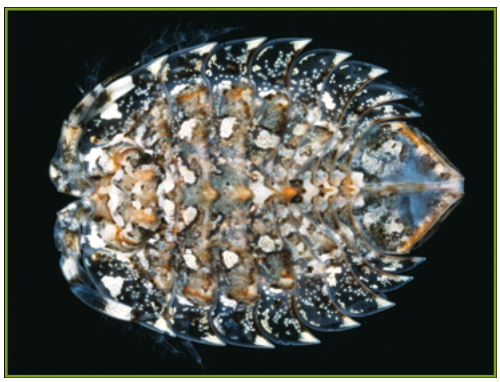
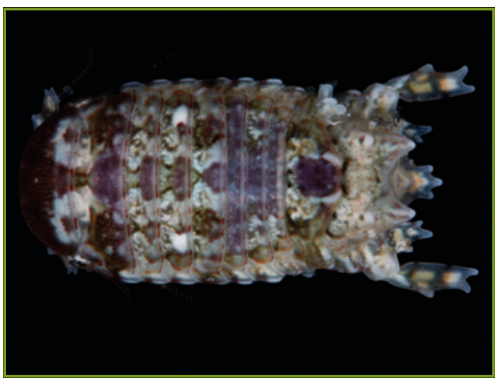
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Marine Crustacea Isopoda: guide to families and genera of the world

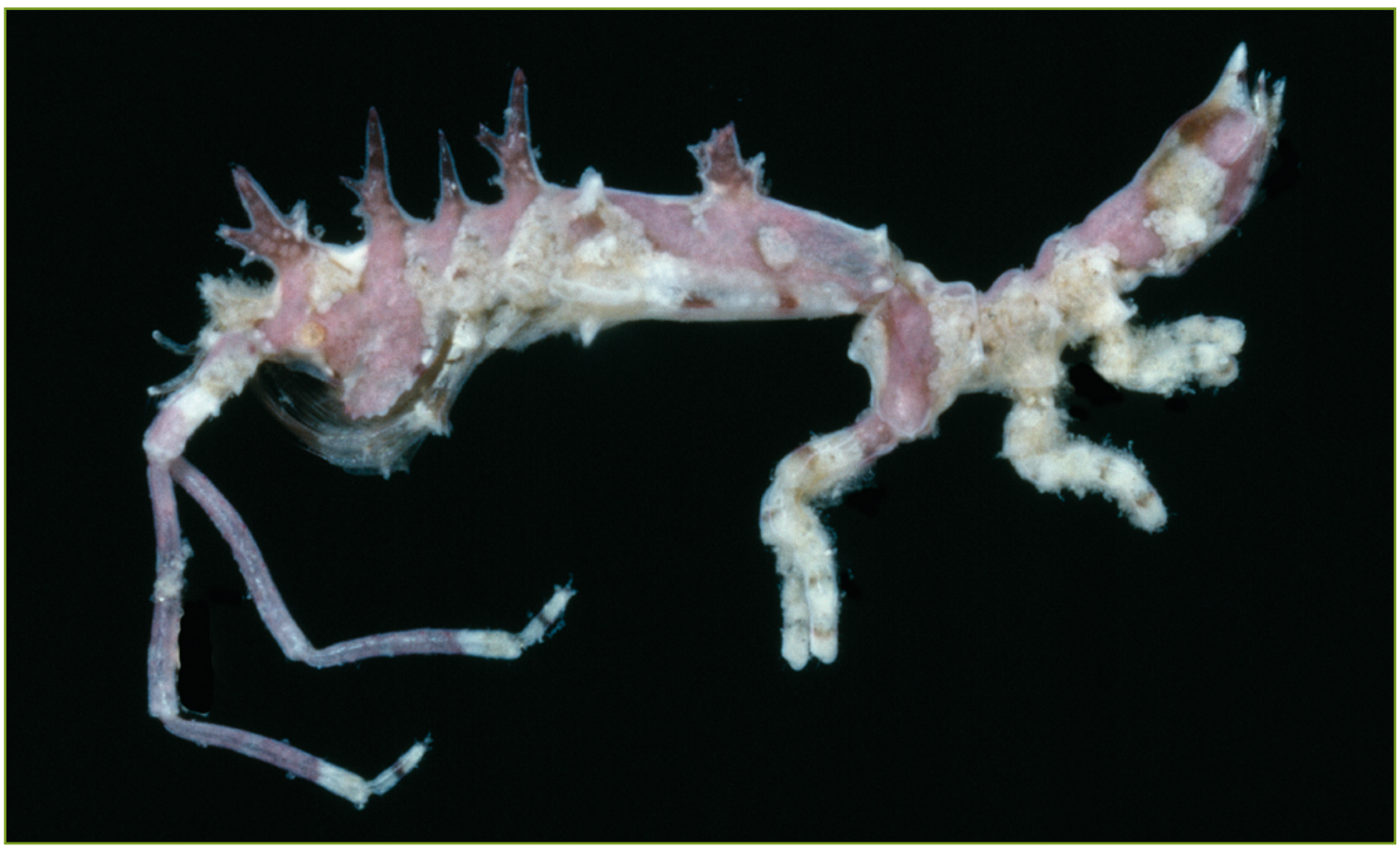
Edited by Gary C. B. Poore

Volume 86 June 2026









Cover images: Top left to bottom, *Serolina delaria* Poore, 1987 (Serolidae); *Paracilicaea septemdentata* (Baker, 1910) (Sphaeromatidae); *Elaphognathia ferox* (Haswell, 1884) (Gnathiidae); *Neastacilla tharnardi* King, 2003 (Arcturidae). All photos by Michael Marmach of isopods collected in Victoria, Australia.

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Marine Crustacea Isopoda: guide to families and genera of the world

Gary C. B. Poore (editor)

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Preface

My interest in crustacean taxonomy, isopods in particular, began in 1969 when I took a job as a benthic ecologist in Victoria, Australia, researching the impact of a sewage farm on a marine ecosystem, Port Phillip Bay. This involved a survey of benthic marine invertebrates which I quickly learned comprised a largely undescribed fauna. An essential reference enabling me to start identifying the crustacean fauna was Jerry Laurens Barnard's book published that same year by the United States National Museum, *The families and genera of marine gammaridean Amphipoda.* This work provided keys to families and genera of a common taxon that at least enabled species to be sorted and given interim family and genus names. It provided a lead to the older literature. Few such compendia existed then for other groups of Crustacea, least of all for marine Isopoda. Jerry visited Australia several times during the 1960s and 1970s and described many amphipod species updating the names in his 1969 book. He also encouraged me to begin describing the many new isopod species being discovered in Port Phillip Bay and nearby Western Port. Now, after 57 years, inspired by the leg-up that *The families and genera of marine gammaridean Amphipoda* gave me, it is long overdue to do the same for marine Isopoda. I have been aided in this endeavour by three other isopod taxonomists, Chris Boyko, Niel Bruce and Jason Williams.

The contributors and I have been encouraged by our opportunities to work with many specialists, in the lab and in the field, whose enthusiasm has rubbed off. We thank them all. Some have since died: Thomas Bowman, Desmond Hurley, Brian Kensley, Bob Menzies, Oleg Kussakin, S. M. Shiino and Torben Wolff. Others continue to be inspirational today: Angelika Brandt, Saskia Brix, Brenda Doti, Bob Hessler, David Holdich, Jean Just, Stephanie Kaiser, Rachael King, Marina Malyutina, John Markham, Kelly Merrin, Noburu Nunomura, Jörundur Svavarsson, Michitaka Shimomura, Wolfgang Wägele, Regina Wetzer and G.D.F. "Buz" Wilson. Other pioneers were inspirational but died before our time: W.T. Calman, James D. Dana, Herbert M. Hale, H. J. Hansen, William E. Leach, Edward J. Miers, H.F. Nierstrasz, Åke Nordenstam, Harriet Richardson, Geog O. Sars, Edith M. Sheppard and Thomas R. R. Stebbing. All of these, either directly or indirectly, helped with this work.

This review has greatly benefitted from ready access to lists of taxa and published works. We appreciate very much the catalogue at WoRMS (World Register of Marine Species) and thank the Database Management Team led by Leen Vendepitte and the isopod editors past and present who keep the catalogue up to date. We are also thankful for the literature available on the Biodiversity Heritage Library and commend all those responsible for making this available.

Although this is largely a synthetic work relying primarily on what has been published, it has only been made possible with access to diverse and well catalogued collections in many museums across the world. Collection and expedition staff museums have enabled us to explore marine isopod diversity.

Most illustrations are original but we thank the publishers of several journals for allowing us to reproduce figures directly: American Museum of Natural History, Australian Museum, Biological Society of Washington, Brill, Cambridge University Press, Carcinological Society of Japan, Columbia University Press, CSIRO Publishing, Elsevier, Florida Fish and Wildlife Conservation Commission, Hong Kong University Press, Japanese Society of Fisheries Science, Kitakyushu Museum of Natural History and Human History, Kyoto University, Leiden University Libraries, Magnolia Press, Musée Océanographique de Monaco, Muséum national d'Histoire naturelle, Paris, Museums and Art Galleries of the Northern Territory, Museums Victoria, Oxford University Press, Pensoft Publishers, Queensland Museum, San Diego Society of Natural History, Science Direct, Scripps Institution of Oceanography, Senckenberg Museum, Smithsonian Institution, Southern California Academy of Sciences, Springer Nature, Taylor & Francis, Universiteit van Amsterdam, University of Copenhagen, University of Guam, Western Australian Museum, Wiley, and the Zoological Society of Japan.

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Chapter 1. Introduction to the Isopoda

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Identification of species, the most fundamental unit in taxonomy, is the essential first step of any biological study. This introduction to a guidebook to families and genera of marine isopods of the world outlines the significance of isopods in marine environments, summarises taxonomical research, explains how the guidebook provides access to what has been written before, and lays out the conventions and information contained in subsequent chapters.

Keywords Isopoda, history, resources

Introduction

Identification of species, the most fundamental unit in taxonomy, is the essential first step of any biological study. Confidence in any report on a species' ecology, physiology or behaviour, and trust in a species list in multispecies research, depend on the study organism, or organisms, being reliably labelled with their current scientifically accepted name. Knowing that one's target organism is several species rather than one, or vice versa, has considerable impact on the conclusions that can be drawn (Schram and Ng, 2012).

Naming of species is managed by taxonomists and is governed by rules and conventions (International Commission on Zoological Nomenclature, 1999). Using the taxonomic literature to ensure that the subject of a researcher's study is identified correctly can be difficult for a non-taxonomist, and troublesome for anyone not familiar with all families in a particular group. Names and the classificatory hierarchy may change with time in the light of research on taxonomic affinities and relationships, but such changes are traceable. The problem is exacerbated in multispecies projects. This guidebook aims to enable biologists to identify any marine isopod to the level of family and genus. The dichotomous keys lead to diagnoses of 86 families, nine subfamilies (of Bopyridae) and 891 genera. A guidebook of over 400 pages cannot be a resource for identification to the species level, but references to key literature are included that should facilitate more precise identification.

Isopods, order Isopoda, are members of Crustacea, a group that includes crayfish, crabs, shrimps and lobsters. Not being large or otherwise easily noticed, marine isopods have few common names, although pill bug (for those that can roll up), sand louse or sea louse (for those that scavenge), fish louse (for those that parasitise fishes), sea centipede (for thin species associated with plants), gribble (for those bore into wood or algae) and sponge mite (for those associated with sponges) are some names adopted by an Australian authority in the 1920s (Hale, 1929). Terrestrial isopods, not covered in this work, are known as slaters or woodlice.

Crustaceans play critical roles in the ecology of the oceans, acting as important trophic links, including as scavengers, predators, parasites and food for many of their cohabitants. Crustaceans range in size from 0.1 mm in maximum diameter (a tantulocarid parasite) to 4 m across (a Japanese spider crab). One species of oceanic copepod, *Oithona similis* Claus, 1866 may be the most common animal on earth (Gallienne and Robins, 2001). Additionally, crustaceans have been found almost as far back in the fossil record as any group of complex animals.

Crustacea generally are most diverse in the marine environment (77% of species occur in the sea) (Poore and Ahyong, 2023) but are represented in fresh water and on land. Isopods are similarly wide-ranging. The global number of marine animals for which we have accepted names is almost 300,000 (as of 21 March 2025), of which 23% (almost 67,000) are crustaceans (Appeltans et al., 2012; Poore and Ahyong, 2023; Vandepitte et al., 2024). On 21 March 2025 the *World Marine, Freshwater and Terrestrial Isopod Crustaceans Database* (Boyko et al., 2025), a subregister of the World Register of Marine Species (WoRMS) listed 10,838 accepted species of Isopoda (13% of Crustacea from all environments), of which 6253 (58%) are marine or brackish (Ahyong et al., 2011; Appeltans et al., 2012; Hartebrodt et al., 2023, updated in 2025 from WoRMS). About a third (36%) of the non-marine species belong to the terrestrial superfamily Oniscoidea. Isopods therefore represent about 17% of all known marine crustacean species, many more than the number of known brachyuran crabs (WoRMS Editorial Board, 2025).

It is widely accepted that the number of described species (those with Linnaean names) is just a small fraction of the true number of species, which has been estimated at 0.3–2+ million for the world's oceans (Appeltans et al., 2012). The reason for this underestimate, for most of Crustacea, is typically not because they are hard to recognise. We know from childhood what a crayfish, crab, shrimp or lobster looks like, and have a general concept of crustaceans. In a catch of animals from a marine habitat it is simple to separate larger crustaceans from fish, snails, worms and seastars. However, crustaceans can be extremely abundant and diverse. Densities may be in thousands of individuals per square metre of sea floor or cubic metre of ocean water, and many different kinds live side by side. Many surveys reveal numerous unnamed crustaceans, particularly in groups such as the isopods that are composed mostly of smaller (<1 cm) species, can be quite cryptic and comprise mostly undescribed species (Brandt et al., 2004; Poore et al., 2014). Based on current rates of species descriptions, over 600 species of isopod are projected to be described by 2100, mostly from marine environments (Hartebrodt et al., 2023). It is predicted that ultimately there remain several times this many undescribed isopod species, especially considering the cryptic species and parasitic groups that have been sampled poorly (Williams and Boyko, 2012).

Environmental awareness exploded in the 1970s, and this was accompanied, particularly in Australia, South Africa, the USSR and the USA, by surveys of marine invertebrates and descriptions of many newly discovered species of marine Isopoda (see species described by G.C.B. Poore, N.L. Bruce, B. Kensley, O.G. Kussakin, T.E. Bowman, J.C. Markham and R.C. Brusca). Until recently, deep ocean basins were little explored (Hessler and Sanders, 1967; Kussakin, 1967) but are now showing that Isopoda are a significant fraction of the benthic fauna. The only survey of a bathyal fauna along the southeastern Australian coast discovered 359 species of isopods (90% new) (Poore et al., 1994), with some subsequently described in the 30-year period since. Isopods accounted for 35% of all peracarid species encountered on the Antarctic shelf (Brandt, 1999; Brökeland et al., 2007), many being undescribed. A study of Gulf of Mexico isopods found 62 of 135 species (46%) to be undescribed (Wilson, 2008). A continent-wide survey of marine invertebrates discovered 118 undescribed species among 127 isopods (93% new) (Poore et al., 2014). A similar percentage (96.8%) of new isopods was found in the Clarion–Clipperton Zone in the deep Pacific Ocean (Rabone et al., 2023). These and exploratory surveys of other marine environments such as coral and rocky reefs have revealed that isopods are a significant but poorly understood component of the fauna. All have and will continue to provide ample material for taxonomic studies.

Among the many reasons for so many species remaining undescribed are that it is difficult to know where to start and naming and description takes some effort. This guidebook is designed to address these issues, although many other taxonomic hurdles remain (Engel et al., 2021; Favret, 2024; Löbl et al., 2023). After the naturalist goes into the field with a dredge or hand-net and collects an isopod, this book should enable identification of the specimen to suborder, family and genus level, even if it is an undescribed species (unless it belongs to an undescribed genus, of course). The citations following each family and genus can be explored to discover whether the species is described.

This introductory chapter explains to the reader how the book has been planned and what to expect from each section. Chapter 2 deals with the higher systematics of Crustacea and explains what an isopod is, how isopods are related to other crustaceans, and clarifies their classification. It includes a glossary explaining novel terms. Chapters 3 to 10 cover the major isopod suborders.

Scope of this work

This guidebook tries to bridge the gap between taxonomists and other marine biologists. These non-taxonomists, such as ecologists, biogeographers and physiologists (to name a few), are the target audience for this volume. The gap exists in part because, while taxonomists are experts in identification, they often write in an arcane language. Additionally, new evidence sometimes causes taxonomists to change accepted Linnaean names, a necessary step but one that can cause considerable problems in both ecological studies and applied settings such as conservation (Sandall et al., 2023). Our aim is to write in a consistent language that is understandable to all and assist future studies relying on accurate identification of isopods.

This guidebook serves to document the state of play in isopod taxonomy in late-2025. Systematics and classification are dynamic disciplines, and the accepted family and generic names published today may not apply in the near or distant future. Nevertheless, these chapters are a point of access to the taxonomic literature. We do not describe new genera or species, or, with few exceptions, undertake any taxonomic revisions. We introduce, for convenience, one new family. However, we discovered errors and inconsistencies in past work and correct these with new interpretations. We rely on the most recent or most generally accepted classifications and lists of names, among which are a few we treat as new synonyms.

The work is confined to marine isopods (all genera of free-living and symbiotic species, including commensal and parasitic ones, are covered). Exclusively freshwater or terrestrial taxa, such as freshwater families and genera of Asellota, Microcerberidea, Cymothoida and Sphaeromatidea, are omitted. The terrestrial and freshwater suborders Calabozoidea, Oniscidea, Phreatoicidea and Tainisopidea are omitted completely. Families with marine, estuarine and freshwater representatives are diagnosed, but exclusively freshwater genera might be listed without appearing in keys. Although regional keys to marine isopods exist (see examples below), this is the first global key to marine isopod families and genera.

History and resources

Like any group of animals, crustaceans have long attracted the attention of biologists. In his *Systema Naturae* Linnaeus (1758) included a pre-Linnaean genus *Asellus* for one isopod species, and introduced *Oniscus* for eight species – an oniscid woodlouse, two valviferans, one aegid and three cymothoid fish lice, as well as one amphipod whale louse. The age of European biological ship-based exploring expeditions began in the late

eighteenth century and continued through to the mid-twentieth century. The series of scientific reports, many taxonomic, associated with ships such as HMS *Challenger*, RIMSS *Investigator*, the *Siboga*, or with the United States Exploring Expedition remain relevant today. Today, research vessels of several nations continue this tradition. Documentation of biodiversity in the Indo-West Pacific has benefitted from the MUSORSTOM, now *Tropical Deep-Sea Benthos*, series of volumes (Bruce, 1996; Lowry and Dempsey, 2006; Markham, 1990; Markham, 1994; Markham, 1999; Poore, 1991; Poore and Brandt, 1997).

General books on Crustacea are found only in speciality libraries. Old books have a fascination of their own because they established the classifications and terminology still used today. Many are now out of print but can be tracked down in the antiquarian market or online. The Reverend T.R.R. Stebbing's *A history of Crustacea: Recent Malacostraca* (1893) and William T. Calman's *The life of Crustacea* (1911) are classics. Patsy McLaughlin's *Comparative morphology of Recent Crustacea* (1980) is a useful practical guide to the definition of living taxa but is not a taxonomic guide and has no ecological information. Alfred Kaestner's (1980) *Crustacea* is a useful translation of a systematic German text. Frederick Schram's more detailed volume, also entitled *Crustacea* (1986), is packed with information and includes all the fossil taxa. Schram and Koenemann (2021) updated it as *Evolution and phylogeny of Pancrustacea: a story of scientific method*, an essential reference book on evolution, taxonomy and general biology for crustacean biologists. The recent and continuing series *The Natural History of the Crustacea* (Watling and Thiel, 2013; Derby and Thiel, 2014; Chang and Thiel, 2015; Thiel and Watling, 2015; Thiel and Wellborn, 2018; Anger et al., 2020; Cothran and Thiel, 2020; Lovrich and Thiel, 2020; Poore and Thiel, 2020; Thiel and Gutow, 2025) deals with all aspects of the biology of Crustacea. Smit et al.'s (2019) *Parasitic Crustacea* serves as a useful resource for background on the natural history and host associations for isopods and related groups.

None of these texts is useful for species identification, although some regional keys are dedicated to that task. While these keys are valuable references, some of the species names given are no longer accepted due to later synonymy or rearrangement of higher classifications. Nevertheless, former species names can usually be traced and updated using the World Marine, Freshwater and Terrestrial Isopod Crustaceans Database (https://www.marinespecies.org/isopoda/, a subregister of WoRMS). Table 1.1 lists the major regional studies geographically. Guides to individual families or genera can be found in the general text. Only works with keys or species diagnoses are listed.

We have referred to these books in the course of research for this volume. However, our task would not have been possible without the following three web-based resources.

(1) The World Marine, Freshwater and Terrestrial Isopod Crustaceans Database https://www.marinespecies.org/isopoda/, a subregister of WoRMS, http://www.marinespecies.org/) is an authoritative classification and catalogue of marine names (WoRMS Editorial Board, 2025). The WoRMS database is managed at the Flanders Marine Institute (VLIZ) and is updated by a team of volunteer taxonomic editors. All family and generic names were checked and downloaded from WoRMS in mid-2025 and these names became the foundation of our review. WoRMS also provides access to much of the relevant taxonomic literature, as citations and often as downloadable publications.

(2) The Biodiversity Heritage Library (https://www.biodiversitylibrary.org/) houses scanned pages of most of the non-copyrighted books and journals held in museums and other institutions, a rich source of old taxonomic literature.

