleni* Leloup,

1953). This association is also noteworthy as it also represents a unique account of a parasite in what is primarily a free-living family (Boxshall and Strong 2006).

The second cyclopoid species discovered by Linnaeus belongs to the genus *Lernaea* Linnaeus, 1758, a widely known genus of freshwater fish parasites, commonly referred to as anchor worms. *Lernaea cyprinacea* was originally described from Europe in 1745 under a trinomial name but was then redescribed by Linnaeus in 1758 (see Kabata 1979). Anchor worms burrow into the skin of its host fish and can cause a disease called lernaecosis where haemorrhagic ulcers occur at the attachment site. Death of the host can occur due to secondary infections and severe bleeding (Khalifa and Post 1976; Kabata 1985). This species has been recorded worldwide and is thought to have been spread through the movement of aquarium species (Innal and Oldewage 2012). The family Lernaeidae is probably one of the most studied cyclopoid groups due to its importance in aquaculture. *Lernaea* spp. have been reported to cause mass mortalities as early as 1880. According to Kocylowski and Miączyński (1960), lernaecosis almost demolished an entire population of crucian carp in the Masurian Lake District (Poland) in 1880. An interesting case of catfish mortality due to gill damage (including epithelial hyperplasia, telangiectasis and haemorrhage) caused by *Lernaea cyprinacea* was also noted in Arkansas by Goodwin (1999). Bighead carp in the same tanks, with approximately the same number of copepods externally, did not die. Fish mortalities due to gill damage from *Lernaea* copepodids had never been reported before. This was most likely due to the polyculturing of the catfish with the bighead carp (an excellent host for *Lernaea*) and the filter-feeding apparatus of the carp preventing large infestations on their gill filaments.

### 2.7.2 *Harpacticoida*

This order includes mainly free-living copepods, although there are some symbiotic and parasitic species. One genus, *Balaenophilus* Aurivillius, 1879 (with three species), known to occur on the external surfaces of turtles, whales and manatees, appears to be both epibionts and parasites. Kazunari Ogawa and colleagues recorded the first copepod on a sea turtle and noticed the turtle's skin inside the gut, which led the authors to the conclusion that the copepods feed on the turtle and not algae or diatoms (Ogawa et al. 1997). According to Badillo et al. (2007), there was definite evidence of *Balaenophilus* ingesting whale and sea turtle host tissue; however, the extent of this on the host is unknown. Mild signs of a tissue reaction was also observed in turtles with large numbers of copepods present at one time (>500). However, when Suárez-Morales et al. (2010) confirmed the presence of these copepods on manatees, they could not see any effect on the hosts. Healthy skin was observed at the site of attachment when *Balaenophilus manatorum* (Ortíz, Lalana & Torres, 1992) was removed, and no difference was seen in their reproduction or behaviour. Thus, their status as parasites remains unclear at this point.

The family Tisbidae contains free-living and symbiotic copepods as well as parasitic copepods. The parasitic species (many from the subfamily Cholidiinae)

are usually found in the gills or on the external surfaces of octopuses (Humes and Voight 1997; Avdeev 2010). Juvenile *Genesis vulcanoctopusi* López-González, Bresciani & Huys, 2000, however, were located within the connective tissue of the octopod integument, indicating the possibility that these parasites may have both endo- and ectoparasitic phases (López-González et al. 2000). The first species described from this family was *Tisbe furcata* (Baird, 1837). Arthur Grover Humes listed specimens labelled as *T. furcata* from the mantle of *Ocnus planci* (Brandt, 1835), a sea cucumber (see Humes 1980); however, the identification was by Monticelli in 1892 and is doubtful. Massy (1909) first reported a copepod on a deep-sea octopus that was later described by Farran (1914) as *Cholidya polypi* Farran, 1914 (see Humes and Voight 1997).

### 2.7.3 *Monstrilloida*

Monstrilloids are only parasitic in the postnaupliar and preadult stages, with adults being free-swimming and non-feeding zooplankters. The endoparasitic forms are known to occur in polychaetes, molluscs and other invertebrates (Davis 1984; Huys et al. 2007). According to Mexican marine biologist and researcher, Eduardo Suárez-Morales (Fig. 2.7f) (2011), the first reported monstrilloid was from a Norwegian fjord in 1842 (Krøyer 1842). A single preadult specimen of *Monstrilla typica* (Krøyer, 1849) (originally named *Thaumatoessa typica* in the 1842 publication) was illustrated by Krøyer but without any description. This description was only provided in 1849 (with a slight alteration to the original name), along with the diagnosis of a new genus (Krøyer 1849). The monstrilloid naupliar stage was first described by Giesbrecht (1893), shortly followed by the drawings and descriptions of the nauplius and development of the endoparasites of *Haemocera* by Malaquin (1901). In 1994, Grygier re-examined the “*Thaumatoessa (Thaumaleus) typica*” type specimen in order to determine its identity and moved it into the genus *Monstrilla* Dana, 1849. Shortly thereafter, Grygier (1995) published an annotated chronological bibliography of the Monstrilloida.

Within this order, only one family, Monstrillidae, is recognised. Until recently, eight genera were considered valid, but Mark Joseph Grygier (Fig. 2.5e) and Susumu Ohtsuka (2008) briefly revised the status of each genus and determined only three should retain their validity, with the other five all being synonymised into the genus *Monstrilla*. They then proceeded to add an additional genus, *Maemonstrilla* Grygier & Ohtsuka, 2008. Six years later, Suárez-Morales and McKinnon (2014) added another genus *Australomonstrillopsis* Suárez-Morales & McKinnon, 2014, giving a current total of five accepted genera.

Most of the species within Monstrilloida have been described by Eduardo Suárez-Morales (Fig. 2.7f) and colleagues (75 valid taxa), including a single genus, 73 species and 1 subspecies. The systematic position of this order however is still unclear. According to Huys et al. (2007), Monstrilloida fall within a fish parasitic clade of the Siphonostomatoida, sharing a common ancestor with caligiform families. However,

this is considered unconfirmed by some researchers, and more information is required before any definitive changes in classification can be made (Suárez-Morales 2011). The original status of the Monstrilloida therefore remains as is at this stage (Suárez-Morales and McKinnon 2014).

#### 2.7.4 *Poecilostomatoida*

Most poecilostomatoid copepods are ectoparasites, attaching to the external surfaces or the gills of their hosts (fish or other invertebrates); however, there are several endoparasitic species that live within the body of their hosts too. The first described species for this order was the ectoparasite *Lernentoma asellina* (Linnaeus, 1758), an uncommon parasite found in the gills of gurnards from the family Triglidae. This copepod is from the family Chondracanthidae that was revised by Ju-shey Ho, from California State University, Long Beach. Ho's work on symbiotic copepods has exceeded 257 publications on these crustaceans from around the world. In 1970 and 1971, Ho revised the Chondracanthidae (when it still was in the order Cyclopoida) in order to clarify the confusion surrounding these crustacean's identification, re-examining and redescribing every specimen and verifying its identity. At the time, only 30 genera were known; however, there are now 51 known genera in this family containing 193 species and 4 subspecies. Recently, Østergaard et al. (2003) used phylogenetic analyses to determine the phylogeny within the family, which clarified some of the questions regarding past and present subfamilies of Chondracanthidae.

The Splanchnotrophidae is a small but interesting family of copepods which parasitise opisthobranch gastropods (including nudibranchs and pteropods) (Huys 2001). They are usually deeply embedded inside their host with only the distal urosome and egg sacs visible (Uyeno and Nagasawa 2012). Currently, there are 6 genera and 31 species within the family. The first two described species were *Lomanotocola brevipes* (Hancock & Norman, 1863) and *Splanchnotrophus gracilis* Hancock & Norman, 1863.

Another family, Ergasilidae, comprises fish parasitic copepods, where only the females are parasitic. Most species are found in freshwater and most attach to the host gills. There are 29 genera, 261 species and 2 subspecies presently regarded as valid species in this family. The first genus to be described was *Ergasilus* von Nordmann, 1832, with two species, *Ergasilus gibbus* Nordmann, 1832, and *Ergasilus sieboldi* Nordmann, 1832. *Ergasilus sieboldi* attaches to the gill filaments using its second antennae and can cause tissue damage or secondary infections at the site of attachment. The nutrition of *E. sieboldi* was noted by Einszporn (1965a, b), and it is known to cause severe fish losses in aquaculture (see Piasecki et al. 2004). Over the years, several researchers mentioned different life stages of *E. sieboldi*, but there were many discrepancies between the different reports as they were often not complete studies on the life cycle. In 1991, Abdelhalim et al. (1991) were able to provide complete information on all of the different life stages for this species.

The family Taeniacanthidae has 21 genera with 121 species. These copepods are parasitic on marine fishes and sea urchins. The first species of taeniacanthid described was *Tucca impressus* Krøyer, 1837, an ectoparasite on porcupinefish and pufferfish. Morphologically Taeniacanthidae are closely related to Bomolochida and were previously placed within that family until 1911 when Wilson separated the taeniacanthids and the bomolochids (Wilson 1911). However, it was only in 1932 when Wilson elevated both of these groups to family level, removing them from Ergasilidae. Dojiri and Cressey (1987) revised the family and, including new species descriptions, keys to all genera, host-parasite lists, distribution, morphology, ecology as well as notes on the relationships between the closely related Bomolochidae, Taeniacanthidae and Tuccidae.

### 2.7.5 *Siphonostomatoida*

This order of copepods contains approximately 75% of the fish parasitic copepods. Most are found in marine waters and are recognised by the siphon-like mouth tube containing stylet-like mandibles to attach and feed from their hosts. The first three species described from this order were *Pennella filosa* (Linnaeus, 1758), *P. sagitta* (Linnaeus, 1758) and *Salmincola salmoneus* (Linnaeus, 1758).

Some of the more noticeable siphonostomatoids are commonly referred to as sea lice. These copepods are from the family Caligidae. The first recognised species in this family was *Lepeophtheirus pectoralis* (Müller, 1776), followed shortly thereafter by *Caligus curtus* Müller, 1785. Currently there are approximately 508 known species in this family in 30 genera. These parasites are of particular concern due to their impact on certain commercially important fish species, such as farmed and wild Atlantic salmon. In fact, *Caligus rogercresseyi* Boxshall & Bravo, 2000, has been recognised as the most pathogenic ectoparasite of farmed salmon in Chile and is also a potential vector for the transmission of the infectious salmon anaemia (ISA) virus (Oelckers et al. 2014; also see Chap. 7).

The family Lernaepodidae is another ecological and economically important group of fish parasites. Most females have large, fleshy bodies that attach to the host via a small chitinous plug called a bulla. The bulla is inserted into the epidermis of the host and held by the maxillary arms (Boxshall 2005). To date there are 48 genera, 334 species and 12 subspecies in the family. *Salmincola salmoneus* (Linnaeus, 1758) was the first lernaepodid species described and is commonly referred to as a gill maggot. Gill maggots from the genus *Salmincola* Wilson, 1915, can occur in large numbers and cause significant mortalities in aquaculture facilities (Sutherland and Wittrock 1985), but they are less abundant in wild populations and have a smaller impact (Amundsen et al. 1997).

Members of the family Eudactylinidae are mostly parasitic on the gills of elasmobranchs (although some genera are found on teleost fishes such as *Heterocladius* Deets & Ho, 1988, and *Jusheyus* Deets & Benz, 1987). There are 12 genera and 57 species known in this family. The earliest record of a species from

this family is the subspecies *Nemesis lamna lamna* Risso, 1826. Damage caused by *Nemesis* species include tissue erosion due to the rasping feeding of the copepod, swollen and pale areas at the site of attachment, thickening of respiratory epithelium, as well as the prevention of water flow between secondary lamellae (Benz 1980; Benz and Adamson 1990).

George William Benz (Fig. 2.7g), in his doctoral thesis, discussed the evolutionary biology of siphonostomatoids that are parasitic on vertebrates based on the 18 families fitting this criterion (Benz 1993). Benz went on to publish numerous articles on these copepods, including the description of a new family, 5 new genera and 17 species. Benz was both a student and close colleague of Kabata, and it seems fitting that his final publication before he passed away in 2015 was a memorial tribute paying homage to his mentor and friend (Benz and Goater 2015).

## 2.8 Branchiura

Superclass Oligostraca Zrzavý, Hypša & Vlášková, 1998

Class Ichthyostraca Zrzavý, Hypša & Vlášková, 1998

Subclass Branchiura Thorell, 1864

These parasitic Crustacea, often referred to as “fish lice”, are small flattened ectoparasites of fish. Occasionally these parasites can occur on other hosts such as alligators (Ringuet 1943), salamanders (Poly 2003) and tadpoles (Stuhlmann 1891; Wolfe et al. 2001). They all belong to the order Arguloidea and family Argulidae with four recognised genera, *Argulus* Müller, 1785; *Chonopeltis* Thiele, 1900; *Dipteropeltis* Calman, 1912; and *Dolops* Audouin, 1837 (see Table 2.1). Approximately 168 species are known worldwide (Ahyong et al. 2011), and only *Argulus* occurs in marine environments, the other genera being exclusively freshwater parasites. William J. Poly summarised the global diversity of all branchiurans in freshwater and highlighted the current distribution of each of the different genera in the different biogeographic regions of the world (Poly 2008). A year later, Ole Sten Møller reviewed the history and taxonomy of this group, giving a chronological account of each group’s history from previously inaccessible literature (Møller 2009). This publication provides valuable information on the Branchiura systematics and morphology and is a helpful aid for any researcher working on these parasites. Recently, Neethling and Avenant-Oldewage (2016) compiled an extensive review of the Branchiura. This compendium features a full overview of the four genera, stating the characteristics and taxonomic changes for each genus, as well as the geographical distributions and host records for each species, and is a comprehensive synopsis of literature on these parasites up to this point.

The phylogenetic position of the branchiurans has been complicated with many different theories and misinterpretations of certain characters that were used to define this unique group (especially with the second maxilla). These parasites were first termed Branchiura (or gill-tails) by Thorell (1864), based on the importance of the



“tail” morphology, but had been previously placed within the siphonostome Copepoda by Heller (1857) and Krøyer (1863). The idea that the Branchiura were more closely linked to the Branchiopoda (“Phyllopoda” in Thorell, 1864) was not widely accepted, and in 1875, Claus reaffirmed that the Branchiura were more closely related to the copepods. Claus (1875) suggested placing the group as a suborder within the Copepoda and Leydig (1889) concurred. In 1902, when Charles Branch Wilson (Fig. 2.7h) revised the parasitic copepods of the family Argulidae, these branchiurans were still viewed as copepods. This extensive review covered 29 species of *Argulus*, 9 species of *Dolops* and 1 species of *Chonopeltis* (Wilson 1902). Finally, Johannes Thiele (Fig. 2.7i) studied the cephalic appendages of the Branchiura and concluded these parasites were not in fact copepods as commonly thought (with no first maxilla in the mouth cone) and should rather be on a level equal to the copepods and phyllopods (Thiele 1904). However, even after this breakthrough, the classification remained unchanged. Almost 30 years later, Martin (1932) completed an in-depth study on the mouth cone and once again suggested Branchiura as a subclass, but it took another 10 years before this new classification was eventually acknowledged in another publication (Ringuelet 1943). Since then (with a few exceptions), the Branchiura and Copepoda have been considered separate groups.