(3) The Ocean Biodiversity Information System (OBIS, https://obis.org/) is a global open-access data and information clearing-house on marine biodiversity for science, conservation and sustainable development. OBIS provides distributional and depth-range data by species and higher taxa derived from museum, fisheries and other sources, and was one of our sources for distributional information.

Table 1.1 Major regional studies of isopod Crustaceans by location.

Southern Australia	Hale, 1929
Southern Africa	Kensley, 1978
Costa Rica	Brusca and Iverson, 1985
Caribbean	Kensley and Schotte, 1989
North America	Richardson, 1905; Schultz, 1969
Southern California, USA	Wetzer et al., 1997; Stebbins and Wetzer, 2023
Great Britain	Naylor, 1972
Norway	Sars, 1896–1899
Russia NW Pacific	Kussakin, 1979, 1982a, 1988
Antarctica	Kussakin, 1967, 1982b
Arctic	Kussakin, 1999, 2003
Indian Ocean	Kensley and Schotte, 2000, 2002; Schotte and Kensley, 2005; Kensley et al., 2007, 2009

The structure of this guidebook, and some advice!

The guidebook follows what is now accepted as the new classification of Isopoda, each chapter devoted to a suborder. All chapters follow the same format: general introduction, diagnosis, a key to families and/or superfamilies, families treated in alphabetical order (each with an introduction, diagnosis and keys to genera), followed by all genera in alphabetical order (sometimes grouped in subfamilies). Each genus is diagnosed and maximum size, depth range, distribution and the number of described species are given.

Diagnoses. Diagnoses of families and genera are original, usually simplified from more detailed diagnoses in the cited literature. Most (Epicaridea excepted) were generated initially from data stored in DELTA databases (Dallwitz et al., 1993 onwards). Diagnoses attempt to characterise each taxon with the same suite of characters, but this was not always possible. DELTA facilitates use of implicit attributes (features that are common to most genera within a family). To save repetition, these features are listed separately following the family diagnosis and only exceptions are included with relevant generic diagnoses.

Ecology. The ecological range of each genus is summarised as depth ranges following widely accepted bathymetric classes. For benthic groups these are intertidal, subtidal (including inshore bays, 20 m or shallower), shelf (20–200 m), slope (200–2000 m), bathyal (2000–3500 m), abyssal (3500–6500 m), and hadal (> 6500 m). Special ecological affinities are also noted for estuarine genera or those living in marine anchialine caves. For the rare pelagic groups depth ranges are as follows: mesopelagic (200–1000 m) and bathypelagic (>1000 m). Actual recorded depth ranges are given when these data were readily available. Sometimes other ecological descriptors such as preferred sediment type or associated fauna are added, but often this detail can be found in the family introduction.

Distributions. Distributions of all benthic genera occurring down to slope depths are given in terms of the 12 realms used in the marine ecoregions of the world (MEOW; Spalding et al., 2006) as follows: Arctic, Temperate Northern Atlantic, Tropical Atlantic, Temperate Northern Pacific, Western Indo-Pacific, Central Indo-Pacific, Eastern Indo-Pacific, Tropical Eastern Pacific, Temperate South America, Temperate Southern Africa, Temperate Australasia, and Southern Ocean (Fig. 1.1). The realms are annotated when they do not adequately describe the distribution. For example, the annotations E and W are added when the known range is only within the eastern and western part of a realm, such as Temperate Northern Pacific or Tropical Atlantic. Further details are added or substituted where appropriate (e.g. Australia or New Zealand to Temperate Australasia). "Indo-West Pacific" is substituted when a genus ranges across the Western Indo-Pacific, Central Indo-Pacific and Eastern Indo-Pacific realms. Distributions of the few benthic genera occurring at bathyal or deeper depths are given in terms of the 14 bathyal provinces used in the Global Open Oceans and Deep Seabed classification (GOODS; UNESCO, 2009) as follows: Arctic, Northern Atlantic, Brazil Basin, Angola & Sierra Leone Basins, Argentine Basin, E Antarctic Basin, W Antarctic, Indian, E Pacific basins, S Pacific, Central Pacific, N Central Pacific, N Pacific, and W Pacific basins (Fig. 1.1).

References. The literature cited, almost 1100 papers, books and chapters, concentrates on the most relevant taxonomic references (i.e. those with more extensive diagnoses and keys to species and/or information on distributions). Single species descriptions are rarely cited unless they are accompanied by more information. Some key ecological works may be cited. References are listed after each family treatment.

Keys and illustrations. Identification is achieved using dichotomous keys adapted from many originally published in the primary literature or developed from scratch. The temptation when using keys is to assume when you reach the last couplet that your specimen belongs in that genus. It is worthwhile to check the diagnosis and the distribution given. The keys are supported by illustrations. Many of the illustrations are reworking of published figures, others are reproductions from the literature. References to elements in black and white figures are given in the key and some diagnoses.

Terminology. Keys written by expert taxonomists for other taxonomists use arcane language. To make matters worse, many specialise in a limited range of taxa using terms that only those specialists appreciate, or they may spell the same term differently. For example, those exploring the diversity of copepods rarely venture into the classification of larger crustaceans (including isopods). One consequence of this is that each group of taxonomists develops its own jargon, sometimes using different terms for the same (i.e. homologous) structure. Further, relative descriptors, such as "small" and "large" are treated as diagnostic terms but are not meaningful to outsiders. Inconsistent taxonomic names, variable terminology and indeterminate descriptors are confusing for the non-specialist. We prepared this guidebook using a consistent terminology that is hopefully understandable by our target audience. The terms used by crustacean taxonomists were compiled by Martin (2005) for the Assembling the Tree of Life (AToL) Decapod project. The illustrated glossary at the end of this volume should be helpful and is illustrated with special terms applicable to only some groups.

Abbreviations. AToL, Assembling the Tree of Life; BL, body length; GOODS, Global Open Oceans and Deep Seabed; MEOW, Marine Ecoregions of the World; mya, million years ago; OBIS, Ocean Biodiversity Information System; VLIZ, Flanders Marine Institute; WoRMS, World Register of Marine Species.

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Credits

Most line illustrations in this work are assembled tracings of figures in the literature, all more or less simplified, undertaken by GCBP using Adobe Illustrator®. Others, listed in each chapter, are reprinted directly with permission of the publisher and/or author or are in the public domain.

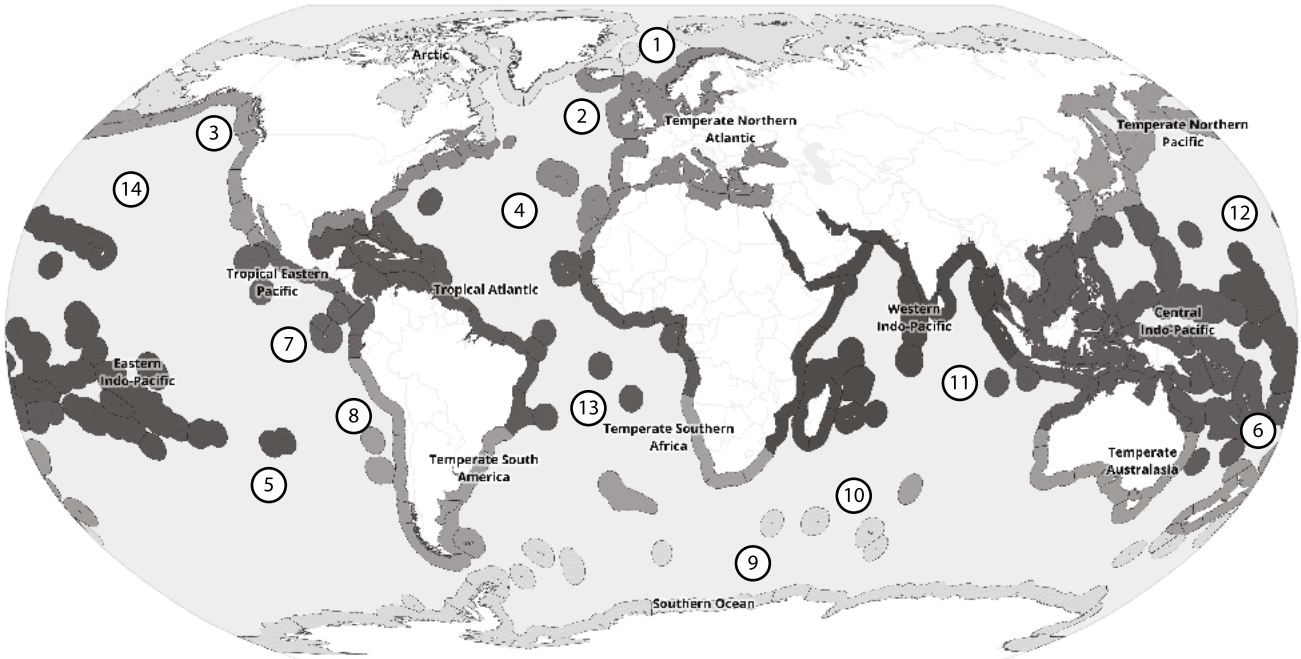


Figure 1.1. Twelve MEOW realms apply from intertidal to slope depths (0–2000 m depth) and are: Arctic, Temperate Northern Atlantic, Tropical Atlantic, Temperate Northern Pacific, Western Indo-Pacific, Central Indo-Pacific, Eastern Indo-Pacific, Tropical Eastern Pacific, Temperate South America, Temperate Southern Africa, Temperate Australasia, and Southern Ocean (Spalding et al., 2006 for detail). Numbers in circles refer to the 14 GOODS lower bathyal provinces (800–3000 m depth) as follows: 1, Arctic, 2, Northern N Atlantic, 3, Northern N Pacific, 4, N Atlantic, 5, SE Pacific ridges, 6, New Zealand/Kermadec, 7, Cocos Plate, 8, Nazca Plate, 9, Antarctic, 10, Subantarctic, 11, Indian, 12, W Pacific, 13, S Atlantic, 14, N Pacific (UNESCO, 2009 for detail). Map supplied by Marine Regions team, VLIZ, Oostende, Belgium.

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Chapter 2. Taxonomy of the Isopoda

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Abstract Poore, G.C.B. 2026. Chapter 2. Taxonomy of the Isopoda. In: Poore, G.C.B. (ed.) Marine Crustacea Isopoda: guide to families and genera of the World. *Memoirs of Museum Victoria* 86: 9–27.

The evolution and classification of the Crustacea are tabulated and discussed briefly. The Isopoda are an order of the superorder Peracarida; molecular evidence suggests they are close to Cumacea and/or Tanaidacea. Isopoda are divided into 12 suborders; species in four suborders inhabit only freshwater or terrestrial environments. The relationships between the suborders are uncertain because the few molecular studies appear to contradict each other and traditional morphological classification. A dichotomous key is provided to separate the eight suborders with marine representatives. An illustrated glossary is provided, explaining terms and conventions used in isopod taxonomy.

Keywords classification, evolution, relationships, Amphipoda, Bochusacea, Cumacea, Ingolfiellida, Isopoda, Lophogastrida, Mictacea, Mysida, Spelaeogriphacea, Stygiomysida, Tanaidacea, Thermosbaenacea, key to suborders, glossary

Introduction

Crustaceans are a group of related animals, meaning they had a common ancestor some time in the past. The features that they share are described in this chapter. Besides being extraordinarily abundant in the sea, crustaceans are among the most morphologically diverse of any taxon. More than 67,000 living species are known (Ahyong et al., 2011), of which more than 51,000 are marine. Most are not crabs, shrimps or lobsters but are small, unfamiliar and rarely have common names. This volume is dedicated to the identification of marine groups of the Order Isopoda.

What is a crustacean?

Insects, spiders, scorpions and millipedes are just some of the Phylum Arthropoda, that large group of animals distinguished from all others by their hard skin (exoskeleton), a segmented body and jointed limbs. Crustaceans belong to this phylum too. Unlike insects, which are usually excluded from marine environments, crustaceans are predominantly marine but can inhabit land and freshwater environments. Crustaceans, then, are arthropods that usually have many pairs of articulated legs, a pair per body segment, and above all have two pairs of antennae (special sensory limbs), one pair on each of the first two segments of the head. Insects, in contrast, have only three pairs of legs, and only one pair of antennae.

Evolution of the Crustacea

For the practical purpose of identification to species, debate about the evolution of Crustacea does not matter. Ancestry does matter, however, when deciding on a classification to follow. In theory at least, a species' genus and family placement should tell us something about its ecology or evolutionary history. It is the attempts of taxonomists to reflect this history that induces them to move species from one genus or family to another.

The crustaceans have origins in deep time. Definitive crustacean fossils date from approximately 500 million years ago in the upper Cambrian Orsten fauna of southern Sweden (Walossek and Müller, 1998). What the first crustacean looked like has been much debated (for review, see Ahyong, 2020; Richter and Wirkner, 2020), but subsequent morphological diversification including increasing body size, most notably from the Silurian onward, has resulted in the major branches of the crustacean tree recognised today: Allotriocarida, Oligostraca and Multicrustacea. The oldest isopod fossils date to the Carboniferous, approximately 300 million years ago (Mya) (Robin et al., 2021 and references therein). Based on molecular data, the ancestor to isopods likely arose in the late Ordovician to mid-Cambrian (~446–521 mya) and the earliest divergence within isopods occurred between Asellota and Phreatoicidea, approximately 425 mya (Thomas Thorpe, 2024). Fossil isopods representing members of the fish parasitic group Cymothoida have been found dating to the Middle Jurassic, approximately 168 mya (Nagler et al., 2017) and branchial swellings of fossil anomurans and brachyurans indicative of epicaridean isopod parasites are known from the Late Jurassic (Klompmaker et al., 2014).

Any discussion of crustacean evolution must mention the unexpected and controversial finding, first touted by molecular phylogenetics, that insects, far from being distant arthropod

relatives of crustaceans, were derived from within Crustacea. That is, insects are, technically speaking, derived crustaceans. Crustaceans were long thought to dominate aquatic habitats but had little success out of the water outside of the terrestrial isopods. Evidently, however, crustaceans have successfully colonised the land more broadly, as insects (Glenner et al., 2006; Oakley et al., 2013; von Reumont and Edgecombe, 2020). This crustacean–insect clade is variously known as Pancrustacea, Tetraconata, or simply Crustacea (Ahyong, 2020; Bracken-Grissom and Wolfe, 2020; Richter and Wirkner, 2020).

Modern distributions of major isopod shallow-water groups reflect the Mesozoic timing of major radiations (Thomas Thorpe, 2024). Because of ancient continental movements that ultimately led to the formation of the Atlantic and Pacific Ocean basins during the Eocene, most warm-water marine isopod groups now have substantially discrete Indo-West Pacific and Atlantic-East Pacific distributions, with few shared species, some shared genera, and mostly cosmopolitan families. This is not the case for cold-water faunas. The Southern Ocean fauna is related to the cold-water fauna of the deep oceans and to that of the Arctic Ocean. Why is this of interest for an identification guide? The deep history of isopod lineages means that, today, most living shallow-water genera (and their species) occur either in the Indo-West Pacific or Atlantic Oceans, but not usually both. Some genera are cosmopolitan, but not most. As a result, knowing the natural geographic range of a genus (indicated in this work) can assist in corroborating or correcting identifications made using the keys. So, if you find a specimen from Brazil that belongs to a genus that is otherwise known only from the Indo-West Pacific, be sure to double-check the identification because it could be incorrect, an introduced species or perhaps a new scientific discovery.

Table 2.1. Classification of living members of the subphylum Crustacea (Isopoda covered in this volume shaded).

Superclass	Class	Subclass	Infraclass/ Superorder	Order	Suborder	Infraorder	Common name
Allotriocarida	Branchiopoda	Phyllopoda	Calmanostraca	Notostraca			shield shrimps
			Diplostraca	Anomopoda			water fleas
				Ctenopoda			water fleas
				Cyclestherida			water fleas
				Haplopoda			water fleas
				Laevicaudata			clam shrimps
				Onychopoda			water fleas
				Spinicaudata			water fleas
		Sarsostraca		Anostraca	Artemiina		fairy shrimps
					Anostracina		
	Cephalocarida			Brachypoda			cephalocarids
	Hexapoda						insects
	Remipedia			Nectipoda			remipedes
Oligostraca	Ichthyostraca	Branchiura		Arguloida			fish lice
		Pentastomida		Cephalobaenida			tongue worms
				Porocephalida			
				Raillietiellida			
				Reighardiida			
		Mystacocarida		Mystacocaridida			mystacocarids
	Ostracoda	Myodocopa		Halocyprida	Cladocopina		seed shrimps, ostracods
					Halocypridina		
				Myodocopida	Myodocopina		
		Podocopa		Platycopida			
				Podocopida	Bairdiocopina		
					Cypridocopina		
					Cytherocopina		
					Darwinulocopina		

Superclass	Class	Subclass	Infraclass/ Superorder	Order	Suborder	Infraorder	Common name
Multicrustacea	Copepoda	Neocopepoda	Gymnoplea	Calanoida			copepods
			Podoplea	Canuelloida			
				Cyclopoida			
				Gelyelloida			
				Harpacticoida			
				Misophrioida			
				Monstrilloida			
				Mormonilloida			
				Siphonostomatoida			
		Progymnoplea		Platycopioida			
	Tantulocarida						tantulocarids
	Thecostraca	Ascothoracica		Dendrogastrida			ascothoracican barnacles
				Laurida			
		Cirripedia	Acrothoracica	Cryptophialida			boring barnacles
				Lithoglyptida			
			Rhizocephala				parasitic barnacles
			Thoracica/ Phosphatothoracica	Iblomorpha			goose barnacles,
			Thoracica/ Thoracicalcarea	Balanomorpha			goose barnacles, wart barnacles, acorn barnacles
				Calanticomorpha			
				Pollicipedomorpha			
				Scalpellomorpha			
				Verrucomorpha			
		Facetotecta					y-larvae
	Malacostraca	Eumalacostraca	Eucarida	Euphausiacea			krill
				Decapoda	Dendrobranchiata		prawns
					Pleocyemata	Achelata	spiny lobsters, bugs
						Anomura (6 superfamilies)	hermit crabs, king crabs, mole crabs, porcelain crabs, squat lobsters
						Astacidea (3 superfamilies)	clawed lobsters, crayfish, yabbies
						Axiidea	ghost and sponge shrimps
						Brachyura (5 ssections)	true crabs
						Caridea (14 superfamilies)	shrimps
						Gebiidea	mud and sponge lobsters
						Glypheidea	glypheid lobsters
						Polychelida	deep-sea blind lobsters
						Procarididea	shrimps
						Stenopodidea	coral shrimps

Superclass	Class	Subclass	Infraclass/ Superorder	Order	Suborder	Infraorder	Common name
			Syncarida	Bathynellacea			bathynellaceans
				Anaspidacea			mountain shrimps
			Peracarida	Amphipoda	Amphilochidea		Amphipods, skeleton shrimps, whale lice
					Colomastigidea		
					Hyperiidea		
					Hyperiopsidea		
					Pseudingolfiellidea		
					Senticaudata		
				Bochusacea			hirsutiids
				Cumacea			comma shrimps, cumaceans
				Ingolfiellida	subdivided		ingolfiellids
				Isopoda	Asellota	4 superfamilies	
					Calabozoidea		
					Cymothoida		
					Epicaridea	2 superfamilies	
					Phoratopidea		
					Limnoriidea		
					Microcerberidea		
					Sphaeromatidea		
					Valvifera	2 superfamilies	
					Oniscidea	3 parvorders	slaters, woodlice, pill bugs
					Phreatoicidea		
					Tainisopidea		
				Lophogastrida			lophogastrids
				Mictacea			mictaceans
				Mysida			opposum shrimps
				Spelaeogriphacea			spelaeogriphaceans
				Stygiomysida			cave mysids
				Thermosbaenacea			thermosbaenaceans
				Tanaidacea	Apseudomorpha		tanaidaceans
					Tanaidomorpha		
		Hoplocarida		Stomatopoda			mantis shrimps
		Phyllocarida		Leptostraca			leptostracans, nebaliaceans

Classification of the Crustacea

Table 2.1 reflects one hierarchy of all the major groups of Crustacea, in which it can be seen that Isopoda is just one order of the superorder Peracarida. This hierarchy of groups within groups is the one adopted by World Register of Marine Species Names (WoRMS, https://www.marinespecies.org/) and is subject to change as more data from morphology and DNA become available (Bracken-Grissom and Wolfe, 2020; Oakley et al., 2013; Regier et al., 2010; Schram and Koenemann, 2021).

The subphylum Crustacea is divided into nine classes, of which three belong to the superclass **Allotriocarida** Oakley, Wolf, Lindgren and Zaharoff, 2013, two to **Oligostraca** Zrzavý, Hypša and Vlášková, 1997 and four to **Multicrustacea** Regier, Shultz, Zwick, Hussey, Ball, Wetzer, Martin and Cunningham, 2010:

Branchiopoda Latreille, 1817: despite a diversity of body forms, branchiopods typically share a series of uniform, phyllopodous trunk limbs and a limbless abdomen (if present). Many branchiopods live in fresh water and only the order Cladocera, popularly known as water fleas, have marine representatives (Olesen, 2009).

Cephalocarida Sanders, 1955: microscopic thin animals with a broad, shield-like cephalon, followed by a thorax of eight and an abdomen of 12 segments, of which the last abdominal segment bears paired caudal rami. Cephalocarids live between the sand grains on beaches and marine sediments (Hessler and Elofsson, 2013).

Remipedia Yager, 1981: an unusual group of many-legged centipede-like predators, that, uniquely among crustaceans, produce venom delivered through the maxillae. They are confined to fresh water in caves and anchialine aquifers (Koenemann et al., 2003).

Ichthyostraca Zrzavý, Hypša and Vlášková, 1997: includes two groups of parasitic crustaceans. Branchiura are external parasites of fishes and amphibians (Moller, 2009) while Pentastomida, or tongue worms, are lung parasites of vertebrates, especially reptiles (Christoffersen and Assis, 2015).

Mystacocarida Pennak and Zinn, 1943: a group of vermiform interstitial crustaceans from sandy beaches (Boxshall and Defaye, 1996).

Ostracoda Latreille, 1802: sometimes called seed shrimps, this group is rich in species in marine, freshwater and terrestrial environments. They have a bivalved carapace and are well represented as fossils. Relationships among the major groups are unresolved (Wolfe and Hegna, 2014).

Copepoda H. Milne Edwards, 1840: diverse and abundant in marine environments with a wide range of pelagic and benthic forms (Boxshall and Halsey, 2004; Huys and Boxshall, 1991). Many copepods are parasitic or symbiotic.

Tantulocarida Boxshall and Lincoln, 1983: minuscule parasites on other crustaceans, most frequently found in the deep sea (Boxshall, 1991, 1996).

Thecostraca Gruvel, 1905: includes a wide range of attached, boring and parasitic barnacles (Chan et al., 2020; Høeg, 1995; Newman, 1996).

The last class, **Malacostraca** Latreille, 1802, includes the most familiar crustaceans. They are variously divided into three subclasses, three superorders and 18 extant orders.

All **Eumalacostraca** Grobben, 1802 have 20 body segments (all except the first with paired limbs) plus a terminal telson. The body segments, or somites, are arranged into three sections, or tagmata: head or cephalon, thorax (or pereon) and pleon (or abdomen). The head has eight pairs of limbs involved in sensation and feeding, the thorax has eight pairs of limbs that are usually locomotory and variously involved with feeding, and the pleon has six pairs of limbs involved with respiration, reproduction and swimming.

The superorder **Eucarida** Calman, 1904 is characterised by a carapace, the shield or shell, encasing the segments of the head and thorax in such a way that the segmentation is concealed. In most other crustaceans many of the segments are quite visible. All eucarids have eyes on moveable stalks. Eucarids comprise two orders, Euphausiacea or krill (Baker et al., 1990; Jarman, 2001; Mauchline, 1980), pelagic crustaceans famous for their role in the diet of whales, and Decapoda. Decapods are the most familiar crustaceans (due in large part to their commercial importance), and this group includes crabs, shrimps, prawns and lobsters.

The superorder **Syncarida** Packard, 1886 are mostly found in fresh water and include Anaspidacea Calman, 1904, or mountain shrimps (Ahyong, 2016), and more cryptic cave and interstitial forms in Bathynellacea Chappuis, 1915 (Camacho et al., 2018a; Camacho et al., 2018b).

Isopoda are one order of the superorder **Peracarida** Calman, 1904, which includes 12 orders of small benthic or epibenthic crustaceans. Some are exceptionally abundant in marine environments. The diverse and common **Amphipoda** Latreille, 1816 were separated from the rarer **Ingolfiellida** by Lowry and Myers (2017). **Cumacea** Krøyer, 1846, unlike many other crustacean groups, are taxonomically stable although relationships between the families are debatable (Haye et al., 2004). **Lophogastrida** Boas, 1883, **Mysida** Boas, 1883 and **Stygiomysida** Tchindonova, 1981, epipelagic or mesopelagic shrimps, were once united but now treated as three orders (Meland and Willassen, 2007; Meland et al., 2015). **Tanaidacea** Dana, 1849 too are abundant but their diversity is only recently being realised (Błażewicz-Paszkowycz et al., 2012). Their relationships have begun to be addressed (Bird and Larsen, 2009; Drumm, 2010; Larsen and Wilson, 2002). **Thermosbaenacea** Monod, 1927 are a group of 45 species in four families, living in fresh and brackish water in caves and thermal springs (Wagner, 1994). The remaining peracaridan orders contain few species and are rare: **Bochusacea** Gutu and Iliffe, 1998, **Mictacea** Bowman, Garner, Hessler, Iliffe and Sanders, 1985 and **Spelaeogriphacea** Gordon, 1957 (Poore, 2015).

The subclass **Hoplocarida** Calman, 1904, mantis shrimps, are marine, mostly benthic predators that are most common on tropical shores. They are recognised by their short, shield-like carapaces, triflagellate antennulae and their trademark adaptations of praying mantis-like raptorial or club-like claws and highly complex eyes (Ahyong and Jarman, 2009; Van Der Wal et al., 2017).

The subclass **Phyllocarida** Packard, 1879 includes only **Leptostraca** Claus, 1880 (Walker-Smith and Poore, 2001) but has from time to time also included Hoplocarida (Stomatopoda) (Ahyong, 2020; Richter and Scholtz, 2001).

Diagnosis of the Isopoda

Peracarida is diagnosed as containing species having a brood pouch in females formed from oostegites, medially directed modifications of the thoracopodal epipods (Poore, 2005; Schram and Koenemann, 2021; Watling, 1999). They share a lacinia mobilis, a specialised spine in the spine row between the mandibular incisor and molar process (Richter et al., 2002) and are certainly monophyletic (Wirkner and Richter, 2010). Isopods are most easily differentiated from other peracaridans by having the telson fused to the sixth pleonite, usually having five pairs of respiratory pleopods and a single pair of uropods with two uniarticulate rami. They differ from the most similar order, Tanaidacea, where the head incorporates two thoracomeres rather than one, the first pereopod is always chelate, pleopods are absent or tiny, and the uropods are uniramous and multisegmented. Isopods have so-called biphasic moulting in which the posterior exoskeleton sheds separately before the anterior region (Sahadevan et al., 2022). Isopods belong to the mancoid group of Peracarida, with Tanaidacea and Cumacea, in which the first instar hatches from the brooded egg without the last pair of pereopods (Boyko and Wolff, 2014; Hessler, 1982).

Diagnosis. Carapace absent. Eyes sessile. Antennula uniramous. Antenna uniramous (antennular scale/exopod rare). Head comprising cephalic somites and first thoracomere. Maxilliped (thoracopod 1) with basal endite and 5-articled palp (articles sometimes fused); maxillipedal epipod large, flap-like protecting lateral mouth-field. Pereopods 1–7 (thoracopods 2–8) uniramous; coxa sometimes with dorsal coxal plate. Pleon of 5 pleonites plus pleotelson (fused pleomere 6 and telson). Pleopods 1–5 typically biramous, with laminar respiratory rami. Uropods usually biramous.

Relationship of Isopoda to other Peracarida

Early naturalists recognised the similarities between isopods and tanaidaceans. Sars (1896–1899), for example, included Chelifera (now Tanaidacea) as one of his tribes of Isopoda. Hansen (1893) was the first to suggest that Tanaidae should be treated as an order separate from Isopoda, a proposition adopted by Calman (1909), who used both Isopoda and Tanaidacea. "Isopoda Chelifera" persisted with Nierstrasz (1913), who referred to isopods as "Isopoda Genuina" (Nierstrasz and Brender à Brandis, 1923a, b; Nierstrasz, 1931, 1941).

The relationships between the orders of Peracarida are poorly understood (Schram and Koenemann, 2021), but there seems to be general agreement from morphological (Richter and Scholtz, 2001; Siewing, 1957; Wirkner and Richter, 2010) and molecular evidence (Bernot et al., 2023; Höpel et al., 2022) that Amphipoda are a sister group to all other peracaridan orders. The idea that Amphipoda are most closely related to Isopoda (Poore, 2005; Schram and Hof, 1998) has not survived (Wilson, 2009). Wirkner and Richter (2010) found Isopoda more related to Cumacea and Tanaidacea than to Amphipoda based on circulatory structures. Höpel et al. (2022) found the same result, but no other infraorders were included in their analysis. Most recently, Bernot et al. (2023) found evidence that Isopoda is sister to Cumacea.

Classification and relationships of the Isopoda

Carl Linneaus was the first to formally name any crustaceans that would eventually be known as isopods, including seven species from the group in *Systema Naturae* (Hadfield, 2019). Latreille (1816) introduced the name Isopodes as his fourth order of Crustacés; it was immediately Latinised to Isopoda. He included a wide range of genera of what are now considered isopods: *Oniscus*, *Ligia*, *Philoscia*, *Porcellio*, *Armadillo*, *Anceus*, *Praniza*, *Bopyrus*, *Ione*, *Cymothoa*, *Sphaeroma*, *Idotea* and *Asellus*. He also included a stomatopod, a tanaidacean and four amphipod genera: *Squilla*, *Apseudes*, *Proto*, *Caprella*, *Cyamus* and *Typhis*. Curiously, Latreille characterised this order as lacking mandibular palps, but noted the legs were simple and designed for locomotion or gripping.

The classification of Isopoda has changed substantially since the early nineteenth century and was reviewed two or three decades ago by Brusca and Wilson (1991), Brandt and Poore (2003) and Schmidt (2008), and more recently by Schram and Koenemann (2021). Not all historical classifications mentioned by them are cited here. Milne Edwards (1840) divided Isopoda into three sections: Marcheurs (walkers); Nageurs (swimmers) and Sédentaires (sitters). His allocation of genera to "familles" within these sections bore little resemblance to any modern classification, nor did Dana's (1852) division of the tribe Isopoda into three subtribes: Idotaeidea, Oniscidoidea and Cymothoidea. Sars (1896–1899), in his review of the isopods of Norway, divided Isopoda into six tribes: Chelifera (now the separate order Tanaidacea), Flabellifera, Valvifera, Asellota, Oniscoidea, and Epicarida. Richardson (1905) followed the same arrangement in her review of the isopods of North America but gave the tribes different superfamily names: Tanaioidea, Cymothoidea, Idoteoidea, Aselloidea, Oniscoidea and Bopyroidea.

Monod (1922) provided a more hierarchical classification of what he called Euisopoda: A. Decempedes (a. Gnathiidea); B. Quatuordecempedes I. Aberrantia (a. Anthuridea); II. Normalia (a. Asellota; b. Valvifera; c. Flabellifera; d. Epicaridea; e. Oniscidea); and III. Gammariformes (a. Phreatoicidea). The separation between the ten-legged gnathiids and other isopods with 14 legs has been largely ignored, Hurley and Jansen (1977) excepted, but the suborder status of Gnathiidea persisted until at least until Kensley and Schotte's (1989) guidebook, and of Anthuridea well after Poore's (2001) review.

Kussakin's (1979) review of the anatomy and evolution of Isopoda concluded with a phylogenetic diagram that Bruce (1981) adapted and redrew. Kussakin derived Epicaridea from Flabellifera, particularly Cymothoidae. An important reappraisal of the relationships between isopods (Dreyer and Wägele, 2001; Wägele, 1989) did away with the commonly used grouping Flabellifera altogether. Wägele (1989) divided Isopoda into eight suborders: Phreatoicidea, Calabozoidea, Asellota, Oniscidea, Valvifera, Anthuridea, Sphaeromatidea and Cymothoida. He retained Anthuridea but included Bopyridae (aka Epicaridea) and Gnathiidae within Cymothoida. Dreyer and Wägele (2001) concluded that Bopyridae (crustacean parasites) are most closely related to the

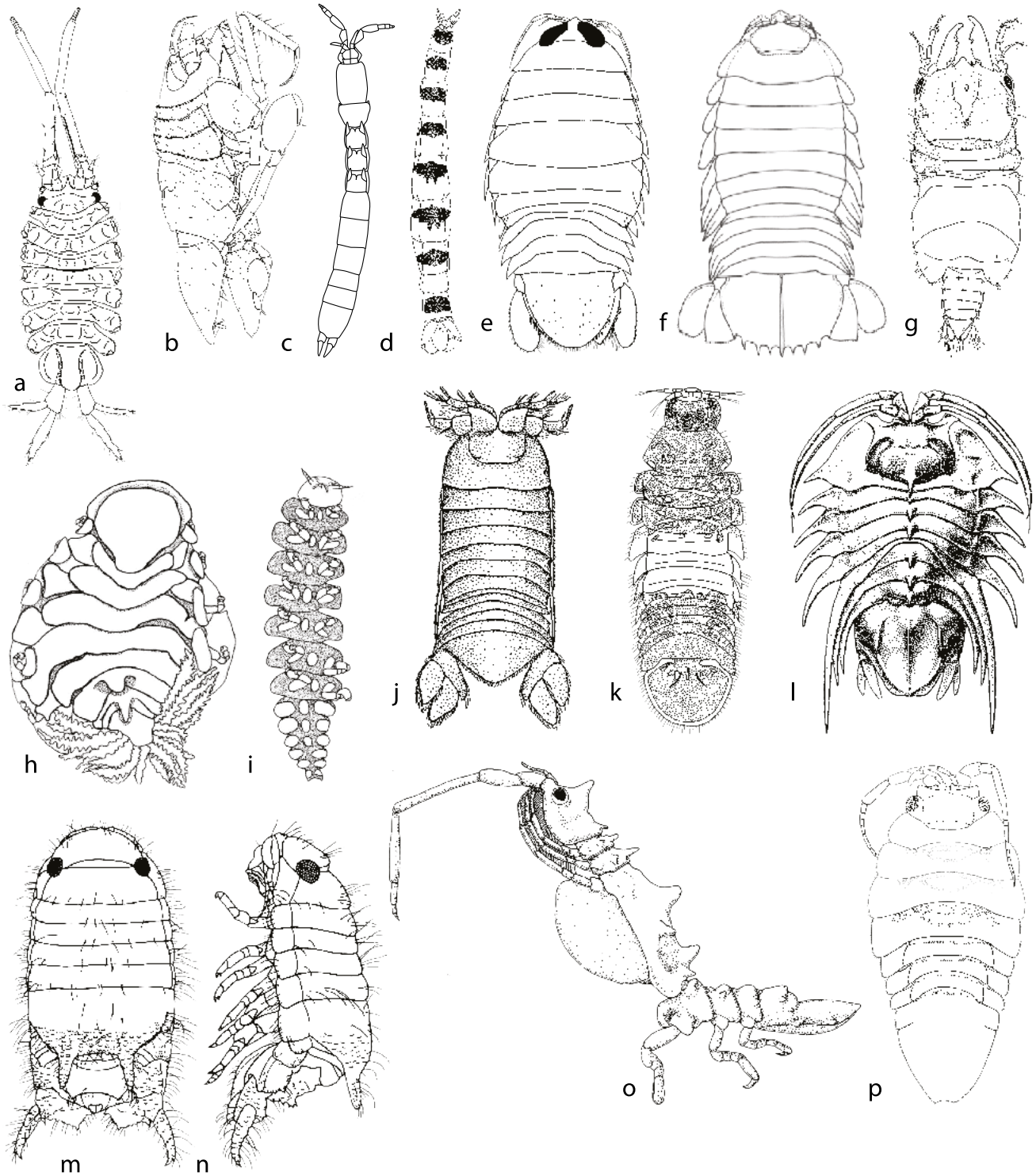


Figure 2.1. Representatives of suborders of Isopoda (not to same scale). **Asellota**: a, Janiridae, *Iathrippa sarsi* (Pfeffer, 1887); b, Munnopsidae, *Tytthocope megalura* (G.O. Sars, 1872). **Microcerberidea**: c, Microcerberidae, *Robustura* sp. **Cymothoida**: d, Anthuridae, *Chelanthura calaena* (Poore and Lew Ton, 1986); e, Aegidae, *Rocinela bonita* Bruce, 2009; f, Cirolanidae, *Bathynomus lowryi* Bruce and Bussarawit, 2004; g, Gnathiidae, *Gibbagnathia europalothrix* Cohen and Poore, 1994. **Epicaridea**: h, i, Bopyridae, *Megacepon sheni* An, Boyko and Li, 2012 (female and male). **Phoratopidea**: j, Phoratopodidae, *Phoratopus remex* Hale, 1925. **Limnoriidea**: k, Limnoriidae, *Limnoria glaucinosa* Cookson, 1991. **Sphaeromatidea**: l, Serolidae, *Acutiserolis spinosa* (Kussakin, 1967); m, n, Sphaeromatidae, *Dynamene curalii* Holdich and Harrison, 1980 (male, dorsal and lateral). **Valvifera**: o, *Neastacilla tarni* King 2003; p, Idoteidae, *Synidotea grisea* Poore and Lew Ton, 1993.

family Cymothoidae (fish parasites), as had Kussakin (1979) before them. While critical of Wägele's (1989) analysis, Brusca and Wilson (1991) agreed from their own cladistic results that Anthuridea, Gnathiidea and Epicaridea appeared to derive from within Flabellifera. Their largely unresolved cladogram did not support the separation of Sphaeromatidea and Cymothoida. Dreyer and Wägele (2002) proposed a new taxon of unspecified rank, Scutocoxifera, on the basis of a genetic analysis of 18S rRNA. Its monophyly was supported by reappraisal of morphological characters in an earlier paper (Dreyer and Wägele, 2001). Scutocoxifera comprises Oniscidea, Valvifera, Sphaeromatidea, Anthuridea and Cymothoida. Brandt and Poore (2003) used a morphological cladistic analysis of Flabellifera *sensu lato* and Scutocoxifera that largely supported the conclusion of Wägele (1989) and Dreyer and Wägele (2001). The most significant difference was the inclusion of "Anthuridea" within Cymothoida close to Gnathiidae. They also found that Cirolanidae warranted superfamily status, but this has not been widely adopted (Wetzer et al., 2013). Brandt and Poore (2003) summarised the competing cladograms of Wägele (1989) and Brusca and Wilson (1991), concluding that Phreatoicidea are sister taxon to all other isopods (Wilson, 2009) and that Calabozoidea, Asellota and Oniscidea are basal to Scutocoxifera.

Molecular attempts to understand the phylogeny of Isopoda have been based on few genes and mostly few representatives. Several are contradictory and have reported difficulties with isopod genetics that have hindered resolving phylogenetic relationships (Hua et al., 2018; Kilpert et al., 2012; Zhang et al., 2019; Zou et al., 2020). Some studies have concluded that Phreatoicidea are among the more derived isopods, contrary to morphological evidence (Lins et al., 2012, 2017). The Bayesian estimate of isopod phylogeny, based on a mitonuclear dataset from 192 species of Lins et al. (2017), supports most of the suborders (except Asellota and Oniscoidea, which are biphyletic) but the relationships between them are at odds with an understanding based on morphology. Zou et al. (2018) found *Cymothoa* basal to all Isopoda.

Bernot et al. (2023), in determining part of a pancrustacean phylogeny, used sequences from only nine species to derive a relationship that can be summarised as (Asellidae ((Idoteidae+Sphaeromatidae) + Oniscidea))). Zhang et al. (2019) found something similar, with Asellota being the basal isopod group. In a study concentrating on Sphaeromatidae, Wetzer et al. (2013) upheld Scutocoxifera. Their analyses placed Valvifera within Sphaeromatidea as sister to Serolidae, and Valvifera + Serolidae as sister to Ancinidae. In contrast to the morphological evidence, Plakarthriidae is nested deep within Sphaeromatidae based on molecular data (Thomas Thorpe, 2024). According to Wetzer et al. (2013), Oniscidea are a monophyletic clade but exclude *Ligia*. Limnoriidea is the sister group to Cymothoida. There is morphological and molecular evidence that Ligiidae is more related to Sphaeromatidea and Valvifera than to other Oniscoidea (Michel-Salzat and Bouchon, 2000; Schmidt, 2008; Zhang et al., 2019; Zou et al., 2020). On the other hand, Thomas Thorpe (2024) found Oniscidea, including *Ligia*, to be monophyletic and that the colonisation of land occurred only once. Thomas Thorpe (2024) also concluded, based on molecular evidence, that Asellota, Sphaeromatidea and Valvifera and most of Cymothoida are monophyletic. Important differences in her findings were that Anthuroidea and Gnathiidae were well separated from most Cymothoida and that Epicaridea was a monophyletic group even further removed from Cymothoida. Previous studies (e.g., Boyko et al., 2013; Yu et al., 2018) called into question whether epicarideans (crustacean parasites) evolved from cymothoids (a group that includes many fish parasites). Epicaridea was recognised as its own suborder of isopods by An et al. (2022), who used molecular evidence to show it is monophyletic and does not form a sister group with any cymothoids. These results indicate that the morphologically based classification may need updating. Regardless, parasitism has been an evolutionarily successful strategy in isopods: about 6% of species of all isopods (11% of marine isopod species) are parasites (or temporary blood feeders) of fish hosts, and about 8% of species are parasites of crustacean hosts (14% of marine isopod species) (Boyko and Williams, chapter 6 of this work; Poore and Bruce, 2012; Williams and Boyko, 2012; Wilson, 2008).

The current classification of Isopoda into 12 suborders is accepted, while it is acknowledged that not all are monophyletic. Eight suborders have marine representatives and are covered in the following chapters, but the following four are terrestrial or inhabit fresh water entirely (Marin and Tiunov, 2023) and so are excluded from this volume.

Calabozoidea Van Lieshout, 1983 is a small group of three species of stygiobont isopods from wells and caves in South America (Prevorčnik et al., 2012; Van Lieshout, 1983, 1986).

Oniscidea Latreille, 1802 include woodlice, pillbugs and slaters and is the only large group of crustaceans to have colonised terrestrial environments (Sfenthourakis et al., 2020). The families Actaeciidae Vandel, 1952 (Lewis and Green, 1994), Ligiidae Leach, 1814 (Schmalfuss and Ferrara, 1978), Scyphacidae Dana, 1852 (Taiti and Ferrara, 1989) and Tylidae Dana, 1852 (Schmalfuss and Vergara, 2000) are supralittoral, almost exclusively found along sandy or rocky seashores. These families are not included in this volume.

Phreatoicidea Stebbing, 1893 are a group of approximately 120 species of terrestrial and freshwater isopods from Australia, India, New Zealand and South Africa (see Wilson and Humphrey, 2020; Wilson and Keable, 2001).

Tainisopidea Brandt and Poore, 2003 include one family of three species in hypogean fresh water aquifers of Western Australia (Wilson, 2003; Wilson and Ponder, 1992).