### 2.8.1 *Argulus*

The first branchiuran species described was *Argulus foliaceus* (Linnaeus, 1758) (originally named *Monoculus foliaceus*), although Branchiura are thought to be mentioned as early as tenth century China. According to Piasecki and Avenant-Oldewage (2008), a monk named (Kao) Tsan-ning mentioned how goldfish that eat bark from poplar trees will not breed “lice”, and this was most likely referring to an *Argulus* species (Møller 2009). Wilson (1902) had originally stated that fish lice were first mentioned by a fisherman from Strasbourg, Léonard Baldner, in 1666. Baldner apparently described and pictured the birds, fishes and aquatic animals of the neighbourhood and specifically mentioned “Pou des poissons” (fish louse).

*Argulus* is the most specious genus of the family Argulidae, with approximately 127 species, and is widely distributed around the world. The genus was named in recognition of the numerous ommatidia in the compound eyes (diminutive of the mythical Greek beast, *Argus*, which had a hundred eyes) (Wilson 1902). The majority of the earlier studies focused on the first *Argulus* species, *A. foliaceus*. The nervous and genital systems as well as other microscopic anatomy of *A. foliaceus* were described by Leydig (1850, 1889), with studies on the larval development initiated by Claus (1875). Wilson (1902, 1904a, b) continued the larval and hatching research, with additional data added on the genital system and the circulatory system. Wilson also covered the taxonomic studies of North American *Argulus* (Wilson 1916, 1920a, b, 1921, 1923, 1924), some of which were revised by Meehan (1940). Wilson (1944) admired some of the new data provided by Meehan,

especially the key to the genus, but disagreed with the taxonomic species revisions calling it a “serious encroachment upon the genus”. The taxonomy and identification keys of African *Argulus* species were completed by Cunnington (1913), Monod (1928), Fryer (1956, 1959, 1961a, b, 1965a, b, 1968) and Rushton-Mellor (1994a, b, c), while the South American species were covered by Brian (1947) and Ringuelet (1943, 1948).

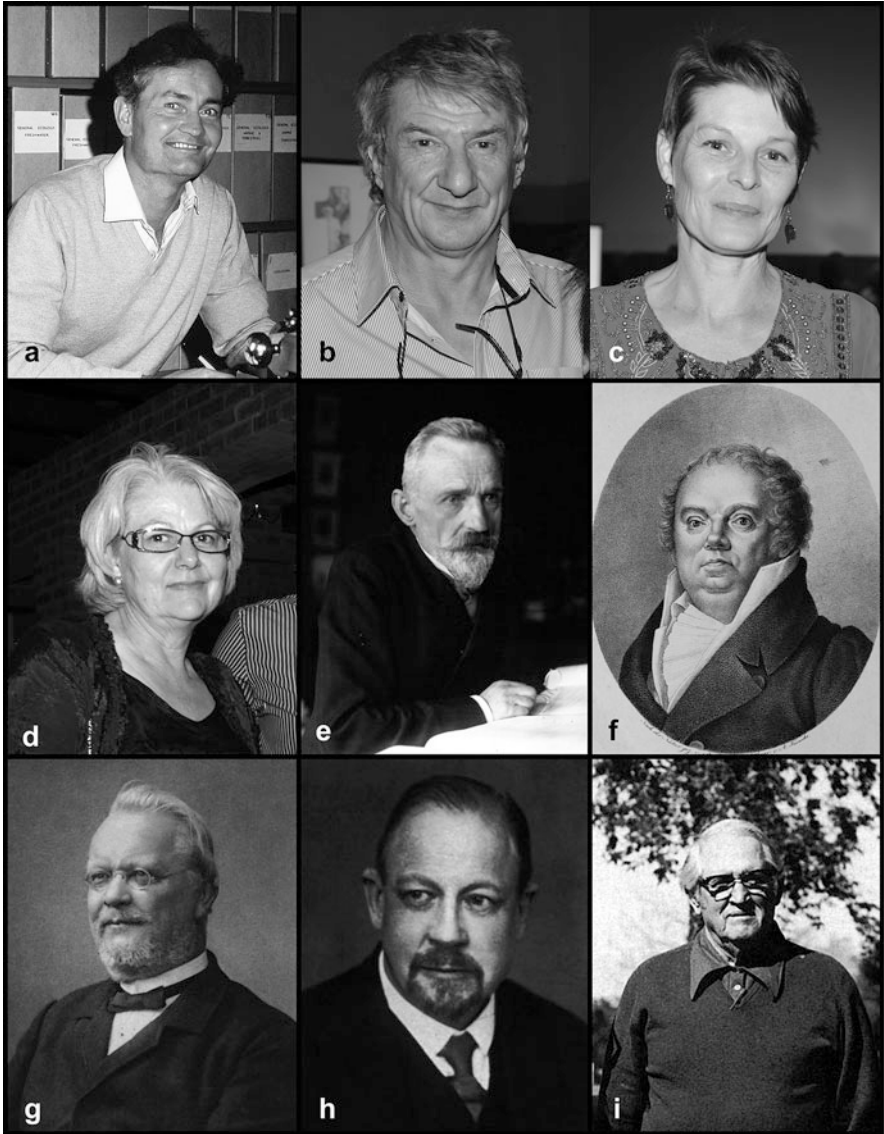
More recently, research has focused on histology and ultrastructure analysis of various *Argulus* structures and how they relate to the ecology of these parasites. Tam and Avenant-Oldewage (2006) used gut ultrastructure to determine that the first larval stage uses yolk, and not blood, as the primary source of nutrition. Three years later, Tam and Avenant-Oldewage (2009) also used the digestive cell ultrastructure to determine that the elaborate enteral diverticula are part of the anterior midgut, and not similar to the midgut glands seen in other Crustacea.

## 2.8.2 *Chonopeltis*

This genus is endemic to sub-Saharan Africa and currently has 13 valid species. The first species described was *Chonopeltis inermis* Thiele, 1900 from Lake Rukwa. The genus is named in reference to the “cone- or funnel-shaped shield” (Møller 2009). Other than three publications (Wilson 1902; Thiele 1904; Monod 1928), almost 40 years passed from when the genus was established to new data being published on it (Brian 1940).

Probably one of the main contributors to our knowledge on this genus is Geoffrey Fryer (Fig. 2.8a). Fryer recognised three different species from the single variant species, *C. inermis* var. *schoutedeni* described by Brian (1940). One species was established as *C. schoutedeni* Brian, 1940, while the other two species were described by Fryer as new to science (*C. congicus* Fryer, 1959, and *C. flaccifrons* Fryer, 1960a). This discovery made him the authority of more than half of the *Chonopeltis* species known at the time (Fryer 1959, 1960a). Furthermore, Fryer completed noteworthy ecological studies on this genus, noting for the first time that the adults are sedentary (Fryer 1956), and there is a lack of cephalic lobe rods in *C. flaccifrons* (see Fryer 1960a). Fryer went on to describe several more species, produce a key for the genus and show the difference between *Chonopeltis* and the already known *Argulus* and *Dolops* larvae with the lack of metanauplius or juvenile-like morphology in the first descriptions of the *Chonopeltis* larval stages (Fryer 1964, 1974, 1977).

The majority of the more recent species descriptions and distributions have been by South African researchers, Jo and Liesl van As (another husband and wife team) (Fig. 2.8b, c) (van As 1986, 1992; van As and van As 1993, 1996, 1999a, b) as well as Annemarië Avenant-Oldewage (Fig. 2.8d) (Avenant-Oldewage 1991; Avenant-Oldewage and Knight 1994, 2008). Additionally, van As and van As (1996) provided the first SEM image of the *Chonopeltis* larva; and Avenant-Oldewage and colleagues used histology to elucidate the morphology of the digestive system



**Fig. 2.8** (a) Geoffrey Fryer, (b) Jo van As, (c) Liesl van As, (d) Annemarië Avenant-Oldewage, (e) Eugène Louis Bouvier, (f) Karl Asmund Rudolphi, (g) Karl Georg Friedrich Rudolf Leuckart, (h) Richard Heymons, (i) John Teague Self. Images (a), (e), (f) and (g) © Wikipedia Commons public domain; image (h) from Röhlig et al. (2010); image (i) from Janovy (1996)

(Swanepoel and Avenant-Oldewage 1993; Avenant-Oldewage et al. 1994). In 2017, Van As et al. revised the southern African species of *Chonopeltis* and found that contrary to earlier theories, each river system does not have its own species of *Chonopeltis*. After careful examination of all *C. meridionalis* Fryer, 1964; *C. victori* Avenant-Oldewage, 1991; and *C. koki* Van As, 1992, material, it was concluded that all are indeed the same species, *C. meridionalis*, and occur in multiple river systems but only on cyprinid hosts (Van As et al. 2017).

### 2.8.3 *Dipteropeltis*

Until recently, *Dipteropeltis* was a monotypic genus, with the sole species being *Dipteropeltis hirundo* Calman, 1912, described by William Thomas Calman (a Scottish zoologist). However, recently Neethling et al. (2014) described a second species, *Dipteropeltis campanaformis* Neethling, Malta & Avenant-Oldewage, 2014, from Brazil. This genus is only known from South America and is the only branchiuran genus endemic to that region. These parasites infect piranhas (Carvalho et al. 2003) and can sometimes occur in certain areas with a prevalence as high as 73% (Mamani et al. 2004). As *Dipteropeltis* species have not been collected very often, and studies on members of this genus are very limited, information on other life stages, development and ecology is scanty.

### 2.8.4 *Dolops*

All but 2 of the 13 known *Dolops* species are known from South America. *Dolops ranarum* (Stuhlmann, 1891) and *D. tasmanianus* Fryer, 1969 are known from sub-Saharan Africa and Tasmania (Australia), respectively, making this genus widespread but confined to the southern hemisphere. The first *Dolops* was noticed by the French entomologist Jean Victoire Audouin (1837) who thought the specimens looked like *Argulus* but without the suction discs. The meaning of the generic name is uncertain but has a Greek mythology origin. Unaware of the naming of *Dolops*, Heller described *Gyropeltis* Heller, 1857, which was based on the South American species. Although it was described after Audouin, Heller's description contained detailed drawings and notes not seen in the publication by Audouin. Due to this, some authors used *Gyropeltis* rather than *Dolops* (see Krøyer 1863; Thorell 1864). Only 33 years later (and 60 years after describing *Dolops*) did Bouvier (1897) use the correct genus name and explain how, even if it seems less informative, *Dolops* was sufficiently described by Audouin and is the accepted authority for the genus.

Most of the information on the South American *Dolops* stems from the work of the French carcinologist Eugène Louis Bouvier (1897, 1898, 1899a, b) (Fig. 2.8e). New species and keys have been published over the years, but there is much that is

still unknown about these parasites. Ringulet (1943, 1948) provided a key to the South American *Dolops* species. Weibezahn and Cobo (1964) described species from Venezuela, while José Celso de Oliveira Malta and colleagues (Malta 1982; Malta and Varella 1983) described species from the Brazilian Amazon. Recent publications from this area focus on the development of young as well as combined host-parasite interactions (Gomes and Malta 2002; Carvalho et al. 2003; Mamani et al. 2004).

Fryer also studied the sperm transfer of several *Dolops* species (Fryer 1958, 1960b, 1969), described a new species from Tasmania (Fryer 1969) and made observations on the distribution of the species in this genus (Fryer 1969). Interestingly, most of the information known about *Dolops* has been completed on a single species from South Africa, *Dolops ranarum*. The major contributors to this knowledge are Annemarië Avenant-Oldewage (Fig. 2.8d) and colleagues. These contributions include a complete redescription of the species (Avenant et al. 1989a), second published drawing of a *Dolops* larva (Avenant et al. 1989b), digestive system morphology (Avenant-Oldewage and Van As 1990), as well as the feeding behaviour and effect on its host fish (Avenant-Oldewage 1994).

## 2.9 Pentastomatida

Superclass Oligostraca Zrzavý, Hypša & Vlášková, 1998

Class Ichthyostraca Zrzavý, Hypša & Vlášková, 1998

Subclass Pentastomida Diesing, 1836

Pentastomes are obligate vermiform parasites and are commonly referred to as “tongue worms” due to the resemblance of some species to a vertebrate tongue. The adult parasites have two pairs of retractile hooks on either side of the mouth, creating a grouping of five anterior appendages from which the group’s name is derived (“five mouths”, although only one is an actual mouth). They are often found in the upper and lower respiratory tracts of vertebrates (birds, reptiles, amphibians, mammals and even humans) where they lay eggs (Paré 2008). These eggs are excreted out via the digestive system of the definitive host and then ingested by an intermediate host (most often a fish or small herbivorous mammal).

The French veterinarian Philibert Chabert (1787) noticed the first tongue worm inside the nasal cavities of horses and dogs. However, the first species, *Linguatula serrata* Frölich, 1789, was only named 2 years later, from the lung of a hare. This species is one of the most synonymised pentastomes with 13 junior synonyms. The Swedish-born “father of helminthology”, Karl Asmund Rudolphi (Fig. 2.8f), recognised that these worms were different to others and placed them into a single group, the genus *Pentastomum* Rudolphi, 1812. However, he was still unable to place them (like many others after him), and they have been grouped with various taxa including annelids, mites, myriapods, onychophorans and tardigrades (see Abele et al. 1989). Dujardin (1845) believed these parasites were different from all the

other worms and most closely resembled arthropods based on their striated muscles. Using molecular techniques, Abele et al. (1989) concluded that pentastomids belong in the Crustacea as they are more closely related to fish lice (*Argulus*) rather than any of the other possible taxa mentioned above. Almeida and Christoffersen (1999) also used cladistics on the pentastomids and challenged some of the older ideas. With the recent discovery of fossil data, there is even more discussion on the phylogenetics and status of this group (see Castellani et al. 2011).