Marine and estuarine families and genera of the remaining suborders are covered in this volume.

Chapter 3. Suborder **Asellota** Latreille, 1802 (freshwater families not covered)

Chapter 4. Suborder **Microcerberidea** Lang, 1961 (freshwater genera not covered)

Chapter 5. Suborder **Cymothoida** Leach, 1818 (freshwater genera not covered)

Chapter 6 Suborder **Epicaridea** Latreille, 1825.

Chapter 7. Suborder **Phoratopidea** Brandt and Poore, 2003

Chapter 8. Suborder **Limnoriidea** Brandt and Poore *in* Poore, 2002

Chapter 9. Suborder **Sphaeromatidea** Wägele, 1989 (freshwater genera not covered)

Chapter 10. Suborder **Valvifera** G.O. Sars, 1883

A **glossary** follows because we have no choice but to learn a new language to identify these animals. General morphology is dealt with, and specialist terms introduced. Diagrams help to explain the special terms applicable to different groups of isopods.

Key to suborders of Isopoda with marine representatives

1. Parasitic on crustaceans. Body of adult female often asymmetrical and always highly modified from typical isopod body plan (fig. 2.1h); male always symmetrical and of typical isopod body plan (fig. 2.1i) ..... Epicaridea ... Chapter 6

– Free-living or parasitic on fishes. Body bilaterally symmetrical (asymmetrical only if parasitic) 2

2. Uropods lateral to margin of pleotelson, articulating in longitudinal axis and folding down alongside and enclosing branchial space (figs. 2.1o, p, 2.2c). Mandibular palp absent (fig. 2.2g, h; one exception) ..... Valvifera ... Chapter 10

– Uropods posterior or sublateral on pleotelson, not enclosing branchial space (figs 2.1a–n, 2.2a, u). Mandibular palp usually present (fig. 2.2f) 3

3. Uropods terminal, peduncle and rami more or less linear. Pereopodal coxal dorsal plates absent, coxa reduced to simple ring (fig. 2.1a–c) 4

– Uropods terminal, peduncle and rami more or less laminar. Pereopodal coxal dorsal plates present, usually overlapping laterally or ventrally bases of pereopods, sometimes fused to pereonal tergite (fig. 2.1d–n) 5

4. Pleopod 1 uniramous in male, sometimes interacting with groove on pleopod 2, absent in female (fig. 2.2r). Pleopod 2 biramous in male, endopod modified as complex gonopod (fig. 2.2s); pair fused as operculum in female (fig. 2.2t) ..... Asellota ... Chapter 3

– Pleopod 1 absent in both sexes (rarely present in male). Pleopod 2 biramous in male, variously digitate; absent in female (fig. 2.1c) ..... Microcerberidea ... Chapter 4

5. Pleotelson underside vaulted, branchial chamber defined by ridges along mesial margin of lateral edge. Uropodal rami lateral to margin of pleotelson, articulating in longitudinal axis and folding down alongside branchial space. Pleonites 4–6 variously fused into pleotelson, at most pleonites 1–3 free (fig. 2.1l–n) ..... Sphaeromatidea ... Chapter 9

– Pleotelson underside flat, without ventrolateral ridges (pleopods not enclosed laterally). Uropodal rami ventral to pleotelson, articulating from side to side in vertical axis inside branchial space. Pleonites 1–5 usually free, sometimes fused, rarely some pleonites fused into pleotelson 6

6. Mandibular molar absent. Maxillipedal endite reaching at least distal margin of palp article 4, non-tapering, slender (except *Keuphylia*) (fig. 2.1k) ..... Limnoriidea ... Chapter 8

– Mandibular molar usually present (fig. 2.2f). Maxillipedal endite rarely reaching distal margin of palp article 4, usually much shorter or vestigial (fig. 2.2m) 7

7. Coxal dorsal plate 7 absent (dorsal coxal plate 6 and pleonal 1 or 2 epimeron in contact). Merus–propodus of pereopods 4 and 5 much wider than those of pereopods 2 and 3. Pereopods 3–7 with reduced dactyli (fig. 2.1j) ..... Phoratopidea ... Chapter 7

– Coxal dorsal plate 7 present. Merus–propodus of pereopods 2–5 similar. All pereopods with curved dactyli (fig. 2.1e–g) ..... Cymothoida ... Chapter 5

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Credits

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al. (1978); d, Poore and Lew Ton (1986); e, Bruce (2009); f, Bruce and Bussarawit (2004); g, Cohen and Poore (1994); h, i, An, Boyko and Li (2012); j, Hale (1925); k, Cookson (1991); l, Kussakin (1967); m, n, Holdich and Harrison (1980); o, King (2003); p, Poore and Lew Ton (1993).

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Glossary

Peracaridans are built on essentially the same body-plan: head, segmented pereon and segmented pleon. Homologies exist between orders for all the limbs. Terminology is much the same for all isopods but has changed over the decades. Early workers tended to use more complex words than are used now, e.g., coxopodite for coxa, epipodite for epipod. In the last third of the twentieth century taxonomists used antenna 1 and antenna 2 for antennula (antennule) and antenna, and maxilla 1 and maxilla 2 for maxillula (maxillule) and maxilla. We prefer to number all segments and limbs using Arabic numerals (1, 2, 3, etc.) although some authors in the past and even currently use Roman numerals (I, II, III, etc.). Multiple organs are numbered in sequence, e.g., pereopods 1–7, rather than first to seventh pereopods. Synonymous terms not used in this volume are cross-referred to our preferred term. The glossary includes most of the specialised terms but hybrid words, like anterolateral, are not defined. Plurals and adjectival forms are given for some. This glossary relies on earlier ones for isopods (Kensley and Schotte, 1989; Wilson, 1989; Wetzer et al., 1997).

The terms "spines" and "teeth" are confined to cuticular expansions or protrusions. Setae are usually thin tapering flexible hair-like structures hinging on the exoskeleton. Thick unbending setae, sometimes flagellate or otherwise ornamented, especially on pereopods, are referred to as "robust setae" or "spiniform setae", not as "spines". For additional details on terminology of crustacean setae see Watling (1989), Garm (2004), and Garm and Watling (2013).

Orientation

Anterior and **posterior** refer to the head and tail ends of a typical isopod, **dorsal** and **ventral** to the top and bottom surfaces when the animal is oriented normally. In some literature dorsal and ventral, or anterior and posterior, are also used to refer to one or other edge of a limb when the terms **upper** and **lower, superior** or **inferior,** or **extensor** and **flexor** are anatomically more correct. Extensor and flexor refer to the action of the internal muscles along each margin. Similarly, strictly speaking, legs do not have a dorsal and ventral, or anterior and posterior, surface or edge because they do not have fixed orientation; anterior pereopods tend to face forward while posterior pereopods orient posteriorly. **Medial** refers to a structure in the midline of the animal and **mesial** to the face of a paired limb facing the midline. **Lateral** is the opposite of mesial or refers to a position away from the midline. **Sublateral** is used to indicate, for example, a spine between the medial and lateral spines. **Proximal** and **distal** describe the attached and remote ends of a limb. Adjectives describing orientation are frequently combined to indicate intermediate conditions (e.g., **posterolateral**, **anteroventral,** etc.).

The body and appendages are divided into segments. The segments of the body are here called **somites**, arranged in three sections (**tagmata**), **head**, **pereon** and **pleon** (Fig. 1.2). In isopods the head, sometimes called the cephalon, incorporates all the fused cephalic somites with their paired limbs plus the first thoracomere with its paired maxillipeds. The pereon comprises seven somites, pereonites (or pereomeres) 1–7 (equivalent to thoracomeres 2–8) with paired pereonites 1–7. The pleon is isopods comprises five pleonites (or pleomeres), each with a pair of pleopods, although in some parasitic taxa there are fewer, plus a pleotelson which is a fusion of pleonite 6 and the telson with a single pair of uropods, although these may be lacking in parasites. The segments of appendages or limbs are called **articles**. The word segment is used for both somite and article in some literature.

abdomen see pleon

aesthetasc chemosensory seta covered by delicate cuticle projecting from antennular flagellum articles

antenna (pl. antennae; adj. antennal) second cephalic appendage, usually with peduncle of five articles and multiarticulate flagellum (synonym, antenna 2). Plural sometimes used to refer to both antennulae and antennae

ambulatory walking, typical pereopod with acute dactylus

anal cone tapered projection beyond body surface, extending dorsally in females, ventrally to posteriorly in males (epicarideans)

anchialine aqueous habitat near the sea; referring to saltwater or brackish pools fluctuating with the tides, but with no surface connection to the sea

antennula (pl. antennulae; adj. antennular) first cephalic appendage, usually with peduncle of three articles and multiarticulate flagellum (synonyms, antennule or antenna 1)

apical referring to apex or tip

appendage any articulated structure used for feeding, locomotion, sensory reception, e.g., mouthparts, antennae, pereopods, pleopods, uropods

appendix masculina (pl. appendices masculinae) rod-like branch on inner margin of pleopod 2 endopod of males (synonym, copulatory stylet)

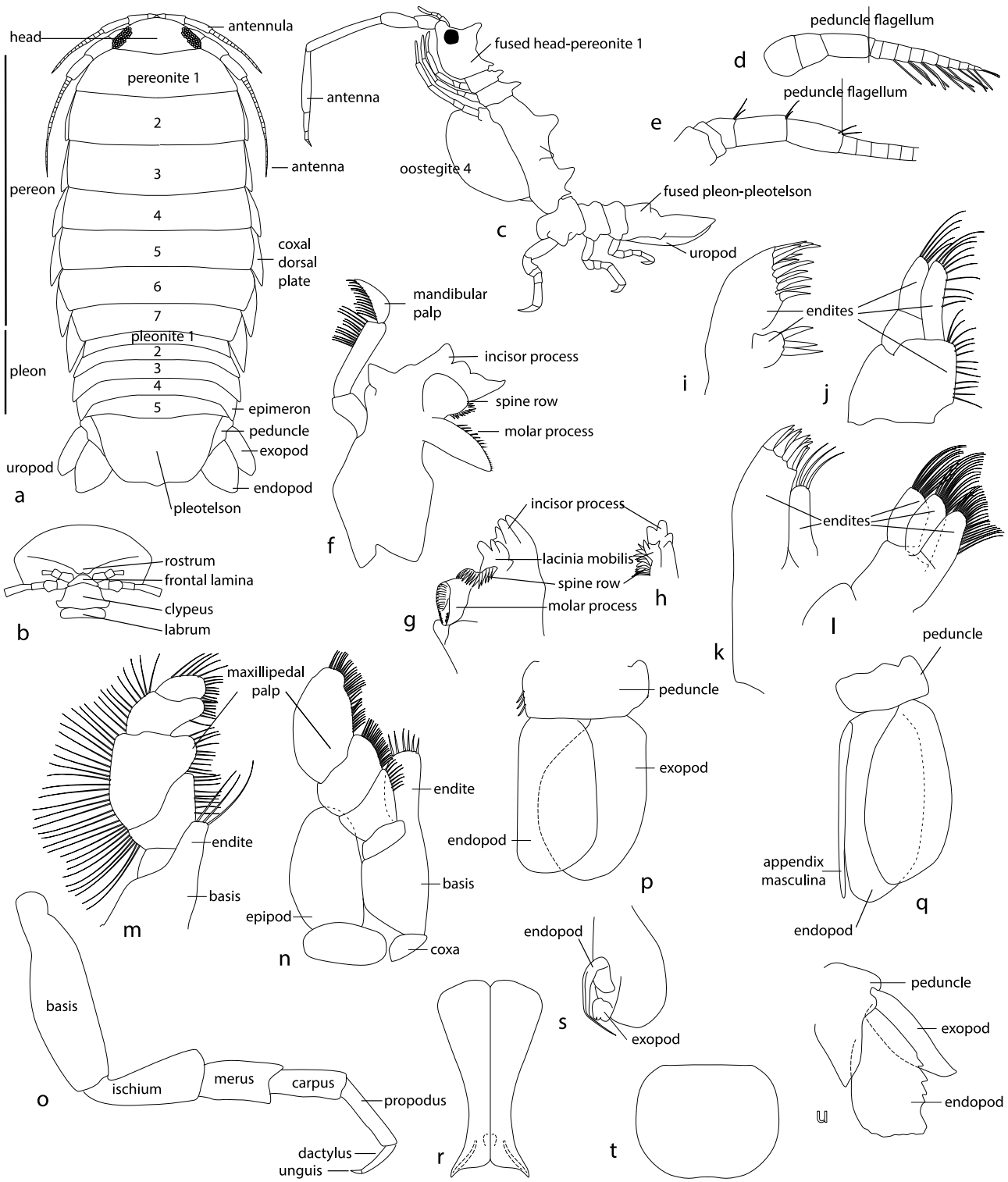


Figure 2.2. Illustrations of morphological terms used in isopod morphology. a, typical cymothoidan isopod; b, anterior view of cymothoidan head; c, lateral view of typical arcturid (Valvifera); d, typical cymothoidan antennula; e, typical cymothoidan antenna; f, typical cymothoidan mandible; g, right mandible of idoteid (palp absent); h, apex of left mandible of idoteid; i, typical cymothoidan maxillula; j, maxillula of idoteid; k, typical cymothoidan maxilla; l, maxilla of idoteid; m, typical cymothoidan maxilliped; n, maxilliped of idoteid (palp articles 4 and 5, propodus and dactylus, fused); o, typical pereopod (coxa not shown); p, typical cymothoidan pleopod 1; q, typical cymothoidan male pleopod 2; r, asellote fused pair of male pleopods 1; s, asellote male pleopod 2; t, asellote female fused opercular pleopods 2; u, typical cymothoidan uropod.

article any of the segments of a limb or appendage (see coxa, basis, ischium, merus, carpus, propodus, dactylus)

barbula posteroventral border of the head, often with lateral projections (epicarideans) (synonym, posterior ventral lamina)

basis (pl. bases; adj. basial or basal) second article of limb; first article articulating with coxa fixed to body (synonym, article 2)

bathypelagic pelagic at bathyal depths, 200 to 2000 m depth

benthic living on the sea floor; **epibenthic** species walk over the surface (cf. *pelagic*)

biramous composed of two rami or branches

broodpouch see marsupium; in Sphaeromatidae restricted to auxilliary anterior and posterior midventral cavities

branchial chamber space under the pleon enclosing pleopods; in Valvifera closed by opercular uropods and in Asellota covered by anterior pleopods (synonym, pleopodal cavity). Also the lateral space under the carapace of decapods where epicaridean isopods live (synonym, gill chamber)

buccal cone anterior projection of all mouthparts together (Cymothoida)

carina (adj. **carinate**) keel, acute ridge, crest

carpus (pl. carpi) fifth article of limb (synonym, article 5)

cephalon body segments bearing eyes, antennulae, antennae, mandibles, maxillulae and maxillae (sometimes synonymous with head and including first thoracomere and maxillipeds)

cephalosome fused somites of the cephalon and thoracomeres 1 and 2 (Gnathiidae only)

chelate claw or pincer, derived from interacting fixed finger (extension from palm of propodus) and moveable finger (dactylus)

clavate club-shaped; having one end thickened

clypeus unpaired unit of the cephalon bearing the labrum postero-medially and in contact with the frontal lamina anteriorly

concave side shorter side of body of female (epicarideans)

conglobate able to roll up into a ball, as in some sphaeromatid and oniscidean isopods

connate spine triangular marginal spine not separated at base from surrounding integument

continental shelf sea floor between low water level and shelf break, usually about 200 m depth

continental slope sea floor between edge of continental shelf, usually about 200 m depth, and top of continental rise, about 1000 m depth (often refers to slope and rise)

continental rise sea floor between lower limit of continental slope and abyssal plain (about 1000 to 4000 m)

convex side longer side of body of female (epicarideans)

copulatory stylet see appendix masculina

coxa (pl. coxae) first article of limb (closest to the body), fixed to body in isopods, not articulating; except in Asellota with dorsolateral and ventral expanded plates

coxal dorsal plate plate-like laterally- or ventrally-directed extension of coxa, covering basis of pereopod (synonym, coxal plate)

crenulate having a scalloped edge with rounded teeth, usually referring to the margin of a structure

cryptoniscus larva third larval stage that leaves the intermediate host and seeks the definitive host (epicarideans)

dactylus (pl. dactyli) seventh article of limb (last article interacting with fixed finger to form chela in chelate limb) (synonym, article 7)

dentate edged with teeth

denticulate edged with fine teeth

dextral distortion of body axis with right side longer and head displaced to left (epicarideans)

digitiform finger-like

distal situated away from the base or point of origin or attachment

distortion angle forms by intersection of lines drawn along longitudinal axes of head and pleon of female (epicarideans)

dorsolateral boss rounded knob-like process on anterodorsal surface of pereomeres of females (epicarideans)

emarginate with concave margin

endite lobe, mesial or distal, of proximal articles of limbs, especially mouthparts

endopod inner of two branches of biramous limb, comprising ischium through to dactylus; in many the dominant or only branch

endopodite see endopod

entire complete, usually meaning with smooth margin

epicaridium larva first larval stage that leaves marsupium and seeks an intermediate host (epicarideans)

epimeron (pl. epimera) lateral extension of somite, especially pleonite

epipod branch of limb, lateral to endopod and exopod; present only on maxilliped in Isopoda (synonym, epipodite)

epipodite see epipod

epistome anterior region above the mouth between front of head, antennulae and buccal region

excavate hollowed, concave

exopod outer of two branches of biramous limb, comprising one or few articles arising from basis (peduncle); pleopods and uropod only in Isopoda

exopodite see exopod

falcate sickle shaped, curved and tapering to a point

flagellum (pl. **flagella**) multiarticulate distal extension beyond 3-articulate peduncle of antennula and beyond 5-articulate peduncle of antenna

frons anterior part of the cephalon bearing the clypeus, found between the antennulae and antennae, and below the rostrum

frontal lamina plate arising between the bases of the antennae and probably homologous to the epistome; in many isopods the frontal lamina may extend anteriorly and be visible dorsally

geniculate bent at an abrupt angle, as in the body of many arcturoid isopods

gnathopod (adj. gnathopodal) a subchelate pereopod 1 (with dactylus closing on the propodal palm); in valviferans, epicarideans and some asellotes

habitus appearance of the whole animal

hirsute bearing dense long hairs

hypogean underground

hypopharynx the labium plus maxilla in Anthuroidea

hyposphenians projections on the medioventral surface of the posterior pereomeres and anterior pleomeres; in some male entoniscids

immersed sunken into, as with head into pereonite 1

incisor see incisor process

incisor process terminal process of mandible, cutting blade, often toothed (synonym, *incisor*)

indurate heavily sclerotized or calcified, and often rough

ischium (adj. ischial) third article of limb (first article of endopod or maxillipedal palp) (synonym, article 3)

interstitial living in the interstices, spaces, between sand grains, gravel or rubble

labium lobe-like structure posterior to mouth, typically divided into two lobes (**paragnaths**) (synonym, lower lip).

labrum unpaired, flat segment of the cephalon articulating with the clypeus, and anteriorly covers the mandibles (synonym, upper lip)

lacinia mobilis toothed, movably articulated process between spine row and incisor process on left mandible (replaced on the right mandible by a larger spine similar to others in the spine row)

lamina dentata serrate platelike structure in the mandible of anthuroids, formed by the fusion of spines of the spine-row

laminar flattened, broad

lanceolate lance-shaped, narrow, tapering to a point

lateral plate lateral extention of pleomere, often resembling ramus of pleopod (epicarideans)

linguiform tongue-shaped

lower lip see labium

manca first three instars following hatching from brooding embryos, lacking or with undeveloped pereopods 7

mandible (adj. mandibular) third limb of cephalon, comprising a thick body with mesial **molar process**, intermediate **lacinia mobilis** and **spine row**, terminal **incisor process,** and **mandibular palp**, usually of 3 articles

marsupium structure in which eggs and embryos are retained and brooded by female, typically formed by overlapping medial plates (**oostegites**) arising from some pereonal coxae (synonym, broodpouch)

maxilla third limb of cephalon; usually comprising three lobes being endites of two proximal articles (coxa and basis) and third article (synonym, maxilla 2)

maxilliped first thoracic limb covering more anterior cephalic mouthparts; comprising coxa, basis usually with terminal endite; palp with up to 5 articles (ischium–dactylus; palp articles often numbered 1–5); and epipod (often adhering to body)

maxillula second limb of cephalon; usually comprising two lobes being endites of two proximal articles (coxa and basis) but often reduced (synonyms, maxillule, maxilla 1)

median in the middle or midline

mesial directed toward the middle or midline

merus (pl. meri; adj. meral) fourth article of limb (synonym, article 4)

mesopelagic midwater over continental slope, beyond 200 m depth

microniscus larva second larval stage attached to the intermediate host (epicarideans)

middorsal boss rounded to pointed process arising from central dorsal region of pereomere of female (epicarideans)

midventral tubercles rounded to conical projection in midventral region of pereomere or pleomere of male (epicarideans)

midwater pelagic

molar process grinding or piercing or slicing structure, arising midbasally on body of mandible (synonym, pars molaris)

monophyletic describing a higher taxon comprising all the species descendant from a common ancestor

mouthparts all cephalothoracic limbs involved with feeding: mandible through to maxilliped

multiarticulate composed of many articles (antennular flagellar for example)

natatory adapted for swimming, rather than walking

obsolete scarcely developed, indistinct; of a spine, tooth, lobe or eye

ommatidia (pl.) individual visual components of the compound eye

oostegite medially directed laminar structure arising from coxa of pereopod or maxilliped in female, forming part of the broodpouch or marsupium

operculiform/operculate in the form of a cover or lid

operculum a cover or lid sometimes formed by anterior pleopods, especially in asellotes

ovarian processes projections on the pereomeres that contain portions of the ovary; in some entoniscids

palm flexor margin of propodus sometimes opposing the closed dactylus

palp up to 3 free articles of the mandible attached laterally to the mandible body, or up to 5 free articles of the maxilliped attached to the maxillipedal basis

paragnath *see labium*

paraphyletic describing a group comprising some but not all species descendant from a common ancestor

pectinate having fine teeth like a comb

peduncle proximal article or articles of uniramous or biramous limb, especially of antennula, antenna, pleopods and uropod (synonyms, *protopod* or *sympod*)

pelagic free-swimming in water mass or associated with drift algae (cf. *benthic*)

penes see penial processes

penial plate fused pair of penial processes (Valvifera)

penial processes paired submedian processes from vas deferens on sternum of male pereonite 7 or pleonite 1 (synonym, penes)

pereonite one of 7 segments of the pereon

pereomere (term preferred by epicaridean taxonomists) see pereonite

pereopod non-maxilliped thoracic limbs; seven pairs in Isopoda (thoracopods 2–8). Each pereopod comprises seven articles, coxa, basis, ischium, merus, carpus, propodus, dactylus but can have fewer articles.