In 1851, the first family, Linguatulidae, was established. Nine years later, the German zoologist, Karl Georg Friedrich Rudolf Leuckart (Fig. 2.8g), determined the first comprehensive study on the life cycle of a linguatulid and divided *Pentastomum* into two subgenera, namely, *Linguatula* Frölich, 1789 and *Pentastomum* (Leuckart 1860). Sambon (1922a, b) revised Linguatulidae and identified differences between the different linguatulid groups as well as added new subfamilies and genera. Another German zoologist, Richard Heymons (Fig. 2.8h), published several papers and described ten pentastomid species. Other substantial publications include the monograph on the pentastomids from Africa (Fain 1961), the review of the pentastomid history by Nicoli (1963) and several publications by Haffner on the biology of these parasites (Haffner 1971, 1973).

One of the world authorities on pentastomes was John Teague Self (Fig. 2.8i). From publishing new species to host-parasite interactions and biological relationships, he explored all aspects of these parasites where possible. John Riley, another important contributor to Pentastomida, described 2 genera and 43 species, some with Self. Riley (with over 45 publications on pentastomids) published noteworthy work on the biology of pentastomids (Riley 1986), revisions of several genera (Riley et al. 1990; Riley 1994), and has a genus named in honour of his large contribution to the taxonomy of Pentastomida, *Rileyella* Spratt, 2003. This name has since changed to *Yelirella* Spratt, 2010 (which is an anagram of *Rileyella*) as *Rileyella* was a junior homonym for a tachinid fly from North America (Spratt 2010).

To date there are 4 orders, 2 superfamilies, 7 families, 26 genera, 130 species and 2 subspecies in this subclass (see Table 2.1). Recently, Gary Poore (Fig. 2.4i) has revised the nomenclature of the pentastomids giving a list of all of the valid species (Poore 2012). Brazilian researchers, Martin Lindsey Christoffersen and José Eriberto de Assis, have published a substantial review of Pentastomida. This thorough monograph includes a detailed history on the subclass with information on all the known species (including updated synonymies, host and distribution lists), as well as notes on their phylogeny and effects on their hosts.

## 2.10 Ostracoda

Superclass Oligostraca Zrzavý, Hypša & Vlášková, 1998

Class Ostracoda Latreille, 1802

Ostracods are small crustaceans found in both marine and freshwaters. The body resembles a clam and is encased by two valves, which forms a carapace. Very little was known about these crustaceans eating preferences for many years. The first mention was by Baird (1850) where he stated that most are essentially carnivorous; nothing specific about their feeding mode was noted. Most ostracods these days are considered to be free-living, predators or scavengers, but there are a few instances of symbiotic (and possibly parasitic) relationships.

One of the first records of a parasitic relationship was by Marshall (1903) when he described the first entocytherid ostracode. William S. Marshall, an Assistant Professor of Zoology at the University of Wisconsin, named this species *Entocythere cambaria* Marshall, 1903, and believed it fed on the blood of its crayfish host. Other members of the podocopan family Endocytheridae have also been listed as parasites but were corrected to commensals when the entocytherids were able to survive for long periods without a host (Young 1971). These ostracods are now considered to be obligate ectosymbionts of other crustaceans (Williams and Weaver 2018).

Other ostracods thought to be parasitic are those from the order Myodocopida. Research by Wilson (1913), Monod (1923) and Harding (1966) reported on myodocopidan ostracod parasitism based on the attachment of these crustaceans on their various hosts. Charles Branch Wilson (Fig. 2.7h) was the first to categorically state that these *Cypridina* Milne-Edwards, 1840, ostracods were parasitic (upon the gills of several fish), that the occurrence was not accidental and that it was not temporary (formation of a pocket to keep the crustacean in place). However, it was debated that these crustaceans are not truly parasitic and only attach to injured or unhealthy fish that are trapped (Cohen 1983). According to Stepien and Brusca (1985), adult fishes in large, nearshore cages were attacked at night by zooplankton swarms, primarily consisting of the luminescent ostracod, *Vargula tsujii* Kornicker & Baker, 1977, and the cirolanid isopod, *Cirolana diminuta* Menzies, 1962. Although the ostracods attached and fed on mucus and skin of the fish, they did not appear to inflict serious harm on the host. They were only found inside fish damaged by the cirolanid isopods and thus could not be considered parasites in this instance.

The attachment and actual effects of these myodocopidan ostracods on the hosts needed to be studied, and so Bennett et al. (1997) compared the histopathology and feeding appendages of ostracods with different feeding strategies. The “parasitic” ostracod investigated, *Sheina orri* Harding, 1966, was found in the gills of the epaulette shark, *Hemiscyllium ocellatum* (Bonnaterre, 1788) in Australia. The authors noted that this crustacean used their mandibular and maxillular claws to attach to the gills, which caused damage to the gills. The claws seemed to be adapted for this purpose, and the damage to the gills suggested they had been attached for a considerable amount of time. Thus, it is a parasite for at least part of its life cycle. This study also found that Wilson’s (1913) description of *Photeros parasitica* (Wilson, 1913) (originally as *Cypridina parasitica*) was so similar to *Sheina orri* that it is most likely parasitic too. More individual studies on the different symbiotic ostracods need to be completed in order to determine if true parasitism is found in other ostracod species.

## 2.11 Concluding Remarks

This chapter reviews many of the historical highlights from the different parasitic Crustacea groups and provides a succinct background to these diverse organisms. Reviewing the literature has revealed how many of the earlier discoveries were dependant on research vessels and expeditions which covered only specific areas. With time, these discoveries became more linked to the area where the respective taxonomist was based and what material they had at their disposal. This led to a biased account on species diversity, influenced by the researcher rather than the presence of the parasite. Furthermore, most of the early biologists were involved in many different fields and described new species from diverse taxa. Over the years, this pattern has altered, and there are now more taxa-specific parasitologists working on species from around the world. It is important to note that many of the currently known crustacean parasitologists are however near retirement; thus, young researchers need to be trained to continue their outstanding work. With a better understanding of what has been done, we can now focus on what needs to be done in order to gain further insight into this unique group of parasites and their niche in the aquatic environment.

**Acknowledgements** The author would like to thank Philippe Laval, Wolfgang Zeidler, Niel Bruce, Christopher Boyko, Jason Williams, John Markham, Jianmei An, Jean-Paul Trilles, Nico Smit, Gary Poore, Mark Grygier, Jens Høeg, Gregory Kolbasov, William Newman, Rony Huys, David Damkaer and Eduardo Suárez-Morales for providing photos used in the figures.

## References

- Abdelhalim AI, Lewis JW, Boxshall GA (1991) The life-cycle of *Ergasilus sieboldi* Nordmann (Copepoda: Poecilostomatoida), parasitic on British freshwater fish. *J Nat Hist* 25:559–582
- Abele LG, Kim W, Felgenhauer BE (1989) Molecular evidence for inclusion of the phylum Pentastomida in the Crustacea. *Mol Biol Evol* 6:685–691
- Ahyong ST, Lowry JK, Alonso M, Bamber RN, Boxshall GA, Castro P, Gerken S, Karaman GS, Goy JW, Jones DS, Meland K, Rogers DC, Svavarsson J (2011) Subphylum Crustacea Brünnich, 1772. In: Zhang Z-Q (ed) *Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness*. *Zootaxa* 3148, pp 165–191
- Almeida WO, Christoffersen ML (1999) A cladistic approach to relationships in Pentastomida. *J Parasitol* 85:695–704
- Amundsen PA, Kristoffersen R, Knudsen R, Klemetsen A (1997) Infection of *Salmincola edwardsii* (Copepoda: Lernaepodidae) in an age-structured population of Arctic char – a long-term study. *J Fish Biol* 51(5):1033–1046
- An J, Yu H, Markham JC (2009) First record of the genus *Gigantione* (Epicaridea: Bopyridae: Pseudioninae) from Chinese waters, with description of three new species. *J Nat Hist* 43 (5–6):335–353
- An J, Boyko CB, Li X (2015a) Review of the parasitic genus *Epipenaeon* Nobili, 1906 (Crustacea: Isopoda: Bopyridae), with new records and redescription of four species from China. *J Nat Hist* 48(33–34):2027–2048



- An J, Markham JC, Li X (2015b) A review of the genus *Parapenaeon* Richardson, 1904 (Crustacea: Isopoda: Bopyridae: Orbioninae), with description of three new species from China. *J Nat Hist* 49(41–42):2527–2557
- Audouin JV (1837) Communications. *Annales de la Société Entomologique de France* 6:13 [French]
- Avdeev GV (2010) *Amplipedicola pectinatus* gen. et sp. n. (Copepoda, Harpacticoida, Tisbidae), a parasite of octopuses in the Bering Sea. *Crustaceana* 83(11):1363–1370
- Avenant A, Loots GC, Van As JG (1989a) A redescription of *Dolops ranarum* (Stuhlmann, 1891) (Crustacea: Branchiura). *Syst Parasitol* 13:141–151
- Avenant A, Van As JG, Loots GC (1989b) On the hatching and morphology of *Dolops ranarum* larvae (Crustacea: Branchiura). *J Zool* 217:511–519
- Avenant-Oldewage A (1991) A new species of *Chonopeltis* (Crustacea: Branchiura) from the Kruger National Park, Southern Africa. *J Afr Zool* 105:313–321
- Avenant-Oldewage A (1994) Integumental damage caused by *Dolops ranarum* (Stuhlmann, 1891) (Crustacea: Branchiura) to *Clarias gariepinus* (Burchell), with reference to normal histology and wound-inflicting structures. *J Fish Dis* 17:641–647
- Avenant-Oldewage A, Knight E (1994) A diagnostic species compendium of the genus *Chonopeltis* Thiele, 1900 (Crustacea: Branchiura) with notes on its geographical distribution. *Koedoe* 37:41–56
- Avenant-Oldewage A, Knight E (2008) Aspects of the ecology of *Chonopeltis australis* Boxshall, 1976 in Boskop Dam, North West Province. *S Afr J Wildl Res* 38:28–34
- Avenant-Oldewage A, Van As JG (1990) The digestive system of the fish ectoparasite *Dolops ranarum* (Crustacea: Branchiura). *J Morphol* 204:103–112
- Avenant-Oldewage A, Swanepoel JH, Knight E (1994) Histomorphology of the digestive tract of *Chonopeltis australis* (Crustacea: Branchiura). *S Afr J Zool* 29:74–81
- Badillo FJ, Puig L, Montero FE, Raga JA, Aznar L (2007) Diet of *Balaenophilus* spp. (Copepoda: Harpacticoida): feeding on keratin at sea? *Mar Biol* 115:751–758
- Balbuena JA, Raga JA (1991) Ecology and host relationships of the whale-louse *Isocyamus delphini* (Amphipoda: Cyamidae) parasitizing long-finned pilot whales (*Globicephala melas*) off the Faroe Islands (Northeast Atlantic). *Can J Zool* 69(1):141–145
- Barnard JL (1961) Gammaridean Amphipoda from depths of 400 to 6000 meters. *Galathea Rep* 5:23–128
- Bate CS (1858) On *Praniza* and *Anceus*, and their affinity to each other. *Ann Mag Nat Hist* 16:165–172
- Becker KH (1975) *Basipodella harpacticola* n. gen., n. sp. (Crustacea, Copepoda). *Helgol Wiss Meeresuntersuch* 27:96–100
- Bennett MB, Heupel MR, Bennett SM, Parker A (1997) *Sheina orri* (Myodocopa: Cypridinidae), an ostracod parasitic on the gills of the epaulette shark, *Hemiscyllium ocellatum* (Elasmobranchii: Hemiscylliidae). *Int J Parasitol* 27:275–281
- Benz GW (1980) Tissue proliferations associated with *Nemesis lamna* Risso, 1826 (Copepoda: Eudactylinidae) infestations on the gill filaments of shortfin makos (*Isurus oxyrinchus Rafinesque*). *J Fish Dis* 3:443–446
- Benz GW (1984) Association of the pedunculate barnacle, *Conchoderma virgatum* (Spengler, 1790), with pandarid copepods (Siphonostomatoida: Pandaridae). *Can J Zool* 62(4):741–742
- Benz GW (1993) Evolutionary biology of Siphonostomatoida (Copepoda) parasitic on vertebrates. PhD Thesis, University of British Columbia
- Benz GW, Adamson SAM (1990) Disease caused by *Nemesis robusta* (van Beneden, 1851) (Eudactylinidae: Siphonostomatoida: Copepoda) infections on gill filaments of thresher sharks (*Alopias vulpinus* (Bonnaterre, 1758)), with notes on parasite ecology and life history. *Can J Zool* 68:1180–1187
- Benz GW, Goater TM (2015) In memoriam: Zbigniew Kabata—metamorphosis of a parasitologist, 17 March 1924 – 4 July 2014. *J Parasitol* 101(2):257–264

- Boccone P (1671) Recherches et observations curieuses sur la nature du corail blanc et rouge, vrai de Dioscoride, et sur la sangsue qui se trouve attachée au poisson “Xiphias”. Claude Barbin, Paris
- Boeger WA (2011) Vernon Everett Thatcher: 1929–2011. *Zoologia (Curitiba)* 28(5):690–691
- Bonnier J (1903) Sur deux types nouveaux d'Épicarides parasites d'un Cumacé et d'un Schizopode. *Compte Rendu Hebd Séanc Acad Sci Paris* 136:102–103
- Boschma H (1928) The Rhizocephala of the North Atlantic region. *Danish Ingolf-Exped* 3:1–49
- Boschma H (1933) The Rhizocephala in the collection of the British Museum. *J Linn Soc (Zool)* 38(261):473–552
- Boschma H (1937) The species of the genus *Sacculina* (Crustacea Rhizocephala). *Zool Meded Leiden* 19:187–328
- Boschma H (1950) Notes on Sacculinidae, chiefly in the collection of the United States National Museum. *Zool Verh Leiden* 7:3–55
- Boschma H (1955) The described species of the family Sacculinidae. *Zool Verh Leiden* 27:1–76
- Bouvier EL (1897) Observations sur les Argulidés du genre *Gyropeltis* recueillis par M. Geay au Vénézuéla. *Bull Mus Natl Hist Nat (section A Zoologie, Biologie et Écologie Animales)* 3:13–19
- Bouvier EL (1898) Les crustacés parasites du genre *Dolops* Audouin (première partie). *Bull Soc Philom* 10:53–81
- Bouvier EL (1899a) Les crustacés parasites du genre *Dolops* Audouin (seconde partie). *Bull Soc Philom* 1:12–40
- Bouvier EL (1899b) Sur les Argulidés du genre *Gyropeltis*, recueillis récemment par M. Geay dans la Guyane. *Bull Mus Natl Hist Nat (section A Zoologie, Biologie et Écologie Animales)* 5:39–41
- Bovallius C (1887a) Arctic and Antarctic Hyperids. *Vega-Exped Vetensk Iakttagel* 4:543–582, pls 40–47
- Bovallius C (1887b) Systematical list of the Amphipoda Hyperiidea. *Bihang till K Svenska Vet Akad Handl* 11(16):1–50
- Bovallius C (1887c) Contributions to a monograph of the Amphipoda Hyperiidea, Part I: 1. The Families Tyronidae, Lanceolidae and Vibilidae. *K Svenska Vet Akad Handl* 22(7):1–72, pls 1–10
- Bovallius C (1889) Contributions to a monograph of the Amphipoda Hyperiidea, Part I: 2. The Families Cyllopodidae, Paraphronimidae, Thaumatosidae, Mimonectidae, Hyperiidæ, Phronimidae and Anchylomeridae. *K Svenska Vet Akad Handl* 22(7):1–434, pls 1–18
- Bovallius C (1890) The Oxycephalids. *Nova Acta Regiae Soc Sci Upsal* 3 14:1–141, pls 1–7
- Bowman TE, Gruner H-E (1973) The families and genera of Hyperiidea (Crustacea: Amphipoda). *Smithson Contrib Zool* 146:1–64
- Boxshall GA (2005) Copepoda (Copepods). In: Rhode K (ed) *Marine parasitology*. CSIRO Publishing, Collingwood, pp 123–138
- Boxshall GA, Halsey SH (2004) An introduction to copepod diversity. The Ray Society, London
- Boxshall GA, Lincoln RJ (1983) Tantulocarida, a new class of Crustacea ectoparasitic on other crustaceans. *J Crust Biol* 3:1–16
- Boxshall GA, Lincoln RJ (1987) The life cycle of the Tantulocarida (Crustacea). *Philos Trans R Soc Lond B* 315:267–303
- Boxshall GA, Strong EE (2006) An extraordinary shift in life habit within a genus of cyclopid copepods in Lake Tanganyika. *Zool J Linnean Soc* 146(2):275–285
- Boxshall GA, Vader W (1993) A new genus of Tantulocarida (Crustacea) parasitic on an amphipod host from the North Sea. *J Nat Hist* 27:977–988
- Boyko CB, Williams JD (2016) Methods of detection, collection and preservation of parasitic isopods (Isopoda: Epicaridea). *Proc Biol Soc Wash* 129(1):76–83
- Boyko CB, Moss J, Williams JD, Shields JD (2013) A molecular phylogeny of Bopyroidea and Cryptoniscoidea (Crustacea: Isopoda). *Syst Biodivers* 11(4):495–506
- Bradford JM, Hewitt GC (1980) A new Maxillopodan crustacean, parasitic on a Myodocopid Ostracod. *Crustaceana* 38(1):69–72

- Brandt A, Poore GCB (2003) Higher classification of the flabelliferan and related Isopoda based on a reappraisal of relationships. *Invert Syst* 17:893–923
- Brattström H (1936) *Ulophysema öresundense* n. gen. et sp., eine neue Art der Ordnung Cirripedia Ascothoracica. (Vorläufige Mitteilung). *Arkiv für Zoologi* 28A(23):1–10
- Brattström H (1947) On the ecology of the Ascothoracid *Ulophysema öresundense* Brattström: Studies on *Ulophysema öresundense* 1. Undersökningar över Öresund XXXII. *Lunds Universitets Årsskrift, N.F., Avd. 2, 43(7):*1–75
- Brattström H (1948a) On the larval development of the Ascothoracid *Ulophysema öresundense* Brattström: Studies on *Ulophysema öresundense* 2. Undersökningar över Öresund XXXIII. *Lunds Universitets Årsskrift, N.F., Avd. 2, 44:*1–70
- Brattström H (1948b) On the morphology of the Ascothoracid *Ulophysema öresundense* Brattström: Studies on *Ulophysema öresundense* 3. Undersökningar över Öresund XXXIV. *Kungliga Fysiografiska Sällskapets Handlingar, N.F.* 59:1–31
- Bresciani J, Jespersen Å (1985) The ultrastructure of the integument of *Ulophysema oeresundense* Brattstrom, 1936 (Crustacea, Ascothoracica). *J Crust Biol* 5(1):146–159
- Brian A (1940) Sur quelques argulidés d’Afrique. *Rev Zool Bot Afri* 33:77–98
- Brian A (1947) Los argúlidos del museo argentino de ciencias naturales (Crustacea Branchiura). *An Mus Argent Cien Nat* 42:353–370
- Bruce NL (1984) A new family for the isopod crustacean genus *Tridentella* Richardson, 1905, with description of a new species from Fiji. *Zool J Linnean Soc* 80:447–455
- Bruce NL (1986a) Cirolanidae (Crustacea: Isopoda) of Australia. *Rec Aust Mus (Suppl)* 6:1–239
- Bruce NL (1986b) Revision of the isopod crustacean genus *Mothocya* Costa, in Hope, 1851 (Cymothoidae: Flabellifera), parasitic on marine fishes. *J Nat Hist* 20:1089–1192
- Bruce NL (1987a) Australian *Pleopodias* Richardson, 1910, and *Anilocra* Leach, 1818 (Isopoda: Cymothoidae), crustacean parasites of marine fishes. *Rec Aust Mus* 39:85–130
- Bruce NL (1987b) Australian *Renocila* Miers, 1880 (Isopoda: Cymothoidae), crustacean parasites of marine fishes. *Rec Aust Mus* 39:169–182
- Bruce NL (1987c) Australian species of *Nerocila* Leach, 1818, and *Creniola* n. gen. (Isopoda: Cymothoidae), crustacean parasites of marine fishes. *Rec Aust Mus* 39:355–412
- Bruce NL (1990) The genera *Catoessa*, *Elthusa*, *Ichthyoxenus*, *Idusa*, *Livoneca* and *Norileca* n. gen. (Isopoda, Cymothoidae), crustacean parasites of marine fishes, with descriptions of eastern Australian species. *Rec Aust Mus* 42:247–300
- Bruce NL (1993) Two new genera of marine isopod crustaceans (Flabellifera: Sphaeromatidae) from southern Australia, with a reappraisal of the Sphaeromatidae. *Invertebr Taxon* 7:151–171
- Bruce NL (1994a) The marine isopod *Neocirolana* Hale, 1925 (Crustacea: Cirolanidae) from tropical Australian waters. *Mem Queensl Mus* 37:41–51
- Bruce NL (1994b) Four new genera of marine isopod crustaceans (Sphaeromatidae) from eastern and southern Australia. *Mem Mus Vic* 54:399–438
- Bruce NL (1995) Comment on the proposed conservation of *Lironeca* Leach, 1818 (Crustacea, Isopoda) as the correct original spelling. *Bull Zool Nomencl* 52:69
- Bruce NL (2004) Reassessment of the isopod crustacean *Aega deshaysiana* (Milne-Edwards, 1840) (Cymothoida: Aegidae) – a worldwide complex of 21 species. *Zool J Linnean Soc* 142:135–232
- Bruce NL (2009) The marine fauna of New Zealand: Isopoda, Aegidae (Crustacea). *NIWA Biodivers Mem* 122:1–252
- Brusca RC (1981) A monograph on the Isopoda Cymothoidae (Crustacea) of the eastern Pacific. *Zool J Linnean Soc* 73(2):117–199
- Brusca RC (1983) A monograph on the isopod family Aegidae in the tropical eastern Pacific. The genus *Aega*. *Allan Hancock Monogr Mar Biol* 12:1–39
- Brusca RC, Iverson EW (1985) A guide to the marine isopod Crustacea of Pacific Costa Rica. *Rev Biol Trop* 33(Suppl):1–77
- Brusca RC, Wilson GDF (1991) A phylogenetic analysis of the Isopoda with some classificatory recommendations. *Mem Queensl Mus* 31:143–204

- Bullard SA (2016) In Memoriam: George William Benz (1 January 1954 – 9 February 2015). *Acta Ichthyol Piscat* 46(2):141–162
- Bunkley-Williams L, Williams EH Jr (1994) Parasites of Puerto Rican freshwater sport fishes. Sportfish Disease Project. Puerto Rico Department of Natural and Environmental Resources, San Juan, Puerto Rico and Department of Marine Sciences, University of Puerto Rico, Mayaguez, Puerto Rico
- Bunkley-Williams L, Williams EH Jr (1998) Isopods associated with fishes: a synopsis and corrections. *J Parasitol* 84:893–896
- Bush AO, Fernandez JC, Esch GW, Seed JR (2001) Parasitism: the diversity and ecology of animal parasites. Cambridge University Press, Cambridge
- Carvalho LN, Del-Claro K, Takemoto RM (2003) Host–parasite interaction between branchiurans (Crustacea: Argulidae) and piranhas (Osteichthyes: Serrasalminae) in the Pantanal wetland of Brazil. *Environ Biol Fish* 67:289–296
- Castellani C, Andreas M, Waloszek D, Haug JT (2011) New pentastomids from the Late Cambrian of Sweden – deeper insight of the ontogeny of fossil tongue worms. *Palaeontogr Abt A Palaeozool-Stratigr* 293:95–145
- Cavolini F (1787) Memoria sulla generazione dei pesci e dei granchi. Napoli
- Chabert P (1787) *Traité des maladies vermineuses dans les animaux*, 2e édition. Imprimerie Royale, Paris
- Claus C (1875) Über die Entwicklung, Organisation und systematische Stellung der Arguliden. *Z Wiss Zool* 15:1–68
- Claus C (1879a) Der Organismus der Phronimiden. *Arb Zool Inst Univ Wien* 2:59–146, pls 1–8
- Claus C (1879b) Die Gattungen und Arten der Platysceliden in Systematischer Übersicht. *Arb Zool Inst Univ Wien* 2:147–198
- Cohen AC (1983) Rearing and postembryonic development of the myodocopid ostracode *Skogsbergia lernerii* from the coral reefs of Belize and the Bahamas. *J Crust Biol* 3:235–256
- Cohen BF, Poore GCB (1994) Phylogeny and biogeography of the Gnathiidae (Crustacea: Isopoda) with descriptions of new genera and species, most from South-Eastern Australia. *Mem Mus Vic* 54:271–397
- Coleman CO (2007) Professor Dr. Hans-Eckhard Gruner 15 May 1926 – 6 December 2006. *J Crust Biol* 27(4):694–696
- Cunnington WA (1913) Zoological results of the Third Tanganyika Expedition, conducted by Dr. W.A. Cunnington, 1904–1905. Report on the Branchiura. *Proc Zool Soc Lond* 19:262–283
- Damkaer DM (2000) Harriet Richardson (1874–1958), first lady of isopods. *J Crust Biol* 20(4):803–811
- Damkaer DM (2002) The Copepodologist's cabinet: a biographical and bibliographical history. *Memoirs of the American Philosophical Society*. American Philosophical Society, Philadelphia
- Darwin CR (1851) A monograph on the subclass Cirripedia with figures of all the species. The Lepadidae; or, pedunculated cirripedes. The Ray Society, London
- Darwin CR (1854) A monograph on the sub-class Cirripedia, with figures of all the species. The Balanidae (or sessile cirripedes); the Verrucidae, etc., etc., etc. Ray Society, London
- Davies AJ, Smit NJ (2001) The life cycle of *Haemogregarina bigemina* (Adeleina: Haemogregarinidae) in South African hosts. *Folia Parasitol* 48:169–177
- Davis CC (1984) Planktonic Copepoda (including Monstrilloida). In: Steidinger KA, Walter LM (eds) *Marine plankton life cycle strategies*. CRC Press, Boca Raton, FL, pp 67–91
- Day JH (1939) A new cirripede parasite *Rhizolepas annelidicola* nov. gen. et sp. *Proc Linn Soc Lond* 151:64–79
- de Lacaze-Duthiers H (1865) Mémoire sur un mode nouveau de parasitisme observé chez un animal non décrit. *C R Hebd Séances Acad Sci* 61(20):838–841
- de Lacaze-Duthiers H (1883) Histoire de la *Laura gerardiae*: type nouveau de Crustacé parasite. *Mém Acad Sci Inst France* 42:1–160
- de Lima MC, Valentin JL (2001) New records of Amphipoda Hyperiidea in associations with gelatinous zooplankton. *Hydrobiologia* 448(1):229–235

- Desmarest A-G (1825) *Considérations Générales sur la Classe des Crustacés, et description des espèces de ces animaux, qui vivent dans la mer, sur les côtes, ou dans les eaux douces de la France*. F.G. Levrault, Libraire, Strasbourg, Paris
- Dojiri M, Cressley RF (1987) Revision of the Taeniacanthidae (Copepoda: Poecilostomatoida) parasitic on fishes and sea urchins. *Smithson Contrib Zool* 447:1–250
- Dujardin F (1845) *Histoire naturelle des helminthes ou vers intestinaux*. Libraire Encyclopédique de Roret, Paris
- Einszporn T (1965a) Nutrition of *Ergasilus sieboldi* Nordmann. I. Histological structure of the alimentary canal. *Acta Parasit Pol* 13:151–160
- Einszporn T (1965b) Nutrition of *Ergasilus sieboldi* Nordmann. II. The uptake of food and the food material. *Acta Parasit Pol* 13:373–382
- Fain A (1961) Les pentastomides de l’Afrique Centrale. *Ann Musee Roy Afr Centr Ser 8 Sci Zool* 92:1–115, pls 1–6
- Farran GP (1914) Description of a harpacticoid copepod parasitic on an octopus. *Ann Mag Nat Hist (Ser 8)* 13:472–475, pl XXI
- Ferrari F (1996) Thomas Elliot Bowman III (1918–1995). *J Crust Biol* 16(3):633–635
- Freire PR, Serejo CS (2004) The genus *Trischizostoma* (Crustacea: Amphipoda: Trischizostomidae) from the Southwest Atlantic, collected by the REVIZEE Program. *Zootaxa* 645:1–15
- Frick MG, Zardus JD, Ross A, Senko J, Montano-Valdez D, Bucio-Pacheco M, Sosa-Cornejo I (2011) Novel records and observations of the barnacle *Stephanolepas muricata* (Cirripedia: Balanomorpha: Coronuloidea); including a case for chemical mediation in turtle and whale barnacles. *J Nat Hist* 45:629–640
- Fryer G (1956) A report on the parasitic Copepoda and Branchiura of the fishes of Lake Nyasa. *Proc Zool Soc Lond* 127:293–344
- Fryer G (1958) Occurrence of spermatophores in the genus *Dolops* (Crustacea: Branchiura). *Nature* 181:1011–1012
- Fryer G (1959) A report on the parasitic Copepoda and Branchiura of the fishes of the Lake Bangweulu (Northern Rhodesia). *Proc Zool Soc Lond* 132:517–550
- Fryer G (1960a) Studies on some parasitic crustaceans on African freshwater fishes, with descriptions of a new copepod of the genus *Ergasilus* and a new branchiuran of the genus *Chonopeltis*. *Proc Zool Soc Lond* 133:629–647
- Fryer G (1960b) The spermatophores of *Dolops ranarum* (Crustacea, Branchiura): their structure, formation and transfer. *Q J Microsc Sci* 101:407–432
- Fryer G (1961a) The parasitic Copepoda and Branchiura of the fishes of Lake Victoria and the Victoria Nile. *Proc Zool Soc Lond* 137:41–60
- Fryer G (1961b) Larval development in the genus *Chonopeltis* (Crustacea: Branchiura). *Proc Zool Soc Lond* 137:61–69
- Fryer G (1964) Further studies on the parasitic Crustacea of the African freshwater fishes. *Proc Zool Soc Lond* 143:79–102
- Fryer G (1965a) Crustacean parasites of African freshwater fishes, mostly collected during the expeditions to Lake Tanganyika, and to Lakes Kivu, Edward and Albert by the Institut Royal des Sciences Naturelles de Belgique. *Bull Inst R Sci Nat Belg* 41:1–22
- Fryer G (1965b) Parasitic crustaceans of African freshwater fishes from the Nile and Niger systems. *Proc Zool Soc Lond* 145:285–303
- Fryer G (1968) The parasitic Crustacea of African freshwater fishes; their biology and distribution. *J Zool* 156:45–95
- Fryer G (1969) A new freshwater species of the genus *Dolops* (Crustacea: Branchiura) parasitic on a galaxiid fish of Tasmania – with comments on disjunct distribution patterns in the southern hemisphere. *Aust J Zool* 17:49–64
- Fryer G (1974) Une nouvelle espèce de *Chonopeltis* (Crustacea: Branchiura) parasite d’un poisson congolais. *Rev Zool Afri* 88:437–440