pleon posterior part of body, of five segments or pleonites sometimes including pleotelson

pleonite segment of the pleon

pleomere (term preferred by epicaridean taxonomists) see pleonite

pleopod one of paired limbs on pleonites 1–5, usually biramous

pleotelson fused pleonite 6 and telson

pleural lamellae lateral extensions of the pleon forming part of the brood pouch (analogous to oostegites; possibly homologous with lateral plates) (entoniscids)

pleuron (pl. pleura) lateral part of body wall of pleonites, produced ventrally or laterally

polyphyletic describing a group comprising unrelated species descendant from different common ancestors

praniza juvenile, immature stage of family Gnathiidae

prehensile adapted for holding or clinging, pereopods in which the dactyl is as long or longer than the propodus and strongly recurved

propodus (pl. propodi) sixth article of limb (synonym, propod, article 6)

protandrous in sequential hermaphroditic forms, becoming a functional male (producing spermatozoa) before becoming a functional female (producing eggs)

protogynous in sequential hermaphroditic forms, becoming a functional female (producing eggs) before becoming a functional male (producing spermatozoa)

protopod(ite) see peduncle

proximal situated close to the base or point of origin or attachment

pylopod second thoracopod (pereopod 1) in Gnathiidae

ramus (pl. rami) branch of limb; **endopod** is inner branch and **exopod** is outer branch

rostrum (adj. rostral) prolongation of median part of anterior carapace between eyes (not the epistome or frontal lamina)

setose bearing setae

scale small lateral article beside antennular flagellum (homologous to exopod in other limbs; rarely seen in Isopoda)

seamount submarine mountain, usually volcanic and steep-sided, reaching much shallower water than surrounding continental slope or abyssal depths

sinistral distortion of body axis with left side longer and head displaced to right (epicarideans)

somite body segment, as in thoracic somites 1–8 and pleonites 1–5

spine row spinose lobe on the mandible, between the molar and incisor processes

statocyst cavity filled with fluid and particles acting as organ of orientation in telson in some Anthuroidea

sternite ventral plate of integument (cf. *tergite*)

sternum ventral surface of body, to which limbs are attached

stygobiont cave organism

styliform long, slender, stiletto-like

sub- prefix meaning almost or close to (as in submedian, sublateral)

subchelate having a subchela formed by the dactylus folding back on to the propodal palm (cf. chelate)

sympod see peduncle

telson plate attached medially to terminal segment of pleon and fused in Isopoda

tergal projection extended process on lateral posterodorsal surface of pereomere of female (epicarideans)

tergite dorsal plate of integument (cf. *sternite*)

thoracic somite one of the eight segments of the thorax (thoracic somites 2–8 are pereonites 1–7 in isopods)

thoracomere see thoracic somite

thorax middle body region of eight somites bearing maxilliped and pereopods 1–7

tricuspid bearing 3 cusps or points

trifid divided into 3 parts or lobes

truncate appearing to be abruptly cut off

tuberculate bearing knob-like or wart-like prominences or tubercles

unguis modified seta on the tip of the dactylus (synonym, claw)

uniramous with only a single branch (ramus)

uropod paired limb of sixth pleonite, combining with telson to form tailfan

walking leg see pereopod

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Chapter 3. Suborder Asellota

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Abstract Poore, G.C.B. 2026. Chapter 3. Suborder Asellota. *In*: Poore, G.C.B. (ed.) Marine Crustacea Isopoda: guide to families and genera of the world. *Memoirs of Museum Victoria* 86: 29–129.

Diagnoses and illustrated keys are provided for 30 families and 234 genera of marine families of asellote isopods. The ecology and distribution of each taxon are discussed with citation of literature critical for further investigation and identification to species.

Keywords Acanthaspidiidae, Basoniscidae, Dendrotionidae, Desmosomatidae, Echinothambematidae, Gnathostenetroididae, Gnathostenetroidoidea, Haplomunnidae, Haploniscidae, Ischnomesidae, Janirellidae, Janiridae, Janiroidea, Joeropsididae, Katianiridae, Lepidocharontidae, Macrostylidae, Mesosignidae, Microparasellidae, Mictosomatidae, Munnidae, Munnopsidae, Nannoniscidae, Paramunnidae, Pleurocopidae, Pseudojaniridae, Santiidae, Stenetriidae, Stenetrioidea, Thambematidae, Urstylidae, Vermectiadidae, Xenosellidae, dichotomous keys

Introduction

The Asellota Latreille, 1802 are a diverse group of mostly small isopods, usually 3–5 mm long, but *Bathyopsurus sonnei* Brandt and Kelch, 2025 can reach a body length of 65 mm. Asellotes inhabit most marine environments but extremely abundant and diverse in the deep-sea (Hessler et al., 1979; Wolff, 1962) or in cold waters (Kaiser et al., 2007). In deep waters most are benthic, associated with soft sediments, but some are wholly or partially mesopelagic (Osborn, 2009). Asellotes also associate with subtidal rocky or coral reefs. Some inhabit fresh water (superfamily Aselloidea) but are not discussed further here.

Asellota have specialised reproductive structures that distinguish them from all other isopods. Pleonites 4 and 5 (and often pleonite 3) are fused to the pleotelson, making an enlarged posterior segment. Pleonites 1 and 2 are vestigial. Pleopods 1, 2 and/or 3 are fused to form an operculum covering the remaining pleopods; this way this happens defines the superfamilies. In the male, pleopods 2 form a specialised copulatory apparatus involving enlarged peduncles, a folded endopod and sturdy exopod (Harrison, 1987). One family, Vermectiadidae, thought to be the most primitive asellote, displays only some of these features (Just and Poore, 1992), which led to uncertainty about the relationships between the four accepted superfamilies.

Diagnosis. Head-pereonite 1 usually free. Dorsal pereopodal coxal plates absent. At least pleonites 4–6, sometimes pleonites 1–3, fused into pleotelson. Pleotelson underside flat, without ventrolateral ridges (pleopods not enclosed laterally). Penial processes at bases of pereopod 7. Mandibular lacinia mobilis present on both sides; molar usually a cylindrical process with triturative flat end; palp usually present. Maxilla trilobed. Maxillipedal endite reaching at least distal margin of palp article 2, usually distally truncate and setose. Pereopods 1–7 similar, directed more or less laterally. Pleopodal exopods biarticulate. Pleopod 1 uniramous in male, sometimes interacting with groove on pleopod 2, absent in female. Pleopod 2 biramous in male, endopod modified as complex gonopod; uniramous or pair fused as operculum in female. Pleopod 3 biramous (uniramous in Vermectiadidae); endopod more or less oval or rectangular, rounded distally. Telsonic region of pleotelson short, anus situated posteriorly on pleotelson. Uropod terminal; peduncle not operculate; rami terminal.

Key to Vermectiadidae and four superfamilies of Asellota

1. Pleotelson with 3 free pleonites. Male pleopods 1, 2 not operculate (fig. 3.1) ..... Vermectiadidae ... p. 31
– Pleotelson with 0–3 free pleonites. Male pleopods 1, 2 operculate 2
2. Male pleopods 1 and 2 and female pleopods 2 much smaller than pleopods 3, which form an operculum over pleopods 4 and 5 3

– Male pleopods 1 and 2 and fused female pleopods 2 large, forming an operculum totally covering pleopods 3–5 4

3. Left and right male pleopods 1 and female pleopods 2 distinctly separate ..... Aselloidea

– Peduncles of male pleopods 1 fused. Female pleopods 2 forming small, pear-shaped operculum (fig. 3.47) ..... Stenetrioidea ... p. 122

4. Peduncles of male pleopods 1 short, totally fused; rami separate, large, entirely covering succeeding pleopods (fig. 3.2f). Female operculum (fused pleopods 2) with broad median terminal incision (fig. 3.2e). Mandible with large tusk-like antero-exterior prolongation in terminal male (fig. 3.2d), small acute process in female (not seen in most specimens) ..... Gnathostenetroidoidea ... p. 32

– Peduncles of male pleopods 1 elongate, coupled (sometimes fused) with each other along midline, covering interior margins of pleopods 2. Pleopods 1 and 2 of male together cover succeeding pleopods (fig. 3.15). Female operculum (fused pleopods 2) rarely with median terminal incision. Mandibles without antero-exterior prolongation or process ..... Janiroidea ... p. 34

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Credits

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Fig. 3.1a–c, Just and Poore (1992). Fig. 3.2a, Stock and Vonk (1980); b, Malyutina and Bruce (2019); c, Carpenter and Magniez (1982). Fig. 3.3a–d, Brandt (1991); e, f, Just (2001). Fig. 3.4a, Wilson (2024). Fig. 3.5a, b, d, e, Cohen (1998); c, Golovan et al. (2018). Fig. 3.6a, b, Brix (2006a); h, Kaiser and Brix (2007). Fig. 3.9a, Just (2003); b, c, Wilson (1976); d, Brenke and Buschmann (2009). Fig. 3.11a, b, e–h, Merrin and Poore (2003); c, Cunha and Wilson (2006). Fig. 3.13a, l, Winkler and Brandt (1993); b, Kim et al. (2019); c, d, Malyutina (1994); e, f, k, Doti and Wilson (2010); g, Kensley (1976); h, Miller (1967); i, Lemos de Castro and Brasil Lima (1977). Fig. 3.14a, Veuille (1979); b, Doti and Wilson (2010); c, Menzies (1951); d, Wolff (1962); e, Matsumoto (1956); f, Shimomura (2005); g, Schiecke and Fresi (1970); h, Kussakin and Vasina (1984); i, Menzies (1962); j, Menzies and Barnard (1951); j, Chappuis et al. (1956); k, Müller (1993). Fig. 3.16a–c, Just (2001). Fig. 3.17a, Svavarsson (1987); b, Kensley (1984). Fig. 3.18a, Albuquerque et al. (2014); b, Galassi et al. (2016); c, Kim et al. (2017). Fig. 3.19, Riehl and Brandt (2013). Fig. 3.20a, d, George (2003); b, c, Menzies and Frankenberg (1967); e, Menzies (1962). Fig. 3.22a, Beddard (1886); b, c, Vanhöffen (1914); d, Teodorczyk and Wägele (1994); e, Müller (1990); g, Menzies and George (1972). Fig. 3.24a, b, Malytina et al. (2018); c, Wilson (1982b); d, e, h, i, Malyutina and Brandt (2006); f, g, Wilson (1982a); j, k, Wilson and Hessler (1981). Fig. 3.25a, b, e, Sars (1897); c, d, f, g, Merrin (2009); h, i, Merrin (2016); j, k, Merrin (2004). Fig. 3.26a, b, Merrin (2011); c, d, Merrin (2006); e–l, Wilson (1989). Fig. 3.27a, b, Wilson (1982a); c, Sars (1897); d, Beddard (1885); e, Svavarsson (1988). Fig. 3.28a, b, Wilson et al. (1989); c, d, Just (2001); e–h, Malyutina (2011); i, j, Malyutina and Brandt (2004b); k–m, Malyutina (2003); n–q, Haugsness and Hessler (1979). Fig. 3.29a, b, Malyutina and Brandt (2007); c, d, Malyutina (2008); e, f, Mursch et al. (2008); g, Sars (1885). Fig. 3.31d–h, Wilson (1989); i, m, Tattersall (1906); k, l, Just (2001); n–s, Malyutina (2011); t, Haugsness and Hessler (1979). Fig. 3.33a, Kaiser and Brandt (2007); b, c, Kaiser et al. (2021); d, e, Kaiser (2009). Fig. 3.35a, b, Just (1990); c, Chardy (1975); d, Doti and Roccatagliata (2005); e–g, Just and Wilson (2004); h, Shimomura (2009); i, Just and Wilson (2006); j, Just and Wilson (2007). Fig. 3.36a, Kussakin and Vasina (1984); b, Schiecke and Fresi (1972); c, Just (2009); d, Hodgson (1910); e, Choudhury et al. (2011); f–h, Just and Wilson (2004); i, Shimomura and Mawatari (2002). Fig. 3.37a, Doti et al. (2009); b, Amar (1974); c, Kussakin (1982); d, Winkler (1994); e, f, Just and Wilson (2007); g, Just and Wilson (2021); h, Beddard (1885); i, Shimomura (2009); j, Hodgson (1910); k, l, Just and Wilson (2004). Fig. 3.38a, b, g, i, Just and Wilson (2004); c, Just (1990); d, Just (2009); e, k, l, Winkler (1994); f, Golovan and Malyutina (2019); h, Shimomura (2009); j, Just and Wilson (2006). Fig. 3.40b, Shimomura (2009); c, Sars (1896–1899); d, Vanhöffen (1914). Fig. 3.41, Shimomura and Naruse (2015). Fig. 3.42a, Wolff (1989); d, e, Wolff and Brandt (2000). Fig. 3.44, Riehl et al. (2014). Fig. 3.45, Just (2005). Fig. 3.46b, Menzies (1962); c, Beddard (1886). Fig. 3.47a, Serov and Wilson (1999); b, Poore and Just (1990); c, Serov and Wilson (1999). Fig. 3.48a, Bruce and Buxton (2013); b, Serov and Wilson (1995).

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Asellota incerta sedis

Vermectias Sivetsen and Holthuis, 1980 is the only asellote genus with three free pleonites in front of the pleotelson. Other characters considered primitive within the Asellota are lateral penes arising from the base of pereopods 7; a pointed male pleopod 2 stylet with a broad, open lateral sperm groove; and characters of the female reproductive system not needed for identification of this genus. These features exclude the genus and the family erected for it by Just and Poore (1992) from the Janiroidea until the superfamilies are better understood.

Vermectiadidae Just and Poore, 1992

Figure 3.1

Vermectiadids are tiny (<2.5 mm long) elongate asellotes from subtidal environments on subantarctic islands (possibly also occurring in southern Chile).

Diagnosis. Pleonites 1–3 free from pleotelson. Male pleopods 1 and 2 not operculate; peduncles of male pleopods 1 short, fused; rami separate, fused to peduncle. Female pleopods 2 absent. Pleopods 3, 4 enlarged, uniramous, inflated, without setae; peduncle absent.

Vermectias Sivetsen and Holthuis, 1980

Subtidal. Southern Ocean. Tristan da Cunha, Macquarie I., Australia. 2 species (Just and Poore, 1992)

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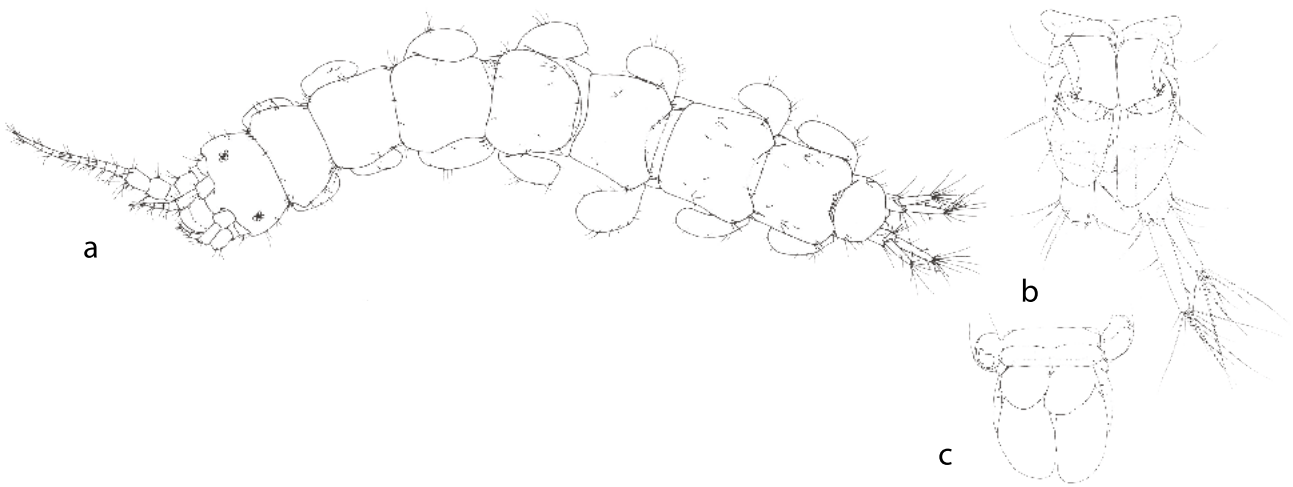


Figure 3.1. Vermectiadidae, *Vermectias nelladanae* Just and Poore, 1992. a, male; b, male pereonite 7, pleon ventral showing penes, pleopods 1–3, uropod; c, female pereonite 7, pleon ventral showing pleopods 1–3.

Superfamily Gnathostenetroidoidea Kussakin, 1967

Gnathostenetroidoidea are characterised by the large male pleopods 1 with unfused operculate rami covering the other pleopods. In other asellote superfamilies the operculum is formed by enlarged pleopods 3 (Stenetrioidea) or pleopods 1 and 2 together (Janiroidea). Gnathostenetroidids are vermiform isopods and like many asellotes are tiny (1–3 mm in length) as adults (Malyutina and Bruce, 2019). Gnathostenetroidoidea comprise two families: Gnathostenetroididae Kussakin, 1967 and Protojaniridae Fresi, Idato and Scipione, 1980. The latter is confined to freshwater interstitial environments and will not be discussed further. For recent information on the seven genera of Protojaniridae consult Fresi et al. (1980), Kensley (1995) and Pérez-Schultheiss and Wilson (2021).

Diagnosis. Mandibles with large tusk-like anteroexterior prolongation in terminal male and a small acute process in female (rarely seen). Male pleopods 1 forming an operculum totally covering pleopods 2–5; peduncles of male pleopods 1 short, totally fused; rami separate, large, entirely covering succeeding pleopods. Female operculum with broad median terminal incision; female pleopods 2 large, forming an operculum totally covering pleopods 3–5.

Gnathostenetroididae Kussakin, 1967

Figure 3.2

Gnathostenetroididae can be distinguished from Protojaniridae by the presence of two free (unfused) pleonites, while Protojaniridae is characterised by absence of free pleonites. All are tiny interstitial isopods of sediments in tropical and subtropical shores or anchialine caves. Malyutina and Bruce (2019) reviewed the family and provided a key to genera.

Diagnosis. Pleonites 1 and 2 free from pleotelson.

Key to genera of Gnathostenetroididae

1. Eyes present. Pleotelson posterolateral margins with indentations and posteriorly directed spines (fig. 3.2b). Pleopod 4 exopod of 1 article, about half as long as endopod (fig. 3.2j) ..... *Gnathostenetroides*

– Eyes absent. Pleotelson posterolateral margins rounded, without indentations and spines. Pleopod 4 exopod of 2 articles, not shorter than endopod 2

2. Body broad, flattened, about 2.5–3.0 times as long as wide (fig. 3.2c). Pleopods 3, 4 endopods of 2 articles. Pleopod 3 exopod narrower than endopod. Pleopod 4 exopod as long as and wider than endopod (fig. 3.2k, l) ..... *Neostenetroides*

– Body vermiform, about 9 times as long as wide (fig. 3.2a). Pleopods 3, 4 endopods of 1 article. Pleopod 3 exopod as wide as endopod. Pleopod 4 exopod about as long and wide as endopod (fig. 3.2g, h) ..... *Caecostenetroides*

Caecostenetroides Fresi and Schiecke, 1968

Diagnosis. Body vermiform, about 9 times as long as wide; pleotelson posterolateral margins rounded. Eyes absent. Pleopods 3, 4 endopods of 1 article. Pleopod 3 exopod as wide as endopod. Pleopod 4 exopod of 2 articles, about as long as wide as endopod.

Intertidal. Temperate Northern and Tropical Atlantic, Temperate Northern Pacific, Eastern Indo-Pacific. 6 species (Stock and Vonk, 1990: 2 species, one as *Dignatroides* Stock and Vonk, 1990, junior synonym; Müller, 1991).

Gnathostenetroides Amar, 1957

Diagnosis. Body elongate, 4.0–5.5 times as long as wide; pleotelson posterolateral margins with indentations and posteriorly directed spines. Eyes present. Pleopods 3, 4 endopods of 1 article. Pleopod 3 exopod narrower than endopod. Pleopod 4 exopod of 1 article, about half as long as endopod.

Intertidal shelf. Tropical Atlantic (including Eastern Mediterranean), Western and Central Indo-Pacific, Tropical Eastern Pacific. 12 species (Müller, 1992: description of 3 species as *Maresiella* Fresi and Scipione, 1980, junior synonym; Malyutina and Bruce, 2019: list and key to species).

Neostenetroides Carpenter and Magniez, 1982

Diagnosis. Body broad, flattened, about 2.5–3.0 times as long as wide; pleotelson posterolateral margins rounded. Eyes absent. Pleopods 3, 4 endopods of 2 articles. Pleopod 3 exopod narrower than endopod. Pleopod 4 exopod of 2 articles, as long and about as wide as endopod.