- Fryer G (1977) On some species of *Chonopeltis* (Crustacea: Branchiura) from the rivers of the extreme South West Cape region of Africa. *J Zool* 182:441–455
- Gannon AT, Wheatly MG (1992) Physiological effects of an ectocommensal gill barnacle, *Octolasmis muelleri*, on gas exchange in the blue crab *Callinectes sapidus*. *J Crustac Biol* 12:11–18
- Giesbrecht W (1893) Systematik und Faunistik der pelagischen Copepoden des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Fauna und Flora des Golfes Neapel. Monographie. Atlas von 54 Tafeln nebst den Tafelerklärungen 19:1–831
- Glenner H, Hebsgaard MB (2006) Phylogeny and evolution of life history strategies of the parasitic barnacles (Crustacea, Cirripedia, Rhizocephala). *Mol Phylogenet Evol* 41:528–538
- Glenner H, Lützen J, Takahashi T (2003) Molecular and morphological evidence for a monophyletic clade of asexually reproducing Rhizocephala: *Polyascus*, new genus (Cirripedia). *J Crust Biol* 23:548–557
- Glenner H, Høeg JT, Stenderup J, Rybakov AV (2010) The monophyletic origin of a remarkable sexual system in akentrogonid rhizocephalan parasites: a molecular and larval structural study. *Exp Parasitol* 125:3–12
- Goater TM, Goater CP, Esch GW (eds) (2014) Parasitism: the diversity and ecology of animal parasites, 2nd edn. Cambridge University Press, Cambridge
- Goddard JHR, Torchin ME, Kuris AM, Lafferty KD (2005) Host specificity of *Sacculina carcini*, a potential biological control agent of the introduced European green crab *Carcinus maenas* in California. *Biol Invasions* 7:895–912
- Gomes AL, Malta JC (2002) Laying, development and hatching of eggs of the *Dolops carvalhoi* Lemos de Castro (Crustacea, Branchiura), reared in the laboratory, parasite from fishes of Central Amazon. *Rev Bras Zool* 19:141–149
- Goodwin AE (1999) Massive *Lernaea cyprinacea* infestations damaging the gills of channel catfish polycultured with bighead carp. *J Aquat Anim Health* 11(4):406–408
- Gordon I (1971) Biographical note on Edward John Miers. F.Z.S., F.L.S. (1851–1930). *Res Crust* 4:123–132
- Grignard JC, Jangoux M (1994) Occurrence and effects of symbiotic pedunculate barnacles on echinoid hosts. In: David B, Guille A, Féral J-P, Roux M (eds) Echinoderms through time. Balkema, Rotterdam
- Grobben K (1899) Carl Claus. *Arb Zool Inst Wien* 11:I–XII
- Gruner HE (1975) Caprellidea II. Fam. Cyamidae. In: Gruner HE, Holthuis LB (eds) Crustaceorum catalogus 5, pp 79–93
- Grutter AS (1996) Parasite removal rates by the cleaner wrasse *Labroides dimidiatus*. *Mar Ecol Prog Ser* 130:61–70
- Grutter AS (2003) Feeding ecology of the fish ectoparasites *Gnathia* sp. (Crustacea: Isopoda) from the Great Barrier Reef, and its implications for fish cleaning behaviour. *Mar Ecol Prog* 259:295–302
- Grutter AS, Morgan J, Adlard R (2000) Characterising parasitic gnathiid isopod species and matching life stages using ribosomal DNA ITS2 sequences. *Mar Biol* 136:201–205
- Gruvel A (1905) Monographie des Cirrhipèdes au Thécostracés. Masson et Cie, Paris
- Grygier MJ (1981) Sperm of the ascothoracican parasite dendrogaster the most primitive found in crustacea. *Int J Inver Rep Dev*:65–74
- Grygier MJ (1983) Ascothoracida and the unity of the Maxillopoda. In: Schram FR (ed) Crustacean issues 1: Crustacean phylogeny. A.A. Balkema, Rotterdam, pp 73–104
- Grygier MJ (1987) Classification of the Ascothoracida (Crustacea). *Proc Biol Soc Wash* 100(3):452–458
- Grygier MJ (1991) Redescription ontogeny and demography of *Parascothorax synagogoides* Crustacea Ascothoracida parasitic on *Ophiophthalmus normani* Ophiuroidea in the bathyal basins off southern California USA. *Proc S Diego Soc Nat Hist* 6:1–20
- Grygier MJ (1992) Laboratory rearing of *Ascothoracidan nauplii* Crustacea Maxillopoda from plankton at Okinawa Japan. *Publ Seto Mar Biol Lab* 35(2–5):235–251

- Grygier MJ (1994) [dated 1993] Identity of *Thaumatoessa* (*Thaumaleus*) *typica* Krøyer, the first described monstrilloid copepod. *Sarsia* 78:235–242
- Grygier MJ (1995) Annotated chronological bibliography of Monstrilloida (Crustacea: Copepoda). *Galaxea* 12:1–82
- Grygier MJ (1996) Sous-classe des Ascothoracides (Ascothoracida Lacaze-Duthiers, 1880). In: Forest J (ed) *Traité de Zoologie sous la direction de P.-P. Grassé*. Vol. 7 Fascicule 2 Généralités (suite) et systématique (Céphalocarides à Syncarides). Masson éditeur, Paris, pp 433–452
- Grygier MJ, Høeg JT (2005) Ascothoracida (ascothoracids). In: Rohde K (ed) *Marine parasitology*, CSIRO Publishing and CABI Publishing, pp 149–154
- Grygier MJ, Newman WA (1991) A new genus and two new species of Microlepadidae (Cirripedia: Pedunculata) found on western Pacific diadematid echinoids. *Galaxea* 10:1–22
- Grygier MJ, Ohtsuka S (2008) A new genus of monstrilloid copepods (Crustacea) with anteriorly pointing ovigerous spines and related adaptations for subthoracic brooding. *Zool J Linnean Soc* 152:459–506
- Gunnerus JE (1763) *Om Sort-Haaen*. Det Trondhjemske Selskabs Skrifter, Anden Deel. København
- Hadfield KA, Smit NJ (2017) Revision of the fish parasitic genus *Pleopodias* Richardson, 1910 (Isopoda, Cymothoidae), with the description of a new species and key to the genus. *ZooKeys* 667:21–37
- Hadfield KA, Bruce NL, Smit NJ (2010) Redescription of the monotypic genus *Cinusa* Schioedte and Meinert, 1884 (Isopoda, Cymothoidae), a buccal-cavity isopod from South Africa. *Zootaxa* 2437:51–68
- Hadfield KA, Bruce NL, Smit NJ (2013) Review of the fish-parasitic genus *Cymothoa* Fabricius, 1793 (Isopoda, Cymothoidae, Crustacea) from the southwestern Indian Ocean, including a new species from South Africa. *Zootaxa* 3640:152–176
- Hadfield KA, Bruce NL, Smit NJ (2014) Review of the fish parasitic genus *Ceratothoa* Dana, 1852 (Crustacea, Isopoda, Cymothoidae) from South Africa, including the description of two new species. *ZooKeys* 400:1–42
- Hadfield KA, Bruce NL, Smit NJ (2015) Review of *Mothocya* Costa, in Hope, 1851 (Crustacea: Isopoda: Cymothoidae) from southern Africa, with the description of a new species. *Afr Zool* 50:147–163
- Hadfield KA, Bruce NL, Smit NJ (2016) Redescription of poorly known species of *Ceratothoa* Dana, 1852 (Crustacea, Isopoda, Cymothoidae), based on original type material. *ZooKeys* 592:39–91
- Hancock A (1849) Notice of the occurrence on the British coast of a burrowing barnacle belonging to a new order of the class Cirripedia. *Ann Mag Nat Hist* 4(23):305–314
- Harbison GR, Biggs DC, Madin LP (1977) The associations of Amphipoda Hyperidea with gelatinous zooplankton – II. Associations with Cnidaria, Ctenophora and Radiolaria. *Deep-Sea Res* 24:465–488
- Harding JP (1966) Myodocopan ostracods from the gills and nostrils of fishes. In: Barnes H (ed) *Some contemporary studies in marine science*. Allen & Unwin, London, pp 369–374
- Harrison K, Smith E (2008) *Rifle-green by nature*. A regency naturalist and his family, William Elford Leach. Ray Society, London
- Heller C (1857) Beiträge zur Kenntniss der Siphono stomen. *Sitzungsber Kaiserl Akad Wiss, Math-Naturwiss Cl* 25:89–108
- Hesse E (1864) Mémoire sur les pranizes et les ancées. *Mém Sav Étr Acad Sci* 18:231–302
- Ho J-S (1970) Revision of the genera of the Chondracanthidae, a copepod family parasitic on marine fishes. *Beaufortia* (No. 229) 17:105–218
- Ho J-S (1971) Parasitic copepods of the family Chondracanthidae from fishes of eastern North America. *Smithson Contrib Zool* 87:1–39
- Høeg JT (1991) Functional and evolutionary aspects of the sexual system in the Rhizocephala (Thecostraca: Cirripedia). In: Bauer RT, Martin JW (eds) *Crustacean sexual biology*. Columbia University Press, New York, pp 208–227

- Høeg JT (1992) Rhizocephala. In: Harrison FW, Humes AG (eds) *Microscopic anatomy of invertebrates, Crustacea*, vol 9. Wiley-Liss, New York, pp 313–345
- Høeg JT (1995) The biology and life cycle of the Rhizocephala (Cirripedia). *J Mar Biol Assoc UK* 75:517–550
- Høeg JT, Lützen J (1993) Comparative morphology and phylogeny of the family Thompsoniidae (Cirripedia, Rhizocephala, Akentrogonida), with description of three new genera and seven new species. *Zool Scr* 22:363–386
- Høeg JT, Lützen J (1995) Life cycle and reproduction in the Cirripedia Rhizocephala. *Oceanogr Mar Biol*:427–485
- Høeg JT, Rybakov AV (1992) Revision of the Rhizocephala Akentrogonida (Cirripedia), with a list of all the species and a key to the identification of families. *J Crust Biol* 12:600–609
- Høeg JT, Pérez-Losada M, Glenner H, Kolbasov GA, Crandall KA (2009) Evolution of morphology, ontogeny and life cycles within the Crustacea Thecostraca. *Arthropod Syst Phylo* 67:199–217
- Hoek PPC (1907) *The Cirripedia of the Siboga Expedition*. A. Cirripedia Pedunculata. Siboga-Expeditie XXXI. EJ Brill, Leiden
- Hope FW (1845) The auto-biography of John Christian Fabricius, translated from the Danish with additional notes and observations. *Trans R Entomol Soc Lond* 4:i–xvi
- Hosie AM (2014) Review of the stalked barnacle genus *Koleolepas* (Cirripedia: Thoracica: Koleolepadidae), with new records from Australian waters. *Rec West Aust Mus* 29(1):1–9
- Humes AG (1980) A review of the copepods associated with holothurians, including new species from the Indo-Pacific. *Beaufortia* 30(4):31–123
- Humes AG, Voight JR (1997) *Cholidya polypi* (Copepoda: Harpacticoida: Tisbidae), a parasite of deep-sea octopuses in the North Atlantic and northeastern Pacific. *Ophelia* 46(1):65–81
- Huys R (1991) Tantulocarida (Crustacea: Maxillopoda): a new taxon from the temporary meiobenthos. *Mar Ecol* 12:1–34
- Huys R (2001) Splanchnotrophid systematics: a case of polyphyly and taxonomic myopia. *J Crustac Biol* 21:106–156
- Huys R (2009) Unresolved cases of type fixation, synonymy and homonymy in harpacticoid copepod nomenclature (Crustacea: Copepoda). *Zootaxa* 2183:1–99
- Huys R, Boxshall GA (1991) *Copepod evolution*. The Ray Society, London
- Huys R, Boxshall GA, Casanova J-P (1993) A redescription of *Cumoniscus* Bonnier, 1903 (Crustacea: Tantulocarida) from a cumacean host in the Bay of Biscay. *Syst Parasitol* 26(1):75–79
- Huys R, Llewellyn-Hughes J, Conroy-Dalton S, Olson PD, Spinks JN, Johnston DA (2007) Extraordinary host switching in siphonostomatoid copepods and the demise of the Monstrilloidea: integrating molecular data, ontogeny and antennular morphology. *Mol Phylogenet Evol* 43:368–378
- Innal D, Avenant-Oldewage A (2012) Occurrence of *Lernaea cyprinacea* on mosquito fish (*Gambusia affinis*) from Kundu Estuary (Antalya-Turkey). *Bull Eur Assoc Fish Pathol* 32(4):140–147
- Itô T, Grygier MJ (1990) Description and complete larval development of a new species of *Baccalaureus* (Crustacea: Ascothoracida) parasitic in a zoanthid from Tanabe Bay, Honshu, Japan. *Zool Sci* 7(3):485–515
- Janovy JJ Jr (1996) In Memoriam: John Teague Self (1906–1995). *J Parasitol* 82(4):687–688
- Jordan HJ (1938) *Levensbericht van H.F. Nierstrasz*. Jaarboek: Huygens Institute – Royal Netherlands Academy of Arts and Sciences (KNAW), pp 195–198
- Kabata Z (1979) *Parasitic Copepoda of the British fishes*. The Royal Society, London
- Kabata Z (1985) *Parasites and diseases of fish cultured in the tropics*. Taylor and Francis, London
- Kaliszewska ZA, Seger J, Rowntree VJ, Barco SG, Benegas R, Best PB, Brown MW, Brownell RL Jr, Carribero A, Harcourt R, Knowlton AR, Marshall-Tilas K, Patenaude NJ, Rivarola M, Schaeff CM, Sironi M, Smith WA, Yamada TK (2005) Population histories of right whales (Cetacea: Eubalaena) inferred from mitochondrial sequence diversities and divergences of their whale lice (Amphipoda: Cyamus). *Mol Ecol* 14(11):3439–3456