Anchialine caves. Tropical Atlantic (Caribbean). 3 species (Botosaneanu and Iliffe, 2007; Carpenter and Magniez, 1982).

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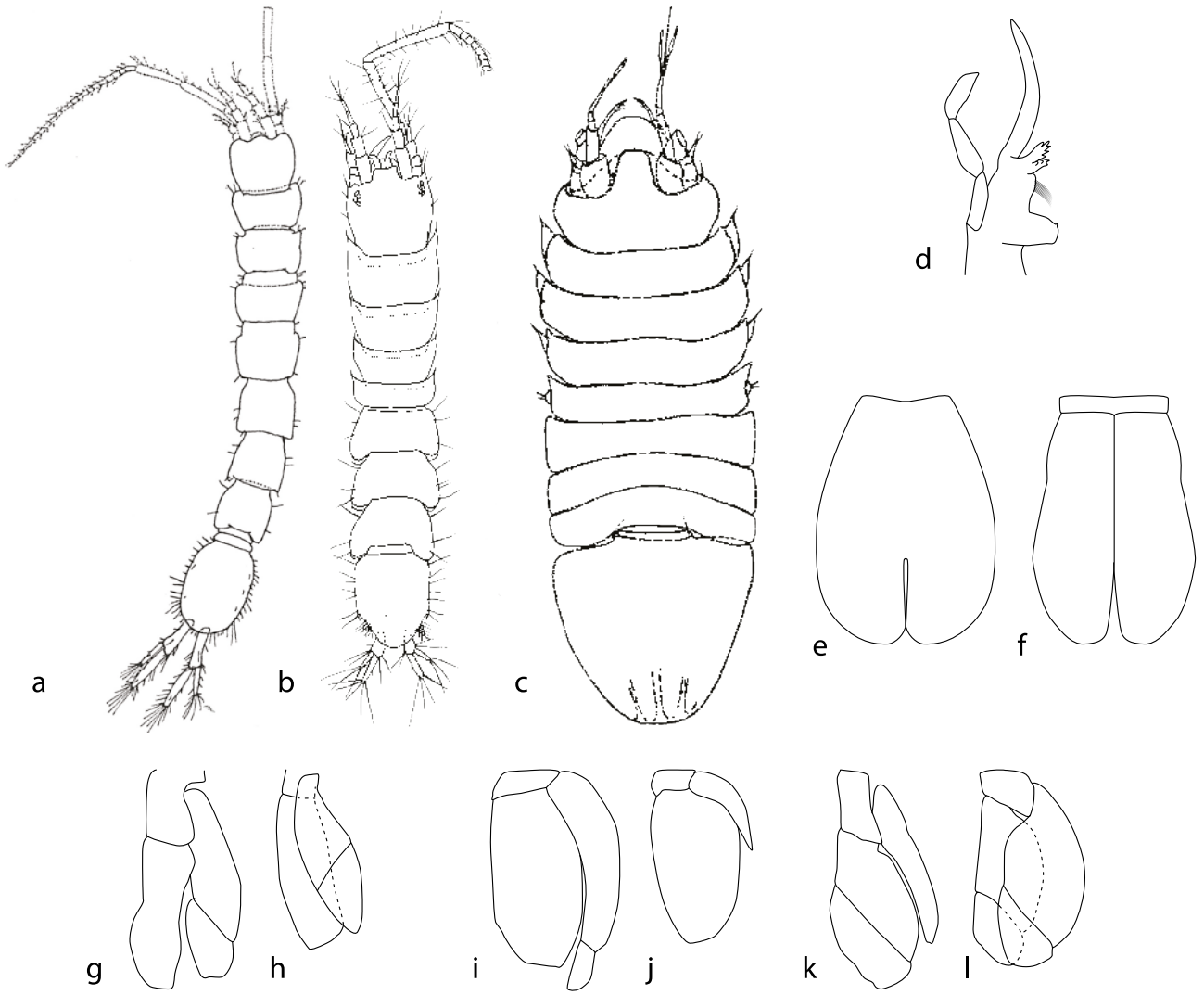


Figure 3.2. Gnathostenetroididae. a, *Caecostenetroides ruderalis* Stock and Vonk, 1990; b, *Gnathostenetroides blazewiczae* Malyutina and Bruce, 2019; c, *Neostenetroides stocki* Carpenter and Magniez, 1982; d, male mandible, *Gnathostenetroides*; e, female pleopods 2, *Gnathostenetroides*; f, male pleopods 2, *Gnathostenetroides*; g, h, pleopods 3, 4, *Caecostenetroides*; i, j, pleopods 3, 4, *Gnathostenetroides*; k, l, pleopods 3, 4, *Neostenetroides*.

Superfamily Janiroidea G.O. Sars, 1897

With 26 families, Janiroidea is the largest superfamily of Asellota. They are recognised by the unique arrangement of the first two pairs of pleopods. In males these pleopods together form an operculum entirely (or sometimes with lateral parts of pleopods 3) covering the more posterior pleopods. In females pleopods 1 are absent and pleopods 2 are fused, forming a discoid operculum.

While some families occur mostly in shallow rocky or coral reefs, sometimes associated with algae, many families occur exclusively in the deep sea. Their invasion and subsequent dominance of bathyal and abyssal benthic faunas has generated considerable discussion (Brandt et al., 2004; Raupach et al., 2004; Wolff, 1962). Janiroidea appear to be the most derived group of all Asellota (Wilson, 1987, 2024).

The key to families used that of Wilson (2013) as a starting point, but is much modified. It contains triplets.

Diagnosis. Pleon with or without free pleonites. Mandibles without antero-exterior prolongation. Male pleopods 1 and 2 forming an operculum totally or mostly covering pleopods 3–5; peduncles of male pleopods 1 elongate, coupled (sometimes fused) with each other along midline, covering interior margins of pleopods 2; rami indistinct. Female pleopods 2 fused, forming a large operculum totally covering pleopods 3–5, rarely with median terminal incision.

Key to families and genera incertae sedis of Janiroidea

1. Antenna geniculate, peduncular article 6 and flagellum folding laterally and backwards under lateral expansion of peduncular article 5. Anterior pereonites with sternal keels (fig. 3.15) ..... Joeropsididae ... p. 65
– Antennal peduncle axis with moderate bend at articles 3–5; distal articles not or scarcely folding against proximal articles. Anterior pereonites without sternal keels 2
2. Uropod peduncle vestigial or absent 3
– Uropod peduncle present 5
3. Pereonites 2–6 with 1 or 2 pairs of prominent lateral projections, often spinose; head and pereonite 1 without lateral processes. Pleonite 1 fused with pleotelson. Pereopod 1 ambulatory (fig. 3.20) ..... Mesosignidae ... p. 70
– Head and pereonites with or without lateral projections. Pleonite 1 free from pleotelson. Pereopod 1 prehensile 4
4. Body subpyriform, without lateral processes. Eyes on prominent lateral processes (if present). Anus not covered by pleopodal operculum (figs 3.22, 3.23) ..... Munnidae ... p. 73
– Body broad, ovate, often with lateral plates. Anus covered by pleopodal operculum (figs 3.35–3.40) ..... Paramunnidae ... p. 101
5. Uropod inserting on anterolateral surface of pleotelson (fig. 3.41) ..... Pleurocopidae ... p. 115
– Uropod inserting on posterolateral margin or on posteroventral surface of pleotelson 6
– Uropod inserting above posterior margin on dorsal surface on pleotelson 26
6. Pereonites 5–7 and pleon integrated into natasome, dorsal surface vaulted (figs 3.24–3.32) ..... Munnopsidae ... p. 76
– Pereonites 5–7 serially homologous, not especially integrated with pleon 7
7. Pereopod 4 coxa inserting on midlateral margin 8
– Pereopod 4 coxa inserting on anterolateral margin 19
8. Pereonites 1–3 more or less fused into rectangular section (fig. 3.19) ..... Macrostylidae ... p. 69
– Pereonites 1–3 not integrated into rectangular section 9
9. Antennula basal article directed anterodorsally 10
– Antennula basal article directed anteriorly 11
10. Body smooth, not spinose; pereonites 2–4 with lateral projections; pleon not swollen, in line with pereon. Uropod comprising single long article. Antennula much shorter than head width. Body dorsal surface without major spines (fig. 3.17) ..... Katianiridae ... p. 67

– Body spinose or setose; pereonites 2–4 without lateral projections; pleon swollen, angled dorsally. Uropod reduced, with 1 or 2 articles. Antennula longer or as long as head width (fig. 3.9) ..... Haplomunnidae ... p. 47

11. Body oval, smooth, without lateral processes. Pleon without free pleonites 12

– Body various, sometimes with lateral processes. Pleon with or without free pleonites 13

12. Uropod peduncle short, rod-like, not covering anus; exopod absent. Pleotelson usually with posteriorly pointing posterolateral angles or processes (fig. 3.10) ..... Haploniscidae ... p. 48

– Uropod peduncle broad, covering anus; exopod minute. Pleotelson without posterolateral angles or processes (fig. 3.4) ..... Basoniscidae ... p. 38

13. Pereonites with lateral projections, bifurcate on pereonites 2–4 or 2–7. Head with prominent narrow rostrum (fig. 3.3) ..... Acanthaspidiidae ... p. 36

– Pereonites without bifurcate lateral projections. Head without rostrum or rostrum minute or broad (never prominent) 14

14. Antennula with 7 articles. Antenna without scale. Maxilliped palp 4-articled, last article sickle-shaped. Pereopods with 3 claws; pereopod 5 sexually dimorphic, in male subchelate, stout (fig. 3.46a) ..... *Angeliera* ... p. 120

– These characters not combined 15

15. Anus covered by pleopodal operculum 16

– Anus not covered by pleopodal operculum 17

16. Pereonite 5 narrowed anteriorly as short stalk (fig. 3.21) ..... Mictosomatidae ... p. 72

– Pereonite 5 not narrowed anteriorly as short stalk (fig. 3.12) ..... Janirellidae ... p. 55

17. Body oval, flat or vaulted (about twice as long as wide), pereonites much wider than long (fig. 3.42) ..... Santiidae ... p. 116

– Body flat, slender (4–10 times as long as wide), pereonites similar, rectangular 18

18. Uropod uniramous, short. Antenna peduncle longer than flagellum. Head with prominent rostrum (mostly freshwater) ..... Microparasellidae ... p. 72

– Uropod biramous, large. Antenna peduncle shorter than flagellum. Rostrum small or absent (fig. 3.18) ..... Lepidocharontidae ... p. 68

– These characters not combined in these ways (figs 3.13–3.15) ..... Janiridae ... p. 57

19. Pereonite 7 or pereonites 6 and 7 fused with pleon. Head frontal margin not projecting anteriorly. Antennula as long as antenna, projecting laterally (fig. 3.8) ..... Echinothambematidae ... p. 46

– Pereonites 6 and 7 not fused with pleon. Head frontal margin projecting anteriorly. Antennula much shorter than antenna length, projecting anteriorly 20

20. Pereonites 2–4 without lateral projections. Pereopods 5–7 coxae oriented ventrolaterally 22

– Pereonites 2–4 tergites with lateral projections. Pereopods 5–7 coxae oriented ventrally 24

21. Anterior pereopods coxae with anterolateral robust setae. Pereon divided in anterior unit of 4 short pereonites and posterior unit of 3 longer depressed pereonites. Head deeper than anterior pereon, ventrally projecting (fig. 3.7) ..... Desmosomatidae ... p. 40

– Anterior pereopods coxae without anterolateral robust setae. Pereonites similar, tagmosis hardly developed. Head about as deep as anterior pereon 21

22. Pereonites 2–7 wider than long. Pleopods 3–5 completely covered by anterior pleopods. Pereopod 1 simple, carpus trapezoidal (fig. 3.44) ..... Urstylidae ... p. 118

– Pereonites 2–7 usually longer than wide. Pleopods 3–5 not completely covered by anterior pleopods. Pereopod 1 subchelate (fig. 3.43) ..... Thambematidae ... p. 118

– Pereonites 2–7 wider than long. Pleopods 3–5 completely covered by anterior pleopods. Pereopod 1 ambulatory 23

23. Pereon parallel-sided, not laterally splayed. Pleonite 1 free. Antennula and antenna about as long as head (fig. 3.46d) ..... *Xostylus* ... p. 120

– Pereon oval-elongate, laterally splayed. Pleon of 1 segment. Antennula and antenna much longer than head (fig. 3.46c) ..... *Trichopleon* ... p. 120

24. Mouthparts projecting strongly anteriorly (head including rostrum twice as long as wide). Pereonites with spinulose lateral extensions. Mandibles lanceolate, exposed in dorsal view (fig. 3.46b) ..... *Sugoniscus* ... p. 120

– Mouthparts not projecting strongly anteriorly (head including rostrum about as long as wide). Mandibles not exposed in dorsal view. Pereonites without lateral extensions 25

25. Pereonite 1 shorter than pereonite 2; pereonite 5 as long as pereonites 6 and 7, sometimes fused (figs 3.33, 3.34) ..... Nannoniscidae ... p. 96

– Pereonites 1, 2 similar; pereonite 5 much longer than pereonites 6, 7 (fig. 3.11) ..... Ischnomesidae ... p. 51

26. Pereonites 5–7 (and 1–4 in male) lateral parts tubular, with large intersegmental gaps; pereonite 5 as long as pereonite 3. Antennula longer than antenna (fig. 3.45) ..... Xenosellidae ... p. 118

– Head and pereonites bearing dorsal spines of long setae; pereonite 5 shorter than pereonite 3. Antennula much shorter than antenna (fig. 3.5) ..... Dendrotionidae ... p. 39

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Acanthaspidiidae Menzies, 1962

Figure 3.3

Acanthaspiids are largely deep-sea isopods with some emerging in shallow shores. Most can be easily recognised by the presence of lateral processes (often bifurcate) on the pereonites, but these are not well developed in some species. Brandt (1991) revised the family and listed the two genera and species then known. Her key to these two genera, *Acanthaspidia* Stebbing, 1893 (now *Iolanthe* Beddard, 1886) and *Ianthopsis* Beddard, 1886 is not reliable, and they appear to overlap for most of the characters in her key. Just (2001) rediagnosed the family, discussing specialisation of the male pleopod 2, and added a third genus. Adults range from 2.5 to 5.4 mm long.

Diagnosis. Body strongly depressed, broadly oval; head usually with prominent narrow rostrum; pereonites with lateral projections, bifurcate on 2–4 or 2–7. Pleon of 1 segment, with serrate margins. Anus covered by pleopodal operculum. Eyes present or absent. Antennal scale long. Maxillipedal palp articles 1–5 narrow, less than half as wide as endite. Pereopods 1–7 ambulatory; pereopod 4 coxa inserting on midlateral margin; pereopodal 2–7 dactyli with 2 claws. Uropod inserting on posterior margin, biramous, usually with long peduncle.

Key to genera of Acanthaspidiidae

1. Eyes present on lateral stalks. Mouthparts produced forwards beyond front of head (fig. 3.3e, f) ..... *Mexicope*

– Eyes absent or not on lateral stalks if present. Mouthparts not or scarcely produced forwards beyond front of head 2

2. Pleotelson about one third as long as and narrow than pereon; lateral margin coarsely or finely serrate (fig. 3.3c, d) ..... *Iolanthe*

– Pleotelson half as long as pereon, narrow anteriorly; lateral margin finely serrate with short curved robust setae (fig. 3.3a, b) ..... *Ianthopsis*

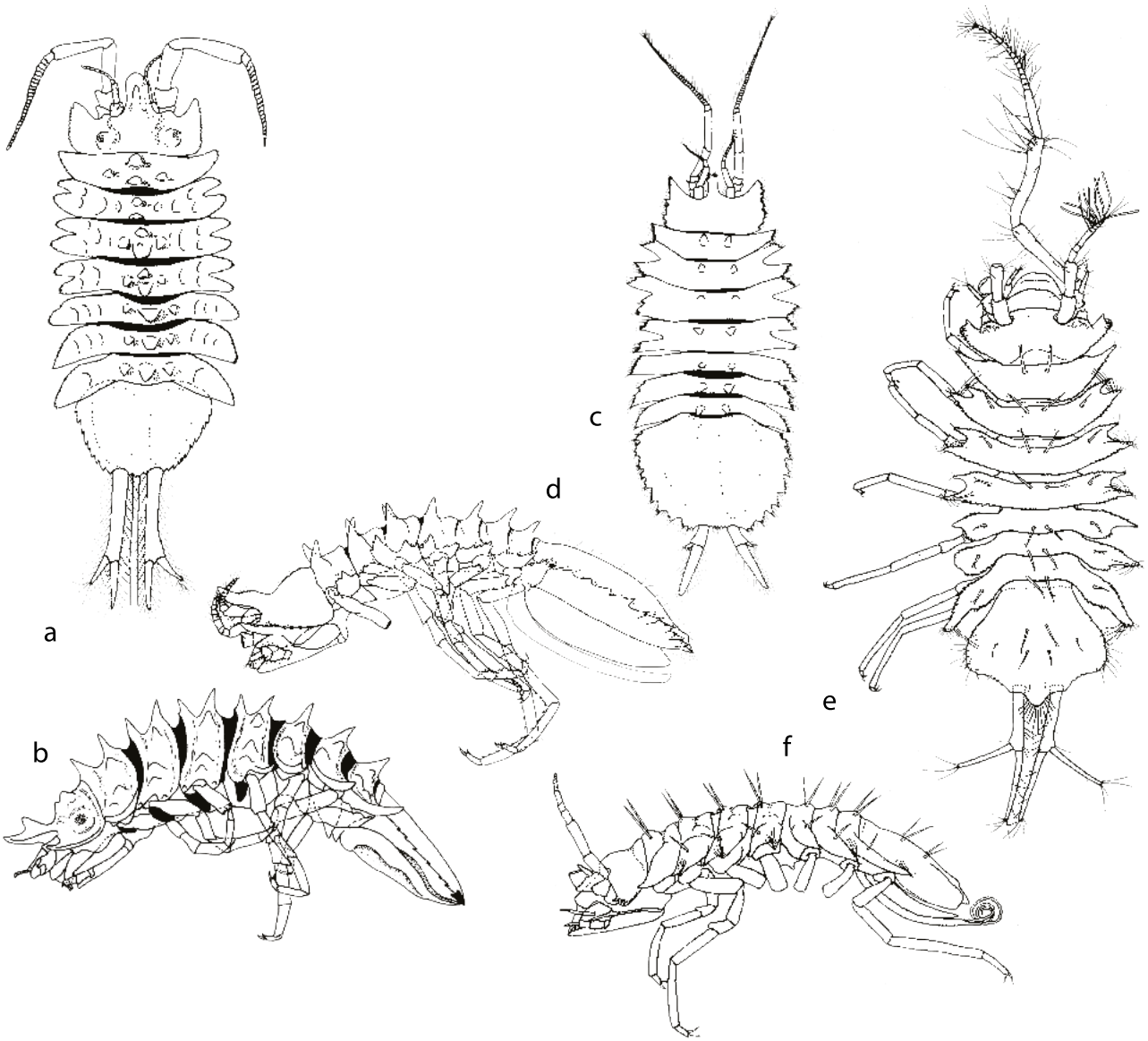


Figure 3.3. Acanthaspidiidae. a, b, *Ianthopsis nasicornis* Vanhöffen, 1914, male, female; c, d, *Iolanthe drygalskii* (Vanhöffen, 1914), female, male; e, f, *Mexicope westralia* Just, 2001, male.

Ianthopsis Beddard, 1886

Diagnosis. Rostrum present. Pleotelson about one third as long as and narrow than pereon; lateral margin coarsely or finely serrate. Eyes present on low bulges, or absent. Mouthparts not or slightly produced forwards.

Subtidal–bathyal. Temperate South America, Temperate Australasia, Southern Ocean. 13 species (Brandt, 1991: rediagnosis, key to 10 species; Just, 2001: rediagnosis, depth distribution; Riehl et al., 2024: rediagnosis, list of species).

Iolanthe Beddard, 1886

Diagnosis. Rostrum present. Pleotelson discoid, about half as long and as wide as pereon; lateral margin with long spines or serrate. Eyes absent. Mouthparts not produced forwards.

Slope–hadal. Arctic, Temperate Northern Atlantic, Temperate Northern W Pacific, Temperate Southern Africa, Southern Ocean. GOODS bathyal provinces: Northern N Atlantic, Northern N Pacific, Antarctic, Subantarctic, Indian, W Pacific, S Atlantic, N Pacific. 20 species (Brandt, 1991: rediagnosis, key to 18 species as *Acanthaspidia*; Just, 2001: depth distribution). Most species in this genus were described or recognised as members of *Acanthaspidia* Stebbing, 1893 but *Iolanthe* is a senior synonym (Merrin and Poore, 2015).

Mexicope Hooker, 1985

Diagnosis. Rostrum absent or short, spine-like. Pleotelson half as long as pereon, narrow anteriorly; lateral margin finely serrate with short curved robust setae. Eyes present on lateral stalks. Mouthparts produced forwards beyond front of head.

Subtidal, shelf. Temperate Northern and Tropical Atlantic, Temperate Australasia. 4 species (Just, 2001: rediagnosis; Bruce, 2004: comment on diagnosis; Riehl et al., 2024: rediagnosis, key to species).

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Basoniscidae Wilson, 2024

Figure 3.4

Basoniscidae was erected for a single genus and species said to be intermediate between Joeropsididae and Haploniscidae (Wilson, 2024).

Diagnosis. Body oval, flat; pereonites 1–7 free, wider than long, with laminar lateral expansions. Coxal plates absent. Pleon without free pleonites, semicircular, flanged. Anus not covered by pleopodal operculum. Eyes absent. Antennal scale lobe-like. Maxillipedal palp articles 1–5 narrow, less than half as wide as endite. Pereopods 1–7 ambulatory. Uropod inserting posteroventrally, peduncle broad, covering anus, biramous, with short exopod.