- Kamens TC (1981) Mechanism of shell penetration by the burrowing barnacle *Trypetesa lampas* (Cirripedia: Acrothoracica): an ultrastructural study. MSc dissertation, University of Delaware, Newark
- Kashenko SD, Korn OM, Rybakov AV (2002) Effects of temperature and salinity on the larvae of *Sacculina polygenea* (Crustacea: Cirripedia: Rhizocephala). *Crust Res* 31:9–17
- Kas'yanov VL, Korn OM, Rybakov AV (1997) Reproductive strategy of Cirripede barnacles. 2: Asexual reproduction, fecundity, reproductive cycles. *Biol Morya* 23(6):337–344
- Kensley BF (1978) Guide to the marine isopods of southern Africa. South African Museum, Cape Town
- Kensley B, Schotte M (1989) Guide to the marine isopod crustaceans of the Caribbean. Smithsonian Institution Press, Washington, DC
- Kensley B, Schotte M, Poore GCB (2009) Gnathiid isopods (Crustacea: Isopoda: Gnathiidae), mostly new, from the Indian Ocean. *Proc Biol Soc Wash* 122(1):32–51
- Khalifa AK, Post G (1976) Histopathological effect of *Lernaea cyprinacea* (a copepod parasite) on fish. *Prog Fish-Cult* 38:110–113
- Kocylowski B, Międzyński T (1960) Choroby ryb i raków [Diseases of fish and crayfish]. PWRiL, Warsaw [in Polish]
- Kolbasov GA (2002) Cuticular structures of some acrothoracican dwarf males (Crustacea: Thecostraca: Cirripedia: Acrothoracica). *Zool Anz* 241:85–94
- Kolbasov GA (2009) Acrothoracica, Burrowing Crustaceans. KMK Scientific Press, Moscow
- Kolbasov GA, Grygier MJ, Høeg JT, Klepal W (2008a) External morphology of the two cypridiform ascothoracid-larva instars of *Dendrogaster*: the evolutionary significance of the two-step metamorphosis and comparison of lattice organs between larvae and adult males (Crustacea, Thecostraca, Ascothoracida). *Zool Anz* 247:159–183
- Kolbasov GA, Yu Sinev A, Tschesunov AV (2008b) External morphology of *Arcticotantulus pertzovi* (Tantulocarida, Basipodellidae), a microscopic crustacean parasite from the White Sea. *Entomol Rev* 88:1192–1207
- Kolbasov GA, Chan BKK, Høeg JT (2014) Acrothoracica. In: Martin JW, Olesen J, Høeg JT (eds) Atlas of Crustacean Larvae. John Hopkins Press, Baltimore, pp 107–110
- Korn OM (1985) Reproductive cycle of the cirripede barnacle *Balanus rostratus* in Peter the Great Bay, Sea of Japan. *Biol Morya* 3:36–43
- Korn OM (1989) Reproduction of the cirripede barnacle *Semibalanus cariosus* in the Sea of Japan. *Biol Morya* 5:40–48
- Korn OM, Rybakov AV, Kashenko SD (2000) Larval development in the rhizocephalan barnacle *Sacculina polygenea*. *Biol Morya* 26(5):353–356
- Korn OM, Shukalyuk AI, Trofimova AV, Isaeva VV (2004) Reproductive stage of the life cycle in the rhizocephalan barnacle *Polyascus polygenea* (Crustacea: Cirripedia). *Russ J Mar Biol* 30(5):328–340
- Krøyer H (1842) Crustacés. In: Gaimard P (ed) Atlas de Zoologie. Voyages de la Commission Scientifique du Nord en Scandinavie, en Laponie, aux Spitzberg et aux Feröe pendant les Années 1838, 1839, et 1840 sur la Corvette La Recherche, Comandée par M Frabvre. Arthus Bertrand, Paris, pp 41–43
- Krøyer H (1849) Carcinologiske Bidrag (Fortsættelse). *Naturhist Tidsskr* 2:561–609, pl VI
- Krøyer H (1863) Bidrag til kundskab om Snyltekrebsene. *Naturhist Tidsskr* 3:1–352
- Larsen SK, Høeg JT, Yusa Y (2016) Host relation, size and reproduction in the burrowing barnacle *Trypetesa lampas* (Hancock) (Crustacea Cirripedia Acrothoracica). *Zool Stud* 55:14
- Laval P (1974) Contribution à l'étude des Amphipodes Hypérides. PhD Thesis, Pierre and Marie Curie University (University of Paris VI)
- Laval P (1980) Hyperiid amphipods as crustacean parasitoids associated with gelatinous zooplankton. *Oceanogr Mar Biol Annu Rev* 18:11–56
- Leach WE (1814) Crustaceology. In: Brewster D (ed) The Edinburgh encyclopaedia. Baldwin, London, pp 383–437

- Leung Y-M (1967) An illustrated key to the species of whale-lice (Amphipoda, Cyamidae), ectoparasites of Cetacea, with a guide to the literature. *Crustaceana* 12:279–291
- Leung Y-M (1970a) First record of the whale-lice genus *Syncyamus* (Cyamidae: Amphipoda) from the western Mediterranean, with notes on the biology of Odontocete cyamids. *Invest Cetacea* 2:243–247
- Leung Y-M (1970b) *Cyamus orcini*, new species of whale-lice [Cyamidae, Amphipoda] from a killer whale. *Bull Inst Fr Afr Noire* 32(3):669–675
- Leung Y-M (1976) Life cycle of *Cyamus scammoni* (Amphipoda: Cyamidae) ectoparasite of gray whale with a remark on the associated species. *Sci Rep Whales Res Inst Tokyo* 28:153–160
- Levin MJ, Pfeiffer CJ (1999) Photoreceptor ultrastructure of the amphipod, *Cyamus ceti* (Linn, 1758), an ectoparasite of bowhead, right and gray whales. *J Submicroscop Cytol Pathol* 31:397–405
- Leydig F (1850) Ueber *Argulus foliaceus*. *Z Wiss Zool* 2:323–349
- Leydig F (1889) Ueber *Argulus foliaceus*. *Neue Mitteilung. Arch Mikrosk Anat* 33:1–51
- Lin H-C, Kobasov GA, Chan BKK (2016) Phylogenetic relationships of Darwin's "Mr. Arthrobalanus": the burrowing barnacles (Cirripedia: Acrothoracica). *Mol Phylogenet Evol* 100:292–302
- Linnaeus C (1758) *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Laurentius Salvius: Holmiae*
- Long DJ, Waggoner BM (1993) The ectoparasitic barnacle *Anelasma* (Cirripedia, Thoracica, Lepadomorpha) on the shark *Centroscyllium nigrum* (Chondrichthyes, Squalidae) from the Pacific sub-Antarctic. *Syst Parasitol* 26:133–136
- López-González PJ, Bresciani J, Huys R, González AF, Guerra A, Pascual S (2000) Discovery of *Genesis vulcanoctopusi* gen. et sp. nov. (Copepoda: Tisbidae) on a hydrothermal vent octopod and a reinterpretation of the life cycle of cholidiynid harpacticoids. *Cah Biol Mar* 41:241–253
- Lörz AN, Bruce NL (2008) Sphaeromatid isopod (Crustacea: Peracarida) assemblages in an algae-sponge association at North Stradbroke Island, southeastern Queensland. *Mem Queensl Mus* 54:253–255
- Löven S (1844) Ny art af Cirripedia: *Alepas squalicola*. *Öfvers Kongl Svenska Vetensk, Acad Förh* 1:192–194
- Lowry JK, Myers AA (2013) A Phylogeny and Classification of the Senticaudata subord. nov. (Crustacea: Amphipoda). *Zootaxa* 3610(1):1–80
- Lütken CF (1873) Bidrag til Kundskab om Arterne af Slægten *Cyamus* Latr. eller Hvallusene. *Vidensk Selsk Skr* 10(3):229–284
- Madin LP, Harbison GR (1977) The associations of Amphipoda Hyperiidea with gelatinous zooplankton – I. Associations with Salpidae. *Deep-Sea Res* 24:449–463
- Malaquin A (1901) Le parasitisme évolutif des Monstrillides (Crustacés Copépodes). *Arch Zool Exp Gén (Troisième Série)* 9:81–232
- Malta JCO (1982) Os argulídeos (Crustacea: Branchiura) da Amazônia brasileira, 2: Aspectos da ecologia de *Dolops geayi* Bouvier, 1897 e *Argulus juparanaensis* Castro, 1950. *Acta Amaz* 12:701–705
- Malta JCO, Varella A (1983) Os argulídeos (Crustacea: Branchiura) da Amazônia brasileira: 3: Aspectos da ecologia de *Dolops striata* Bouvier, 1899 e *Dolops carvalhoi* Castro, 1949. *Acta Amaz* 13:299–306
- Mamani M, Hamel C, Van Damme PA (2004) Ectoparasites (Crustacea: Branchiura) of *Pseudoplatystoma fasciatum* (surubí) and *P. tigrinum* (chuncuina) in Bolivian white-water floodplains. *Ecol Bolív* 39:9–20
- Markham JC (1982) Bopyrid isopods parasitic on decapod crustaceans in Hong Kong and southern China. In: Morton B, Tseng CK (eds) *Proceedings of the first international marine biological workshop: the marine flora and fauna of Hong Kong and Southern China, vol 1. Hong Kong, Hong Kong University Press, pp 325–391*
- Markham JC (1985) Additions to the bopyrid isopod fauna of Thailand. *Zool Verhandl* 224:1–63

- Markham JC (1986) Evolution and zoogeography of the Isopoda Bopyridae, parasites of Crustacea Decapoda. In: Gore RH, Heck KL (eds) Crustacean biogeography. Crustacean issues 4, pp 143–164
- Markham JC (1988) Descriptions and revisions of some species of Isopoda Bopyridae of the north western Atlantic Ocean. Zool Verh (Leiden) 246:1–63
- Marshall WS (1903) *Entocythere cambaria* n. g. n. sp., a parasitic ostracod. Trans Wis Acad Sci Arts Lett 14(1):117–144
- Martin MF (1932) On the morphology and classification of *Argulus* (Crustacea). Proc Zool Soc Lond 1932:771–806
- Martin JW, Heyning JE (1999) First record of *Isocyamus kogiae* Sedlak-Weinstein, 1992 (Crustacea, Amphipoda, Cyamidae) from the Eastern Pacific, with comments on morphological characters, a key to the genera of the Cyamidae, and a checklist of cyamids and their hosts. Bull South Calif Acad Sci 98(1):26–38
- Martínez R, Segade P, Martínez-Cedeira JA, Arias C, García-Estévez JM, Iglesias R (2008) Occurrence of the ectoparasite *Isocyamus deltobranchium* (Amphipoda: Cyamidae) on cetaceans from Atlantic waters. J Parasitol 94(6):1239–1242
- Massy AL (1909) The Cephalopoda Dibranchiata of the coasts of Ireland. Fisheries, Ireland, Scientific Investigations (Series 1907, part I)
- Meehan OL (1940) A review of the parasitic Crustacea of the genus *Argulus* in the collections of the United States National Museum. Proc US Natl Mus 88:459–522
- Melander Y (1950) Studies on the chromosomes of *Ulophysema oresundense*. Hereditas 36:233–255
- Mian A, Watanabe K, Shoja MM, Loukas M, Tubbs RS (2014) Guillaume Rondelet (1507–1566): cardinal physician and anatomist who dissected his own son. Clin Anat 27(3):279–281
- Miers EJ (1876) Descriptions of some new species of Crustacea, chiefly from New Zealand. Ann Mag Nat Hist 17:218–229
- Miers EJ (1877) On a collection of Crustacea, Decapoda and Isopoda, chiefly from South America, with descriptions of new genera and species. Proc Zool Soc Lond 43:653–679
- Miers EJ (1880) On a collection of Crustacea from the Malaysian Region. Part 4. Penaeidae, Stomatopoda, Isopoda, Suctorina and Xiphosura. Ann Mag Nat Hist 5:457–472
- Milne-Edwards H (1840) Histoire Naturelle des Crustacés Comprenent l’anatomie, la physiologie et la classification de ces animaux. Roret, Paris
- Møller OS (2009) Branchiura (Crustacea). Survey of historical literature and taxonomy. Arthropod Syst Phylo 67(1):41–55
- Monod T (1923) Notes carcinologiques (parasites et commensaux). Bull Instit Océanogr Monaco 427:1–5
- Monod T (1924) Parasitologia Mauritanica. Matériaux pour la faune parasitologique en Mauritanie (II Isopoda). Bull Comité Études Hist Sci Afri Occid Franç 9:67–84 (428–445)
- Monod T (1926) Les Gnathiidae. Essai monographique (Morphologie, Biologie, Systématique). Mém Soc Sci Nat Maroc 13:1–668
- Monod T (1928) Les Argulidés du Musée du Congo. Rev Zool Bot Afr 16:242–274
- Monod T (1930) Contribution à l’étude des “Cirolanidae”. Ann Sci Nat Zool (10<sup>e</sup> série) 13:129–183
- Monod T (1931) Sur quelques Crustacés aquatiques d’Afrique (Cameroun et Congo). Rev Zool Bot Afr 21(1):1–36
- Monod T (1934) Isopodes marins des campagnes du ‘de Lanessan’. Note Institut Océanogr Indochine, Saigon 23:1–22, pls 1–45
- Montagu G (1804) Description of several marine animals found on the South Coast of Devonshire. Trans Linn Soc 7:61–84
- Montagu G (1813) Description of several new or rare animals, principally marine discovered of the South Coast of Devonshire. Trans Linn Soc 11:1–26
- Moreira PS, Sadowsky V (1978) An annotated bibliography of parasitic Isopoda (Crustacea) of Chondrichthyes. Bolm Instit Oceanogr, Sao Paulo 27:95–152

- Müller F (1862) On the Rhizocephala, a new group of parasitic Crustacea. *J Nat Hist Ser 3* 10 (55):44–50
- Murphy NE, Goggin CL (2000) Genetic discrimination of sacculinid parasites (Cirripedia, Rhizocephala): implication for control of introduced green crabs (*Carcinus maenas*). *J Crust Biol* 20(1):153–157
- Murphy AE, Williams JD (2013) New records of two trypetesid burrowing barnacles (Crustacea: Cirripedia: Acrothoracica: Trypetesidae) and their predation on host hermit crab eggs. *J Mar Biol Assoc UK* 93:107–133
- Myers AA, Lowry JK (2003) A phylogeny and a new classification of the Coroppiidea Leach, 1814 (Amphipoda). *J Crust Biol* 23:443–485
- Nagler C, Hyžný M, Haug JT (2017) 168 million years old “marine lice” and the evolution of parasitism within isopods. *BMC Evol Biol* 17(1):76
- Neethling LAM, Avenant-Oldewage A (2016) Branchiura – a compendium of the geographical distribution and a summary of their biology. *Crustaceana* 89(11–12):1243–1446
- Neethling LAM, Malta JC, Avenant-Oldewage A (2014) Additional morphological information on *Dipteropeltis hirundo* Calman, 1912, and a description of *Dipteropeltis campanaformis* n. sp. (Crustacea: Branchiura) from two characiform benthopelagic fish hosts from two Northern rivers of the Brazilian Amazon. *Zootaxa* 3755(2):179–193
- Newman WA (1993) Darwin and cirripedology. In: Truesdale F (ed) *History of carcinology. Crustacean issues 8*. Balkema, Rotterdam, pp 349–434
- Nicoli RM (1963) Phylogénèse et systématique. Le phylum des Pentastomida *Ann Parasitol Hum Comp* 38:483–516
- Nierstrasz HF (1931) Isopoda genuina. II. Flabellifera. In: Weber M, De Beaufort LF (eds) *Die Isopoden der Siboga-Expedition. Siboga Expeditie (Uitkomsten op Zoölogisch, Botanisch, Oceanographisch en Geologisch Gebied verzameld in de Oost-Indische 1899–1900 aan boord H.M. Siboga onder commando van Luitenant ter zee 1e kl. G.F. Tydeman)*. E.J. Brill, Leiden, pp 123–233, pls 10–11
- Nierstrasz HF, Brender à Brandis GA (1923) *Die Isopoden der Siboga-Expedition. II. Isopoda Genuina. I. Epicaridea. Siboga Expeditie Monographie* 32b:57–121
- Noll FC (1872) *Mittheilung von Dr. F C Noll Ber Senckenb naturf Ges* 3:21–26
- Norman AM (1903) New generic names for some Entomostraca and Cirripedia. *Ann Nat Hist* 11 (7):367–369
- Oelckers K, Vike S, Duesund H, Gonzalez J, Wadsworth S, Nylund A (2014) *Caligus rogercresseyi* as a potential vector for transmission of infectious salmon anaemia (ISA) virus in Chile. *Aquaculture* 420–421:126–132
- Ogawa K, Matsuzaki K, Misaki H (1997) A new species of *Balaenophilus* (Copepoda: Harpacticoida), an ectoparasite of a sea turtle in Japan. *Zool Sci* 14:691–700
- Øksnebjerg B (2000) The Rhizocephala (Crustacea: Cirripedia) of the Mediterranean and Black seas: taxonomy, biogeography, and ecology. *Isr J Zool* 46:1–102
- Ommundsen A, Noever C, Glenner H (2016) Caught in the act: phenotypic consequences of a recent shift in feeding strategy of the shark barnacle *Anelasma squalicola* (Lovén, 1844). *Zoomorphology* 135:51–65
- Østergaard P, Boxshall GA, Quicke DL (2003) Phylogeny within the Chondracanthidae (Poecilostomatoida, Copepoda). *Zool Scr* 32(4):299–319
- Paré JA (2008) An overview of pentastomiasis in reptiles and other vertebrates. *J Exot Pet Med* 17 (4):285–294
- Peresan L, Roccatagliata D (2005) First record of the hyperparasite *Liriopsis pygmaea* (Cryptoniscidae, Isopoda) from a rhizocephalan parasite of the false king crab *Paralotnis granulosa* from the Beagle Channel (Argentina), with a redescription. *J Nat Hist* 39:311–324
- Pérez-Losada M, Høeg JT, Crandall KA (2009) Remarkable convergent evolution in specialized parasitic Thecostraca (Crustacea). *BMC Biol* 7:15

- Petrulina AS, Neretina TV, Mugue NS, Kolbasov GA (2013) Tantulocarida versus Thecostraca: inside or outside? First attempts to resolve phylogenetic position of Tantulocarida using gene sequences. *J Zool Syst Evol Res* 52(2):100–108
- Pfeiffer CJ (2002) Whale lice. In: Perrin WF, Würsig B, Thewissen JGM (eds) *Encyclopedia of marine mammals*. Academic Press, San Diego, CA, pp 1302–1305
- Pfeiffer CJ, Viers V (1998) Microanatomy of the marsupium, juveniles, eggs and cuticle of cyamid ectoparasites (Crustacea: Amphipoda) of whales. *Aquat Mamm* 24:83–91
- Piasecki W, Avenant-Oldewage A (2008) Diseases caused by Crustacea. In: Eiras JC, Segner H, Wahli T, Kapoor BG (eds) *Fish diseases*. Science Publishers, Enfield, NH, pp 1115–1200
- Piasecki W, Goodwin AE, Eiras JC, Nowak BF (2004) Importance of Copepoda in freshwater aquaculture. *Zool Stud* 43(2):193–205
- Poly WJ (2003) *Argulus ambystoma*, a new species parasitic on the salamander *Ambystoma dumerilii* from Mexico (Crustacea: Branchiura: Argulidae). *Ohio J Sci* 103:52–61
- Poly WJ (2008) Global diversity of fishlice (Crustacea: Branchiura: Argulidae) in freshwater. *Hydrobiologia* 595:209–212
- Rees DJ, Noever C, Høeg JT, Ommundsen A, Glenner H (2014) On the origin of a novel parasitic-feeding mode within suspension-feeding barnacles. *Curr Biol* 24:1429–1434
- Richardson H (1905) A monograph on the isopods of North America. *Bull US Natl Mus* 54:1–727
- Riley J (1986) The biology of pentastomids. *Adv Parasitol* 25:45–128
- Riley J (1994) A revision of the genus *Alofia* Giglioli, 1992 and a description of a new monotypic genus, *Selfia*: Two genera of pentastomid parasites (Porocephalida: Sebekidae) inhabiting the bronchioles of the marine crocodile *Crocodylus porosus* and other crocodylians. *Syst Parasitol* 29:23–41
- Riley J, Spratt DM, Winch JM (1990) A revision of the genus *Sebekia* Sambon, 1922 (Pentastomida) from crocodylians with descriptions of five new species. *Syst Parasitol* 16:1–25
- Ringuelet R (1943) Revisión de los Argúlidos Argentinos (Crustácea, Branchiura) Con el catálogo de las especies Neotropicales. *Rev Mus La Plata (Nueva Serie)*. Sección Zoológica 3(19):43–99
- Ringuelet R (1948) Argúlidos del Mueso de La Plata. *Rev Mus La Plata (Nueva Serie)* 5:281–296
- Risso A (1816) *Histoire naturelle des Crustacés des environs de Nice*. Librairie Grecque-Latine-Allemande, Paris
- Rohde K (2005) *Marine parasitology*. CSIRO Publishing, Melbourne
- Röhlig D, Dunlop JA, Grau JH, Friederichs A (2010) An annotated catalogue of the tongue worms (Pentastomida) held in the Museum für Naturkunde Berlin. *Zoosyst Evol* 86(1):129–154
- Rondelet G (1554) *Libri de Piscibus Marinus, in quibus verae Piscibus effigies expressae sunt*. Matthias Bonhomme, Lyon
- Ross A, Newman WA (1967) Eocene Balanidae of Florida, including a new genus and species with a unique plan of “Turtle Barnacle” organization. *Am Mus Novit* 2288:1–21
- Ross A, Newman WA (1969) A coral-eating barnacle. *Pacific Sci* 23(2):252–256
- Ross A, Newman WA (1995) A coral-eating barnacle, revisited (Cirripedia: Pyrgomatidae). *Contrib Zool* 65:139–175
- Ross A, Newman WA (2000) A new coral-eating barnacle: the first record from the Great Barrier Reef, Australia. *Mem Queensl Mus* 45(2):585–591
- Rowntree VJ (1996) Feeding, distribution, and reproductive behavior of cyamids (Crustacea: Amphipoda) living on humpback and right whales. *Can J Zool* 74:103–109
- Rushton-Mellor SK (1994a) The genus *Argulus* (Crustacea: Branchiura) in Africa: two new species, *A. fryeri* and *A. gracilis*, the previously undescribed male of *A. brachypeltis* Fryer and the identity of the male described as *A. ambloplites* Wilson. *Syst Parasitol* 28:23–31
- Rushton-Mellor SK (1994b) The genus *Argulus* (Crustacea: Branchiura) in Africa: redescription of type-material collected by W.A. Cunningham during the Lake Tanganyika Expedition in 1913, with notes on *A. giganteus* Lucas and *A. arcassonensis* Cuénot. *Syst Parasitol* 28:33–49
- Rushton-Mellor SK (1994c) The genus *Argulus* (Crustacea: Branchiura) in Africa: identification keys. *Syst Parasitol* 28:51–63
- Sambon LW (1922a) A synopsis of the family Linguatulidae. *J Trop Med Hyg* 25:188–206

- Sambon LW (1922b) A synopsis of the family Linguatulidae. *J Trop Med Hyg* 25:391–428
- Savchenko AS, Kolbasov GA (2009) *Serratotantulus chertoprudae* gen. et sp. n. (Crustacea, Tantulocarida, Basipodellidae): a new tantulocaridan from the abyssal depths of the Indian Ocean. *Integr Comp Biol* 49(2):106–113
- Schell DM, Rowntree VJ, Pfeiffer CJ (2000) Stable-isotope and electron-microscopic evidence that cyamids (Crustacea: Amphipoda) feed on whale skin. *Can J Zool* 78(5):721–727
- Schioedte JC, Meinert F (1879) Symbolæ ad monographium Cymothoarum crustaceorum isopodum familiæ. I. Aegidæ. *Naturhistorisk Tidsskrift, Kjøbenhavn* 12:321–414, pls 327–313
- Schioedte JC, Meinert F (1881) Symbolæ ad monographium Cymothoarum crustaceorum isopodum familiæ. II. Anilocridæ. *Naturhistorisk Tidsskrift, Kjøbenhavn* 13:1–166, pls 161–110
- Schioedte JC, Meinert F (1883) Symbolæ ad monographium Cymothoarum crustaceorum familiæ. III. Saophridæ. IV. Ceratothoinæ. *Naturhistorisk Tidsskrift, Kjøbenhavn* 13:281–378, pls 211–286
- Schioedte JC, Meinert F (1884) Symbolæ ad monographium Cymothoarum crustaceorum isopodum familiæ. IV. Cymothoidæ Trib. II. Cymothoinæ. Trib. III: Lironecinæ. *Naturhistorisk Tidsskrift, Kjøbenhavn* 14:221–454, pls 226–213
- Schotte M (2005) Obituary: Brian Frederick Kensley. *J Crust Biol* 25(1):165–174
- Sexton EW (1908) On the amphipod genus *Trischizostoma*. *Proc Zool Soc Lond* 78(2):370–402
- Slabber M (1769) Naturkundige Verlostingingen behelzende Microscopische waarneemingen van in- en uitlandse Water- en Land- Dieren door Martinus Slabber. Haarlem
- Smit NJ, Davies AJ (2004) The curious life-style of the parasitic stages of gnathiid isopods. *Adv Parasitol* 58:289–391
- Smit NJ, Bruce NL, Hadfield KA (2014) Global diversity of fish parasitic isopod crustaceans of the family Cymothoidae. *Int J Parasitol Parasites Wildl* 3:188–197
- Smith G (1904) Metamorphosis and life-history of *Gnathia maxillaris*. *Mitt Zool Stn Neapel* 16:469–474
- Spooner GM (1960) Obituary Mrs E. W. Sexton, F.L.S. (1868–1959). *J Mar Biol Assoc UK* 39(1):1–4
- Spratt DM (2010) *Yelirella* nomen novum for *Rileyella* Spratt, 2003 (Pentastomida: Cephalobaenida), a junior homonym of *Rileyella* Townsend, 1909 (Diptera: Tachinidae). *Parasite (Paris, France)* 17(4):319
- Stebbing TRR (1910a) General catalogue of South African Crustacea. (Part V. of S. A. Crustacea, for the Marine Investigations in South Africa). *Ann S Afr Mus* 6:281–594, pls 216–222
- Stebbing TRR (1910b) Isopoda from the Indian Ocean and British East Africa. No. 6. Reports of the Percy Sladen Trust Expedition to the Indian Ocean in 1905. *Trans Linn Soc Lond Zool* 2:83–122, pls 125–111
- Stepien CA, Brusca RC (1985) Nocturnal attacks on nearshore fishes in southern California by crustacean zooplankton. *Mar Ecol Prog Ser* 25:91–105
- Stuhlmann F (1891) Zur kenntniss der Fauna central-afrikanischer Seen II. Ueber eine neue Art der Arguliden-Gattung *Gyropeltis*. *Zoologische Jahrbucher, Abteilung für Systematik* 5:152–154
- Suárez-Morales E (2011) Diversity of the Monstrilloida (Crustacea: Copepoda). *PLoS One* 6(8): e22915
- Suárez-Morales E, McKinnon AD (2014) The Australian Monstrilloida (Crustacea: Copepoda) I. *Monstrillopsis* Sars, *Maemonstrilla* Grygier & Ohtsuka, and *Australomonstrillopsis* gen. nov. *Zootaxa* 3779(3):301–340
- Suárez-Morales E, Morales-Vela B, Padilla-Saldívar J, Silva-Briano M (2010) The copepod *Balaenophilus manatorum* (Ortíz, Lalana and Torres, 1992) (Harpacticoida), an epibiont of the Caribbean manatee. *J Nat Hist* 44:847–859
- Suriray JSA (1819) Sur les oeufs de Calyge. *J Phys Chim Hist Nat Art* 89:400
- Sutherland DR, Wittrock DD (1985) The effects of *Salmincola californiensis* (Copepoda: Lernaeopodidae) on the gills of farm-raised rainbow trout, *Salmo gairdneri*. *Can J Zool* 63:2893–2901