Basoniscus Wilson, 2024

Bathyal (2974–3183 m depth). GOODS bathyal provinces: New Zealand/Kermadec. 1 species.

Reference

Wilson, G.D.F. 2024. A new family of Asellota (Crustacea, Isopoda) from the deep sea of Zealandia. *European Journal of Taxonomy* 917: 122–151. https://doi.org/10.5852/ejt.2024.917.2393

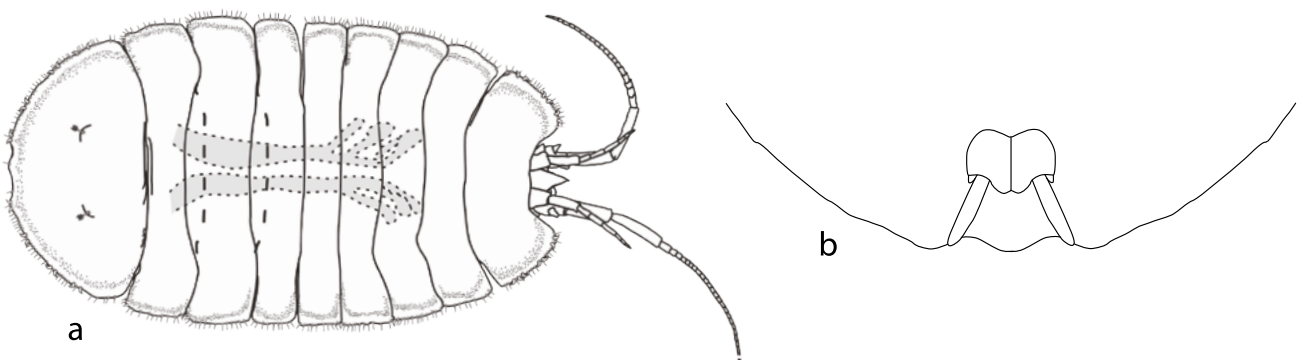


Figure 3.4. Basoniscidae, *Basoniscus hikurangi* Wilson, 2024. a, habitus; posterior pleotelson, uropods (ventral).

Dendrotionidae Vanhöffen, 1914

Figure 3.5

Dendrotionid isopods are confined to the slope and deep sea. They are best recognised by their oval shape, more or less spinose or setose dorsally, and their long spindly legs. The family and its genera were diagnosed and reviewed by Cohen (1998), who noted than half the known species occur in the southern Australasian region. Dendrotiidae is a misspelling of the family name.

Diagnosis. Body bearing dorsal spines or long setae. Pleon of 1 free pleonite plus pleotelson. Antennula much shorter than antenna. Maxillipedal palp articles 1–5 narrow, less than half as wide as endite. Pereopod 1 subchelate; pereopods 2–7 ambulatory, dactlyi with 1 unguis. Uropod inserting dorsally or dorsolaterally, elongate, biramous, often enlarged.

Key to genera of Dendrotionidae

1. Head with prominent lateral process supporting antennae. Antennula basal article elongate (more than 5 times as long as wide) (fig. 3.5d, e) ..... *Dendrotion*

– Head without prominent lateral process supporting antennae. Antennula basal article less than twice as long as wide 2

2. Eyes present. Pereon smooth or bearing many small spines, without dorsolaterally directed spine-like processes (fig. 3.5a, b) ..... *Acanthomunna*

– Eyes absent. Pereon bearing few large dorsolaterally directed spine-like processes, each with apical cluster of spines (fig. 3.5c) ..... *Dendromunna*

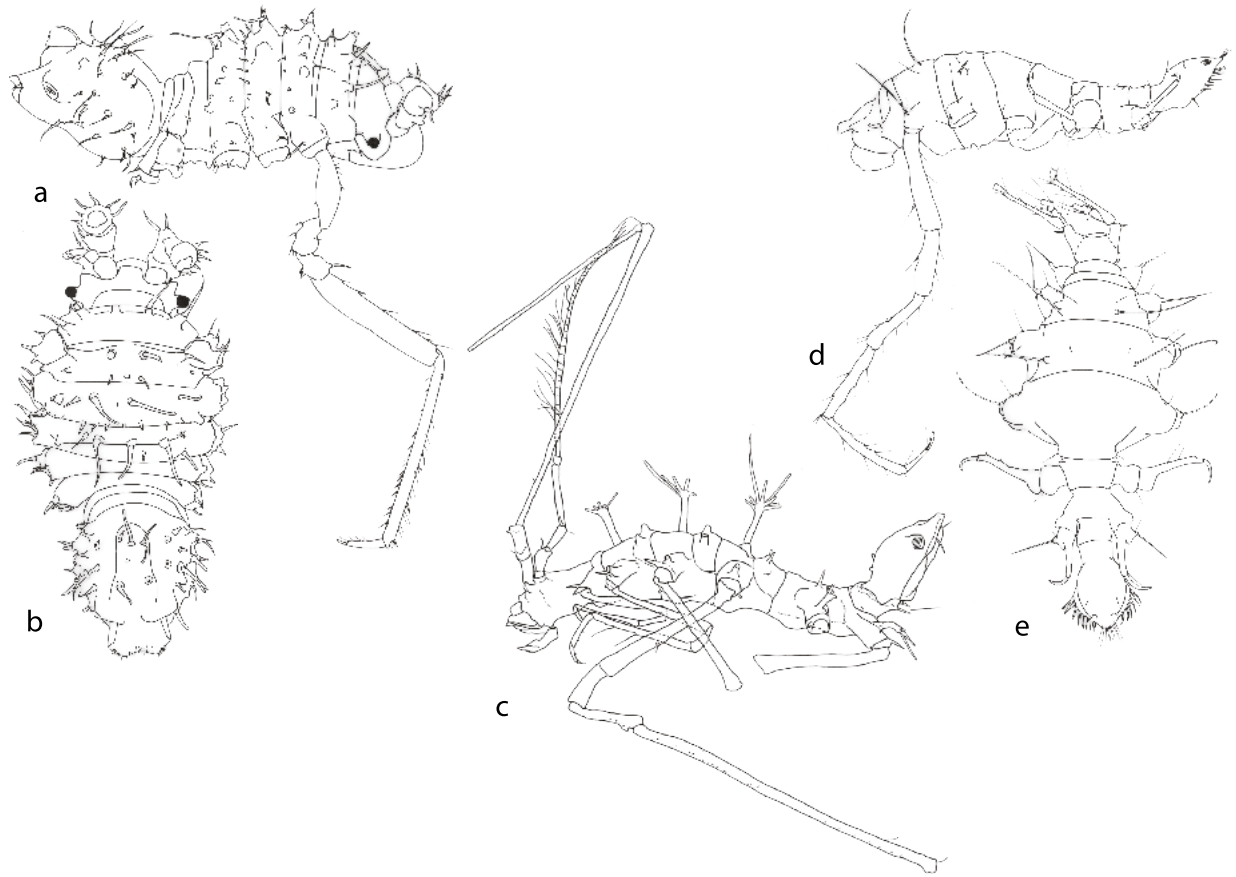


Figure 3.5. Dendrotionidae. a, b, *Acanthomunna potorous* Cohen, 1998; c, *Dendromunna kurilensis* Golovan, Malyutina and Brandt, 2018; d, e, *Dendrotion perodorous* Cohen, 1998.

Acanthomunna Beddard, 1886

Diagnosis. Head without prominent lateral process supporting antennae. Pereon smooth or bearing many small spines, without dorsolaterally directed spine-like processes. Eyes present. Antennula basal article less than twice as long as wide. Pereopod 7 present in adult.

Slope (385–2011 m). Arctic, Temperate Northern Atlantic, Temperate Northern Pacific, Temperate Australasia, Southern Ocean. 10 species (Cohen, 1998: rediagnosis, key to 9 species).

Dendromunna Menzies, 1962

Diagnosis. Head without prominent lateral process supporting antennae. Pereon bearing few large dorsolaterally directed spine-like processes, each with apical cluster of spines. Eyes absent. Antennula basal article less than twice as long as wide. Pereopod 7 absent in adult.

Slope–abyssal (1271–5408 m). GOODS bathyal provinces: Northern N Atlantic, Northern N Pacific, New Zealand/Kermadec, S Atlantic. 6 species (Cohen, 1998: rediagnosis, key to 3 species; Golovan et al., 2018: key to 6 species).

Dendrotion G.O. Sars, 1872

Diagnosis. Head with prominent lateral process supporting antennae. Pereon without dorsal spines, often conspicuously setose. Eyes absent. Antennula basal article elongate (more than 5 times as long as wide). Pereopod 7 present in adult.

Slope (281–2900 m). Arctic, Temperate Northern and Tropical Atlantic, Temperate Australasia. 11 species (Cohen, 1998: rediagnosis, key to 9 species).

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Desmosomatidae G.O. Sars, 1897

Figures 3.6, 3.7

Desmosomatidae are asellote isopods known from all oceanic basins, with many species waiting to be described. Although they are predominantly deep-sea taxa, several species occur on polar and temperate shelves, whereas others have been reported only from hadal depths (Brix et al., 2021). Members of the family are most easily recognised by the separation of a unit comprising the short pereonites 1–4 from the longer and more depressed pereonites 5–7. Adults range from 1.4 to 9.5 mm long.

Hessler (1970) established the fundamentals of the taxonomy of the family, dividing it into two subfamilies and erecting ten new genera. One of his genera has since been moved to another family and another has jumped subfamily; few genera have been established since. While the Desmosomatidae appear monophyletic, the subfamilies and some of the larger genera are para- or polyphyletic, according to Brix et al. (2021), who based this conclusion on morphological and molecular evidence.

Both Hessler (1970) and Brix et al. (2021) offered keys to genera that are augmented and modified here. Substantial additions to described species were made by Malyutina and Kussakin (1996) and Brix and coauthors (Brenke et al., 2005; Brix, 2006a, 2007; Brix and Bruce, 2008; Brix et al., 2021; Brix et al., 2015). *Chelibranchus* Mezhov, 1986 is poorly diagnosed according to Brix et al. (2021) and not included in this key.

Diagnosis. Body elongate, subcylindrical; head frontal margin projecting forward, deeper than pereon; pereon divided into anterior unit of 4 short pereonites and posterior unit of 3 longer depressed pereonites. Pleon of 1 free pleonite plus pleotelson. Anus not covered by pleopodal operculum. Eyes absent. Antennula short, dorsal. Mandibular molar small, triangular, spinulose. Maxillipedal palp articles 1–3 wider than distal articles, as wide or wider than endite. Pereopods 2–7 ambulatory; pereopod 4 coxa inserting on anterolateral margin. Uropod inserting posteroventrally.

Key to genera of Desmosomatidae

The key contains a triplet.

1. Pereonite 1 shorter or as long as pereonite 2 (fig. 3.6d, f, h). Pereopod 1 smaller or similar to pereopod 2, more slender than pereopod 2 (rarely subchelate) (fig. 3.7a, b) ..... Desmosomatinae ... 2

– Pereonite 1 as long or longer than pereonite 2 (fig. 3.6a–c, e, g). Pereopod 1 usually more robust than pereopod 2, chelate or raptorial (fig. 3.7c–f) ..... Eugerdellatinae ... 9

2. Body margins serrate (fig. 3.7c) ..... *Echinopleura*

– Body margins smooth 3

3. Pleotelson enlarged (wider than and at least twice as long as pereonite 7) (fig. 3.6h). Uropods inserting close together, endopod short, almost bulbous (fig. 3.6l). Pereopod 7 ischium upper margin with proximal tooth (fig. 3.7w) ..... *Pseudomesus*

– Pleotelson not enlarged. Uropods extending beyond posterior margin of pleotelson. Pereopod 7 ischium upper margin without tooth 4

4. Pereopod 1 subchelate (dactylus closing on propodus) (fig. 3.7r) ..... *Torwolia*

– Pereopod 1 not subchelate 5

5. Pereopod 1 elongate (carpus and propodus more than 5 times as long as wide) (fig. 3.7a) ..... *Eugerda*

– Pereopod 1 not elongate 6

6. Pereopods 5–7 carpi and propodi wide, flat, with rows of long natatory setae (fig. 3.7u) ..... *Desmosoma*

– Pereopods 5–7 carpi and propodi not wide or flat (fig. 3.7t) 7

7. Pereopods 1–4 coxae sexually dimorphic, in male anteriorly produced, well overlapping more anterior somite (fig. 3.6f). Pereonites 5–7 and pleotelson with lateral flanges ..... *Mirabilicoxa*

– Pereopods 1–4 coxae not sexually dimorphic, with short spine in both sexes. Pereonites 5–7 and pleotelson without lateral flanges 8

8. Pereopod 1 carpus as long as propodus, setae largely confined to row on lower margin (fig. 3.7l) ..... *Momedossa*

– Pereopod 1 carpus shorter than propodus, with rows of setae on lower margin and lateral face (fig. 3.7g) ..... *Balbidocolon*

9. Pereopod 1 raptorial (carpus with more than 1 robust seta on lower margin) (fig. 3.7j, n) 10

– Pereopod 1 chelate (carpus with 1 distal dominating robust seta on lower margin) (fig. 3.7h, i, k, m) 12

10. Pereopod 4 natatory (enlarged, carpus and propodus paddle-like, with numerous setae) (fig. 3.7s) ..... *Paradesmosoma*

– Pereopod 4 ambulatory (fig. 3.7t) 11

11. Pereopod 1 carpus lower margin with distal seta longer than others (fig. 3.73) ..... *Whoia*

– Pereopod 1 carpus lower margin with distal seta shorter than penultimate seta (fig. 3.7c) ..... *Eugerdella*

– Pereopod 1 carpus lower margin with row of setae increasing in length towards claw (fig. 3.7j) ..... *Cryodesma*

12. Pereonites 6, 7 and pleotelson fused (fig. 3.7a, b) ..... *Chelantermedia*

– Pereonites free (fig. 3.7c–h) 13

13. Pleotelson vaulted (fig. 3.6j). Operculum small, rounded (fig. 3.6k) ..... *Oecidiobranchus*

– Pleotelson not vaulted. Operculum almost as wide as pleotelson 14

14. Head with spines lateral to antennae (fig. 3.6i) ..... *Disparella*

– Head without spines 15

15. Maxillipedal palp with 4 articles (fig. 3.6n) ..... *Reductosoma*

– Maxillipedal palp with 5 articles (fig. 3.6m) 16

16. Pereopod 1 carpus distally produced (except *C. stellae*); propodus strongly tapered distally (fig. 3.7i) ..... *Chelator*

– Pereopod 1 carpus not anteriorly produced; propodus not strongly tapered distally 17

17. Pereopod 1 carpus 3.7 times as long as wide, longer than propodus, with 1 slender seta lateral to carpo-propodal articulation between propodus and distal seta (fig. 3.7o) ..... *Parvochelus*

– Pereopod 1 carpus about twice as long as wide, shorter than propodus, with accessory seta next to distal seta and marginal robust seta (fig. 3.7p) ..... *Prochelator*

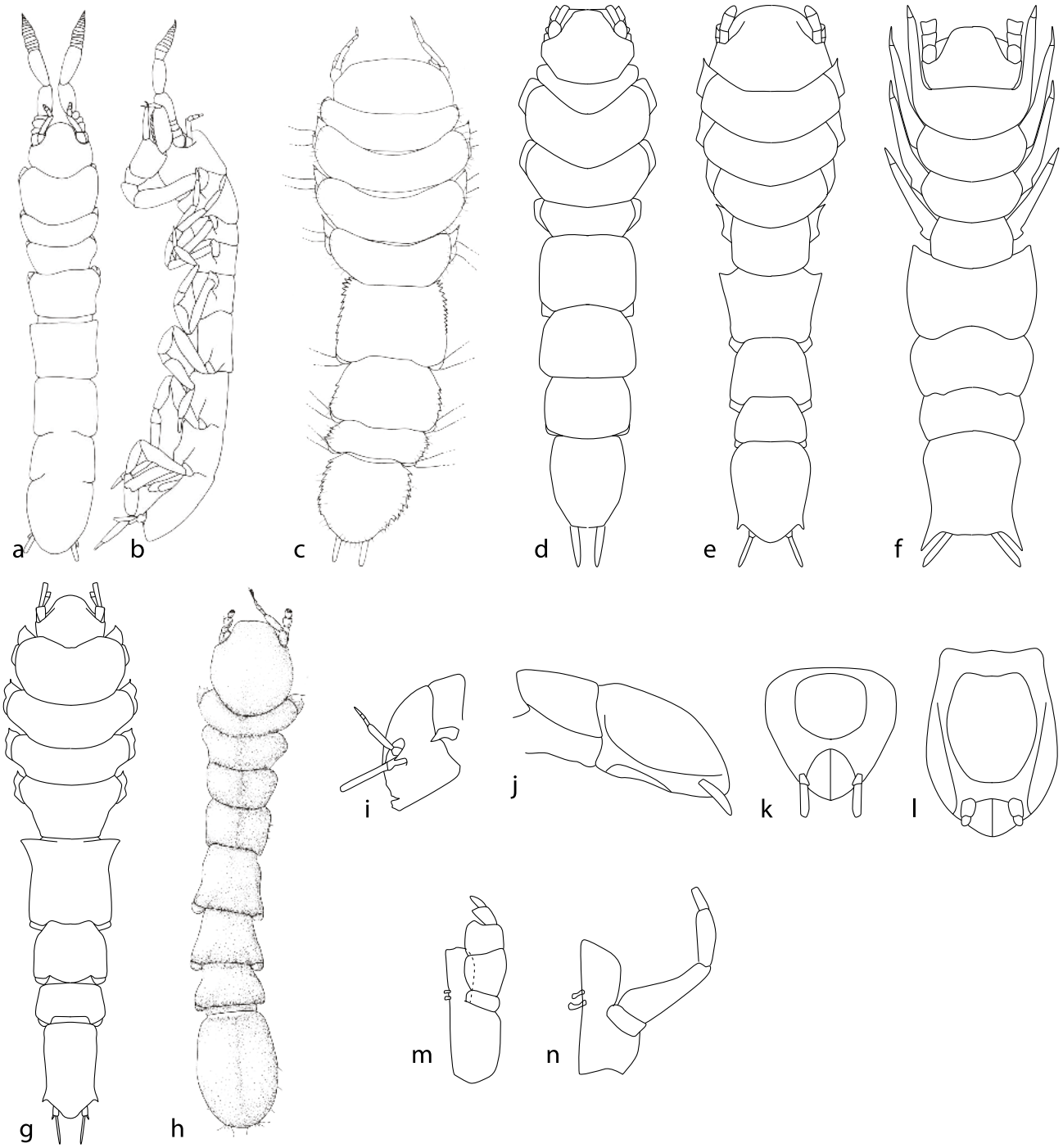


Figure 3.6. Desmosomatidae. a, b, *Chelantermedia composita* Brix, 2006; c, *Echinopleura cephalomagna* Brix, 2006; d, *Eugerda*; e, *Eugerdella*; f, *Mirabilicoxa* (male); g, *Prochelator*; h, *Pseudomesus pitombo* Kaiser and Brix, 2007; i, *Disparella*, lateral head; j, *Oecidiobranchus*, pereonite 7, pleotelson, lateral; k, *Oecidiobranchus*, pleotelson, ventral; l, *Pseudomesus*, pleon, ventral. Maxilliped: m, *Prochelator*; n, *Reductosoma*.

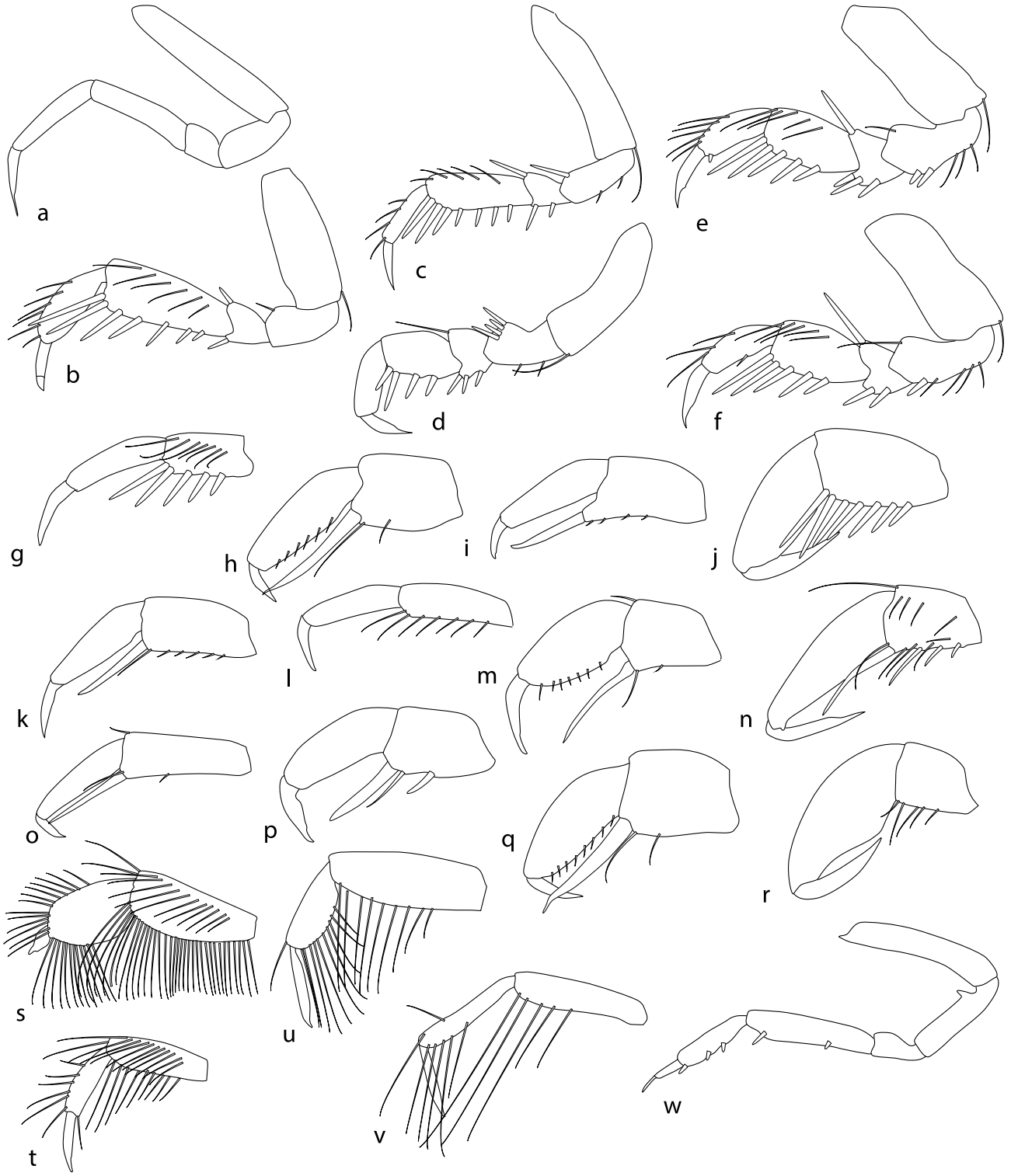


Figure 3.7. Desmosomatidae. Pereopods 1, 2: a, b, Desmosomatinae, *Eugerda*; c, d, Eugerdellatinae, *Eugerdella*; e, f, Eugerdellatinae, *Whoia*. Pereopod 1, carpus–dactylus: g, *Balbidocolon*; h, *Chelantermedia*; i, *Chelator*; j, *Cryodesma*; k, *Disparella*; l, *Momedossa*; m, *Oecidiobranchus*; n, *Paradesmosoma*; o, *Parvochelus*; p, *Prochelator*; q, *Reductosoma*; r, *Torwolia*. Pereopod 4, carpus–propodus: s, *Paradesmosoma*; t, *Whoia*. Pereopod 5, carpus–propodus: u, *Desmosoma*; v, *Mirabilicoxa*. Pereopod 7: w, *Pseudomesus*.