- Swanepoel JH, Avenant-Oldewage A (1993) Functional morphology of the foregut of *Chonopeltis australis* Boxshall (Branchiura). *J Crust Biol* 13:656–666
- Tam Q, Avenant-Oldewage A (2006) The digestive system of larval *Argulus japonicus* (Branchiura). *J Crust Biol* 26:447–454
- Tam Q, Avenant-Oldewage A (2009) The ultrastructure of the digestive cells of *Argulus japonicus*, Thiele 1900 (Crustacea: Branchiura). *Arthropod Struct Dev* 38:45–53
- Thatcher VE (1991) Amazon fish parasites. *Amazoniana* 11(3/4):263–572
- Thatcher VE (1995) Comparative pleopod morphology of 11 species of parasitic isopods from Brazilian fish. *Amazoniana* 13:305–314
- Thatcher VE (1997) Mouthpart morphology of six freshwater species of Cymothoidae (Isopoda) from Amazonian fish compared to that of three marine forms, with the proposal of *Artystonenae* subfam. nov. *Amazoniana* 14:311–322
- Thatcher VE (2000) The isopod parasites of South American fishes. In: Salgado-Maldonado G, Aldrete ANG, Vidal-Martinez VM (eds) *Metazoan parasites in the Neotropics: a systematic and ecological perspective Mexico*. Univ Nacional Autónoma de México, Instituto de Biología, pp 193–226
- Thiele J (1904) Beiträge zur Morphologie der Arguliden. *Mitt Zool Mus Berl* 2:5–51
- Thomas JD (1992) J Laurens Barnard (1928–1991). *J Crust Biol* 12(2):324–326
- Thorell T (1864) Om tvenne europeiske Argulider; jemte anmärkningar om Argulidernas morfologi och systematiska ställning, samt en öfversigt af de för närvarande kända arterna af denna familj. *Öfvers Kongl Vetensk-Akad Förh* 1:7–72
- Tomlinson JT (1969) The burrowing barnacles: (Cirripedia: Order Acrothoracica). *Bull US Natl Mus* 296:1–162
- Tomlinson JT (1987) The burrowing barnacles (Acrothoracica). In: Southward AJ (ed) *Barnacle biology, Crustacean issues 5*. A. A. Balkema, Rotterdam, pp 63–71
- Trilles J-P (1972) Les Cymothoidae (Isopoda, Flabellifera) du Muséum National d'Histoire Naturelle de Paris. Étude critique accompagnée de précisions en particulier sur la répartition géographique et l'écologie des différentes espèces représentées. I. Les Ceratothoinae Schiøedte et Meinert, 1883. *Bull Mus Natl Hist Nat (3ème Série, Zool)* 70:1231–1268
- Trilles J-P (1977) Les Cymothoidae (Isopoda, Flabellifera; parasites de poissons) du Rijksmuseum van Natuurlijke Historie de Leiden. Méditerranée et Atlantique nord-oriental *Zool Meded (Leiden)* 52:7–17
- Trilles J-P (1994) Les Cymothoidae (Crustacea, Isopoda) du Monde. *Prodrome pour une faune. Studia Marina* 21–22:1–288 [for 1991]
- Trilles J-P (2008) Some marine isopods from the Senckenberg Research Institute (Frankfurt am Main, Germany) (Crustacea, Isopoda: Cymothoidae, Aegidae, Corallanidae, Cirolanidae). *Senckenb Biol* 88:21–28
- Truesdale F (1993) *History of carcinology*. CRC Press, Rotterdam
- Tsuchida K, Lützen J, Nishida M (2006) Sympatric three-species infection of *Sacculina* parasites (Cirripedia: Rhizocephala: Sacculinidae) of an intertidal grapsoid crab. *J Crust Biol* 26:474–479
- Uyeno D, Nagasawa K (2012) Four new species of splanchnotrophid copepods (Poecilostomatoida) parasitic on doridacean nudibranchs (Gastropoda, Opisthobranchia) from Japan, with proposition of one new genus. *ZooKeys* 247:1–29
- Väänölä R, Witt J, Grabowski M, Bradbury J, Jazdzewski K, Sket B (2008) Global diversity of amphipods (Amphipoda; Crustacea) in freshwater. *Hydrobiologia* 595(1):241–255
- Van As JG (1986) A new species of *Chonopeltis* (Crustacea: Branchiura) from the Limpopo system, southern Africa. *S Afr J Zool* 21:348–351
- Van As JG (1992) A new species of *Chonopeltis* (Crustacea: Branchiura) from the Zambesi River system. *Syst Parasitol* 22:221–229
- Van As LL, Van As JG (1993) First record of *Chonopeltis inermis* Thiele, 1900 (Crustacea: Branchiura) in the Limpopo River system with notes on its morphology. *Syst Parasitol* 24:229–236

- Van As LL, Van As JG (1996) A new species of *Chonopeltis* (Crustacea: Branchiura) from the southern Rift Valley, with notes on larval development. *Syst Parasitol* 35:69–77
- Van As JG, Van As LL (1999a) *Chonopeltis liversedgei* sp. n. (Crustacea: Branchiura), parasite of the western bottlenose *Mormyrus lacerda* (Mormyridae) from the Okavango Delta, Botswana. *Folia Parasitol* 46:319–325
- Van As LL, Van As JG (1999b) Aspects of the morphology and a review of the taxonomic status of three species of the genus *Chonopeltis* (Crustacea: Branchiura) from the Orange-Vaal and South West Cape River systems, South Africa. *Folia Parasitol* 48:221–228
- Van As LL, Smit NJ, van As JG (2017) Rediscovery of *Chonopeltis meridionalis* Fryer, 1964 (Crustacea: Branchiura) from *Labeo rosae* Steindachner in the River Olifants, Mpumalanga, and the taxonomic status of *C. victori* Avenant-Oldewage, 1991 and *C. koki* Van As, 1992. *Syst Parasitol* 94:797–807
- Vinogradov GM (1991) [A new species of *Trischizostoma* (Amphipoda: Gammaridea) from the Indian Ocean (with a key to species)]. *Zool Zhurnal* 70:25–31 [Russian]
- von Haffner K (1971) Das Pentastomidenproblem (Tagmosis, Metamerie, Organisation, Evolution, systematische Stellung). *Mitt StInst Zool Mus Hamb* 67:53–107
- von Haffner K (1973) Über die Entwicklung, vergleichende Anatomie und Evolution der Extremitäten von Pentastomiden. *Z Zool Syst Evol* 11:241–268
- Voris HK, Jeffries WB, Poovachiranon S (2000) Size and location relationships of stalked barnacles of the genus *Octolasmis* on the mangrove crab, *Scylla serrata*. *J Crustac Biol* 20:485–496
- Wagin VL (1976) Ascithoracida. Kazan University Press, Kazan, USSR. [Russian]
- Walker G (2001) Introduction to the Rhizocephala (Crustacea: Cirripedia). *J Morphol* 249(1):1–8
- Weibezahn FH, Cobo T (1964) Seis argulidos (Crustacea: Branchiura) parasitos de peces dulce-acuicolas en Venezuela, con descripción de una nueva especie del genero *Argulus*. *Acta Biol Venez* 4:119–144
- Williams EH Jr (1978) *Conchoderma virgatum* (Spengler) (Cirripedia Thoracica) in association with *Dinemoura latifolia* (Steenstrup & Lutken) (Copepoda, Caligidea), a parasite of the shortfin mako, *Isurus oxyrinchus* Rafinesque (Pisces, Chondrichthyes). *Crustaceana* 34 (1):109–110
- Williams JD, Boyko CB (2012) The global diversity of parasitic isopods associated with crustacean hosts (Isopoda: Bopyroidea and Cryptoniscoidea). *PLoS One* 7(4):e35350. <https://doi.org/10.1371/journal.pone.0035350>
- Williams EH Jr, Bunkley Williams L (1986) The first *Anilocra* and *Pleopodias* isopods (Crustacea: Cymothoidae) parasitic on Japanese fishes, with three new species. *Proc Biol Soc Wash* 99:647–657
- Williams EH Jr, Bunkley-Williams L (2000) On the generic placement of ‘*Livoneca* sp.’: a critique of Colomni et al. (1997). *Dis Aquat Org* 40:233–234
- Williams BW, Weaver PG (2018) A historical review of the taxonomy and classification of Entocytheridae (Crustacea: Ostracoda: Podocopida). *Zootaxa* 4448(1):1–129
- Williams EH Jr, Bunkley Williams L, Waldner RE, Kimmel JJ (1982) Predisposition of a pomacentrid fish, *Chromis multilineatus* (Guichenot) to parasitism by a cymothoid isopod, *Anilocra chromis* Williams and Williams. *J Parasitol* 68:942–945
- Williams JD, Gallardo A, Murphy AE (2011) Crustacean parasites associated with hermit crabs from the western Mediterranean Sea, with first documentation of egg predation by the burrowing barnacle *Trypetesa lampas* (Cirripedia: Acrothoracica: Trypetesidae). *Integr Zool* 6:13–27
- Wilson CB (1902) North American parasitic copepods of the family Argulidae, with a bibliography of the group and a systematic review of all known species. *Proc US Natl Mus* 25:635–742
- Wilson CB (1904a) A new species of *Argulus*, with a more complete account of two species already described. *Proc US Natl Mus* 27:627–655
- Wilson CB (1904b) The fish parasites of the genus *Argulus* found in the Woods Hole region. *Bull Bur Fish* 24:115–131
- Wilson CB (1911) North American parasitic copepods belonging to the family Ergasilidae. *Proc US Natl Mus* 39:263–400, pl 41–60



- Wilson CB (1913) Crustacean parasites of West Indian fishes and land crabs, with descriptions of new genera and species. *Proc US Natl Mus* 44:189–277
- Wilson CB (1916) Copepod parasites of fresh-water fishes and their economic relations to mussel glochidia. *Bull Bur Fish* 34:331–374
- Wilson CB (1920a) Parasitic copepods from the Congo basin. *Bull Am Mus Nat Hist* 43:1–8
- Wilson CB (1920b) Argulidae from the Shubenacadie River, Nova Scotia. *Can Field Nat* 34:149–151
- Wilson CB (1921) Parasitic copepods from Japan, including five new species. *Ark Zool* 14:1–17
- Wilson CB (1923) New species of parasitic copepods from Southern Africa. *Meddel Göteborg Mus Zool Avd* 19:3–12
- Wilson CB (1924) New North American parasitic copepods, new hosts, and notes on copepod nomenclature. *Proc US Natl Mus* 64:1–22
- Wilson CB (1932) The copepods of the Woods Hole region of Massachusetts. *Bull US Nat Mus* 158:1–635
- Wilson CB (1944) Parasitic copepods in the United States National Museum. *Proc US Natl Mus* 94:529–582
- Winfield I, Hendrickx ME, Ortiz M (2017) A new deep-water species of *Trischizostoma* (Crustacea: Amphipoda: Gammaridea: Trischizostomatidae) from western Mexico, NE Pacific Ocean. *J Mar Biol Assoc UK* 97(1):141–149
- Wolfe BA, Harms CA, Groves JD, Loomis MR (2001) Treatment of *Argulus* sp. infestation of river frogs. *Contemp Top Lab Anim Sci* 40:35–36
- Yano K, Musick JA (2000) The effect of the mesoparasitic barnacle *Anelasma* on the development of reproductive organs of deep-sea squaloid sharks, *Centroscyllium* and *Etmopterus*. *Environ Biol Fish* 59(3):329–339
- Young W (1971) Ecological studies of the Entocytheridae (Ostracoda). *Am Midl Nat* 85:399–409
- Yusa Y, Yamato S (1999) Cropping of sea anemone tentacles by a symbiotic barnacle. *Biol Bull Mar Biol Lab, Woods Hole* 197:315–318
- Yusa Y, Yamato S, Marumura M (2001) Ecology of a parasitic barnacle, *Koleolepas avis*: Relationship to the hosts, distribution, left-right asymmetry and reproduction. *J Mar Biol Assoc UK* 81:781–788
- Zeidler W (2003a) A review of the hyperiidean amphipod family Cystisomatidae Willemöes-Suhm, 1875 (Crustacea: Amphipoda: Hyperiidea). *Zootaxa* 141:1–43
- Zeidler W (2003b) A review of the hyperiidean amphipod superfamily Vibilioidea Bowman & Gruner, 1973 (Crustacea: Amphipoda: Hyperiidea). *Zootaxa* 280:1–104
- Zeidler W (2004a) A review of the hyperiidean amphipod superfamily Lycaeopsoidea Bowman & Gruner, 1973 (Crustacea: Amphipoda: Hyperiidea). *Zootaxa* 520:1–18
- Zeidler W (2004b) A review of the families and genera of the hyperiidean amphipod superfamily Phronimoidea Bowman & Gruner, 1973 (Crustacea: Amphipoda: Hyperiidea). *Zootaxa* 567:1–66
- Zeidler W (2006) A review of the hyperiidean amphipod superfamily Archaeoscinoidea Vinogradov, Volkov & Semenova, 1982 (Crustacea: Amphipoda: Hyperiidea). *Zootaxa* 1125:1–37
- Zeidler W (2009) A review of the hyperiidean amphipod superfamily Lanceoloidea Bowman & Gruner, 1973 (Crustacea: Amphipoda: Hyperiidea). *Zootaxa* 2000:1–117
- Zeidler W (2012) A review of the hyperiidean amphipod families Mimonectidae and Proscinidae (Crustacea: Amphipoda: Hyperiidea: Scinoidea). *Zootaxa* 3533:1–74
- Zeidler W (2015) A review of the hyperiidean amphipod genus *Hyperoche* Bovallius, 1887 (Crustacea: Amphipoda; Hyperiidea: Hyperiidae), with the description of a new genus to accommodate *H. shihi* Gasca, 2005. *Zootaxa* 3905(2):151–192
- Zeidler W, De Broyer C (2009) Catalogue of the Hyperiidean Amphipoda (Crustacea) of the Southern Ocean with distribution and ecological data. In: De Broyer C (ed) *Census of Antarctic marine life: synopsis of the amphipoda of the Southern Ocean*, vol 3. *Bull Inst R Sci Nat Belg Biol* 79(Suppl 1), pp 1–96