Subfamily Desmosomatinae G.O. Sars, 1897

Diagnosis. Pereonite 1 shorter or as long as pereonite 2. Pereopods 1, 2 of similar size and form, or pereopod 1 more slender than pereopod 2, with few setae (Hessler, 1970: diagnosis of subfamily).

Balbidocolon Hessler, 1970

Diagnosis. Pleotelson widest at posterolateral spines, highly vaulted, with flat lateral fields. Pereopod 1 carpus shorter than propodus, with rows of setae on lower margin and lateral face. Uropod uniramous, or uropod with rudimentary exopod.

Slope, bathyal. Temperate Northern and Tropical Atlantic, Temperate Australasia. 2 species (Hessler, 1970).

Desmosoma G. O. Sars, 1864

Diagnosis. Pleotelson without posterolateral angles, vaulted, without lateral fields. Pereopod 1 carpus lower margin lower margin with slender setae; propodus without setae. Pereopods 5–7 carpi and propodi wide, flattened, with rows of long natatory setae. Uropod uniramous.

Shelf–hadal. Arctic, Temperate Northern and Tropical Atlantic, Temperate Northern Pacific, Southern Ocean. GOODS bathyal provinces: N Atlantic, N Pacific. 29 species (Hessler, 1970: rediagnosis; Brix, 2007: rediagnosis).

Echinopleura G. O. Sars, 1897

Diagnosis. Body margins serrate. Pleotelson constricted at base, without posterolateral spines. Pereopod 1 carpus lower margin with few robust setae. Uropod uniramous.

Shelf, slope (15–990 m). Temperate Northern Atlantic, Temperate Australasia. 2 species (Hessler, 1970: rediagnosis).

Eugerda Meinert, 1890

Diagnosis. Pleotelson without posterolateral angles, vaulted, without lateral fields. Pereopod 1 elongate (carpus and propodus more than 5 times as long as wide); carpus lower margin with few small setae. Uropod biramous, exopod well developed.

Shelf–abyssal. Arctic, Temperate Northern and Tropical Atlantic, Temperate Northern W Pacific, Western Indo-Pacific, Temperate South America, Temperate Southern Africa, Temperate Australasia. 17 species (Hessler, 1970: rediagnosis).

Mirabilicoxa Hessler, 1970

Diagnosis. Pereonites 5–7 and pleotelson with lateral flanges. Pleotelson widest anteriorly, tapering, with posterolateral spines. Pereopod 1 carpus lower margin with few robust setae. Pereopods 1–4 coxae sexually dimorphic, in male anteriorly produced, well overlapping more anterior somite. Uropod uniramous, or uropod with rudimentary exopod.

Slope–abyssal. Arctic, Temperate Northern and Tropical Atlantic, Western Indo-Pacific, Temperate South America, Temperate Australasia, Southern Ocean. GOODS bathyal provinces: N Atlantic, W Pacific. 20 species (Hessler, 1970).

Momedossa Hessler, 1970

Diagnosis. Pleotelson with posterolateral angles. Pereopod 1 simple; carpus as long as propodus, setae confined to row on lower margin. Uropod biramous, exopod well developed.

Bathyal, abyssal. GOODS bathyal provinces: Northern N Pacific, N Atlantic, S Atlantic. 29 species (Hessler, 1970: rediagnosis; Brix, 2007: rediagnosis).

Pseudomesus Hansen, 1916

Diagnosis. Pleotelson enlarged, vaulted (wider than and at least twice as long as pereonite 7). Pereopod 1 simple; carpus lower margin with few robust setae. Pereopod 7 ischium upper margin with proximal tooth. Uropods inserting close together, endopod short, almost bulbous.

Shelf–abyssal (80–5441 m). Arctic, Temperate Northern and Tropical Atlantic, Temperate Northern W Pacific, Temperate Australasia. 5 species (Hessler, 1970: rediagnosis; Kaiser and Brix, 2007: rediagnosis, species distributions).

Torwolia Hessler, 1970

Diagnosis. Pleotelson without posterolateral spines. Pereopod 1 subchelate (dactylus closing on propodus); carpus short, broad, lower margin with short robust setae.

Bathyal, abyssal (2000–5395 m). GOODS bathyal provinces: Northern N Atlantic, S Atlantic. 3 species (Hessler, 1970: diagnosis; Brix, 2007: rediagnosis).

Subfamily Eugerdellatinae Hessler, 1970

Diagnosis. Pereonite 1 as long or longer than pereonite 2. Pereopod 1 usually more robust than pereopod 2, chelate or raptorial (Hessler, 1970).

Chelantermedia Brix, 2006

Diagnosis. Pereonites 6, 7 and pleotelson fused. Pleotelson without posterolateral spines. Pereopod 1 large, chelate; carpus lower margin with 1 strong distal seta opposing dactylus plus finer accessory seta. Uropod biramous.

Slope (204 m). Temperate Australasia (SE Australia). 1 species (Brix, 2006a).

Chelator Hessler, 1970

Diagnosis. Pleotelson without posterolateral spines in female, small ones sometimes in male. Pereopod 1 large, chelate; carpus distally produced (except *C. stellae*), as long or shorter than propodus, with small or slender setae; propodus strongly tapered distally. Uropod uniramous.

Shelf–abyssal. Cosmopolitan. 9 species (Hessler, 1970; Brix et al., 2015: rediagnosis, key to 8 species).

Cryodesma Svavarsson, 1988

Diagnosis. Pleotelson with posterolateral angles. Pereopod 1 raptorial; carpus lower margin with row of setae increasing in length towards claw. Uropod uniramous.

Bathyal (970–3627 m). GOODS bathyal provinces: Arctic, Northern N Atlantic. 2 species (Svavarsson, 1988).

Disparella Hessler, 1970

Diagnosis. Head with spines lateral to antennae. Pleotelson with posterolateral angles. Pereopod 1 large, chelate; carpus lower margin with row of small setae proximal to distal robust seta. Uropod uniramous.

Bathyal, abyssal. Temperate Northern Atlantic, Western Indo-Pacific, Temperate Australasia, Southern Ocean. 5 species (Hessler, 1970).

Eugerdella Kussakin, 1965

Diagnosis. Pleotelson with or without posterolateral spines. Pereopod 1 raptorial; carpus lower margin with distal robust seta shorter than penultimate seta. Uropod exopod small or absent.

Shelf. Arctic, Temperate Northern and Tropical Atlantic, Temperate Northern W Pacific, Western Indo-Pacific, Temperate South America, Temperate Australasia, Southern Ocean. 18 species (Hessler, 1970: rediagnosis; Brix, 2006b: rediagnosis).

Oecidiobranchus Hessler, 1970

Diagnosis. Pleotelson vaulted, without posterolateral spines. Pereopod 1 large, chelate; carpus lower margin with strong distal robust seta and finer accessory seta. Uropod uniramous. Branchial chamber and operculum small, rounded.

Shelf–bathyal. Arctic, Temperate Northern and Tropical Atlantic, Temperate Australasia. 5 species (Hessler, 1970).

Paradesmosoma Kussakin, 1965

Diagnosis. Pleotelson without posterolateral spines. Pereopod 1 raptorial; carpus lower margin with row of irregularly-sized robust setae proximal to distal robust seta, 1 slender seta distal to 'claw'. Pereopod 4 natatory (enlarged, carpus and propodus paddle-like, with numerous setae). Uropod uniramous.

Shelf, slope (95–400 m). Temperate Northern Pacific, Temperate Australasia. 3 species (Hessler, 1970: rediagnosis).

Parvochelus Brix and Kihara, 2015

Diagnosis. Pleotelson without posterolateral spines. Pereopod 1 chelate; carpus 3.7 times as long as wide, longer than propodus, with 1 slender seta lateral to carpo-propodal articulation between propodus and distal seta; propodus subparallel.

Abyssal (4863–5180 m). GOODS bathyal provinces: Northern N Pacific, N Atlantic. 2 species (Brix et al., 2015).

Prochelator Hessler, 1970

Diagnosis. Pleotelson with posterolateral spines (sometimes rudimentary). Pereopod 1 large, chelate; carpus about twice as long as wide, shorter than propodus, with accessory seta next to distal seta and marginal robust seta. Uropod biramous.

Shelf–abyssal. Temperate Northern and Tropical Atlantic, Temperate Southern Africa, Temperate Australasia. GOODS bathyal provinces: N Atlantic, Cocos Plate, Antarctic. 12 species (Hessler, 1970; Brix and Bruce, 2008: rediagnosis).

Reductosoma Brandt, 1992

Diagnosis. Pleotelson without posterolateral spines. Maxillipedal palp with 4 articles. Pereopod 1 large, chelate; carpus about 1.5 times as long as wide, shorter than propodus, with accessory seta next to distal seta and marginal slender seta. Uropod biramous.

Abyssal (3981 m). Southern Ocean. 1 species (Brandt, 1992).

Whoia Hessler, 1970

Diagnosis. Pleotelson without posterolateral angles, vaulted, without lateral fields. Pereopod 1 raptorial; carpus lower margin with robust setae, upper margin with fine setae. Uropod exopod small or absent.

Shelf–slope, bathyal (50–1840 m). Temperate Northern and Tropical Atlantic, Temperate Australasia. 5 species (Hessler, 1970).

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Echinothambematidae Menzies, 1956

Figure 3.8

Echinothambematids are rare, known only from very deep water in the Atlantic and Pacific Oceans. They are cylindrical isopods, up to 5.4 mm long, with one or two of the posterior pereonites fused with the pleotelson. The family was rediagnosed by Malyutina et al. (2001), who differentiated the two genera and by Just (2025) who provided a key to species.

Diagnosis. Body elongate, subcylindrical; pereonite 7 or pereonites 6 and 7 fused with pleon (sutures visible dorsally in adults). Coxal plates absent. Pleon widest posteriorly, vaulted. Anus covered by pleopodal operculum. Eyes absent. Antennula as long as antenna, projecting laterally. Maxillipedal palp articles 1–3 wider than distal articles. Pereopods 2–7 ambulatory; pereopod 4 coxa inserting on anterolateral margin; pereopodal 2–7 dactyli with 1 or 2 claws. Uropod inserting posterolaterally, comprising single long article.

Echinothambema Menzies, 1956

Diagnosis. Pereonal and pleonal lateral spines present. Antennula article 1 laterally expanded, longer than article 2. Head and pereonite 1 not fused (fig. 3.8a).

Abyssal (5100 m). GOODS bathyal provinces: N Atlantic, SE Pacific Ridges. 2 species (Menzies, 1962).

Vemathambema Menzies, 1962

Diagnosis. Pereonal and pleonal lateral spines absent. Antennula article 1 stout, similar to article 2. Head and pereonite 1 fused (fig. 3.8b).

Abyssal (4630–5397 m). GOODS bathyal provinces: S Atlantic. 3 species (Just, 20025; Malyutina et al., 2001).

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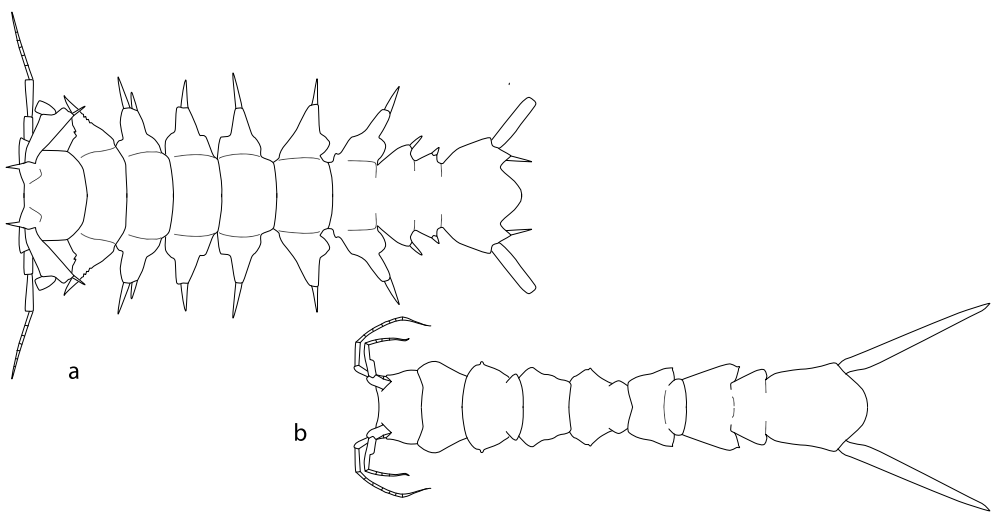


Figure 3.8. Echinothambematidae. Habitus dorsal views: a, *Echinothambema*; b, *Vemathambema*.

Haplomunnidae Wilson, 1976

Figure 3.9

Haplomunnidae were diagnosed by Wilson (1976) and again by Cunha and Wilson (2003). The family includes only deep-water forms, all oval (*Munna*-like), up to 3 mm long, spinose, with strong subchelate pereopods 1 and long ambulatory legs. A key to four genera Wilson (1976) was written before the fifth genus was described (Just, 2003). Just (2003) tabulated differences between all genera. Cunha and Wilson (2003) listed all material known with their distributions including several undescribed species.

Diagnosis. Body dorsal surface spinose or setose; pereonites 5–7 shorter than anterior pereonites. Pleon of 1 segment. Anus covered by pleopodal operculum. Eyes absent. Antennula basal article directed anterodorsally, with many articles. Pereopod 1 subchelate; pereopods 2–7 ambulatory; pereopod 4 coxa inserting on midlateral margin. Uropod reduced, of 1 or 2 articles, inserting near ventral margin.

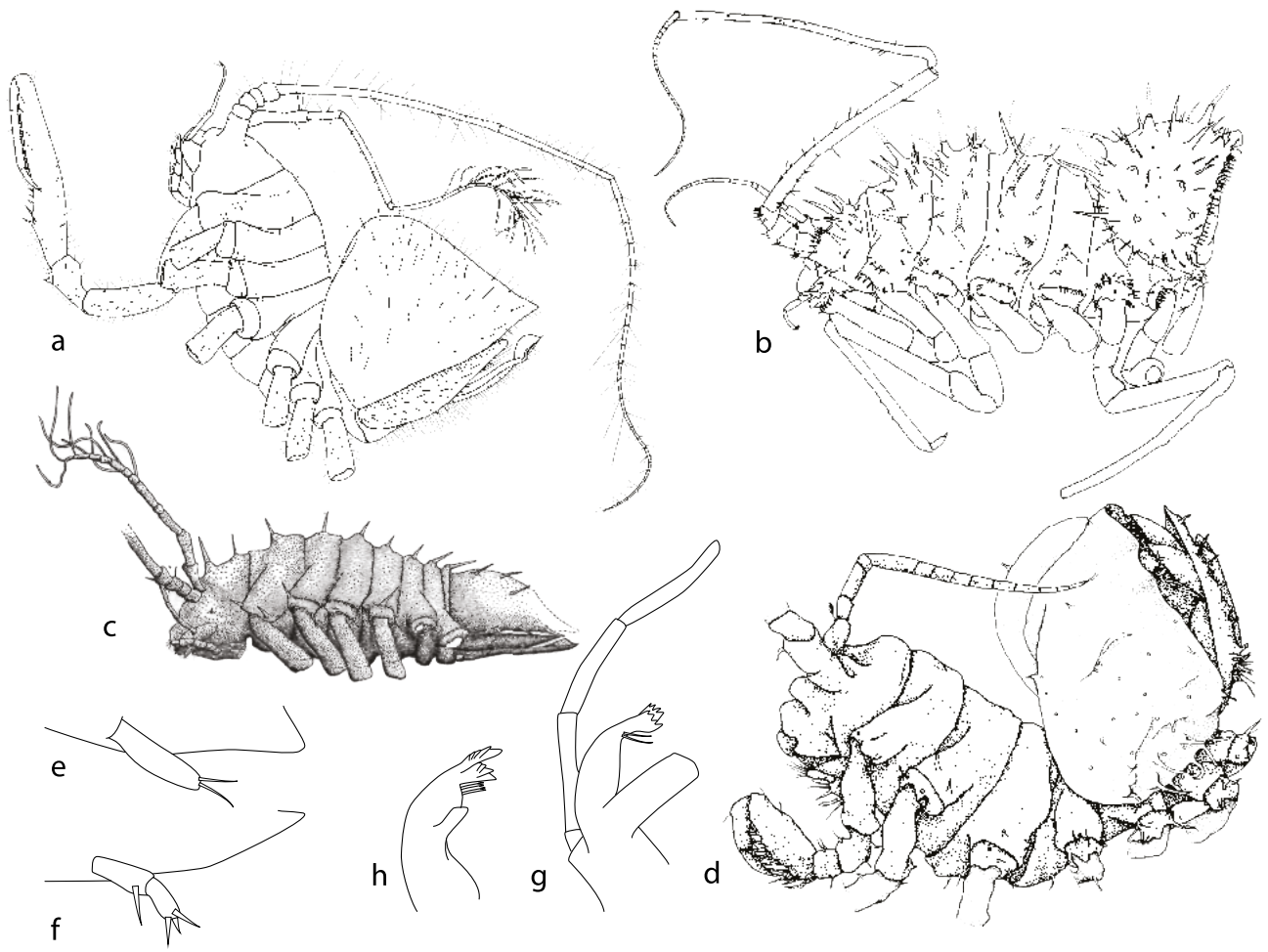


Figure 3.9. Haplomunnidae. Habitus, lateral views, not all pereopods shown: a, *Haplodendron buzwilsoni* Just, 2003 1; b, *Haplomunna hubbsi* Wilson, 1976; c, *Munella gayda* Wilson,1974; d, *Thylakogaster namibiensis* Brenke and Buschmann, 2009. Uropod: e, *Abyssaranea*; f, *Munella*. Mandible: g, *Haplodendron*; h, *Thylakogaster.*

Key to genera of Haplomunnidae

1. Pereonite 7 and pereopods 7 present (fig. 3.9a, b, d) 2

– Pereonite 7 and pereopods 7 absent (fig. 3.9c) 4

2. Pleotelson slightly expanded, half size of pereon (fig. 3.9b) ..... *Haplomunna*
– Pleotelson balloon-like, almost as large as pereon (fig. 3.9a, d) 3
3. Pereonites, pleotelson lateral margins with spines. Antennula and antenna attached directly or on small projection to head (fig. 3.9d). Mandible without palp (fig. 3.9h) ..... *Thylakogaster*
– Pereonites, pleotelson lateral margins setose. Antennula and antenna attached to dorsolateral stalk on head (fig. 3.9a). Mandible with 3-articled palp (fig. 3.9g) ..... *Haplodendron*
4. Uropod with 2 articles (fig. 3.9f). Antenna as long as body (fig. 3.9c) ..... *Munella*
– Uropod with 1 article (fig. 3.9e). Antenna shorter than body ..... *Abyssaranea*

Abyssaranea Wilson and Hessler, 1974

Diagnosis. Pereonite 7 and pereopods 7 absent. Pleotelson balloon-like, almost as large as pereon, in line with axis of pereon. Pleotelson spinose. Antennula and antenna attached directly to head. Antenna shorter than body. Mandible with 3-articled palp. Uropod with 1 article.

Abyssal (3459–4438 m). GOODS bathyal provinces: N Atlantic. 1 species (Wilson and Hessler, 1974).

Haplodendron Just, 2003

Diagnosis. Pereonite 7 and pereopods 7 present. Pleotelson balloon-like, almost as large as pereon, acutely angled with axis of pereon. Pereonites, pleotelson lateral margins setose. Antennula and antenna attached to dorsolateral stalk on head. Antenna longer than body. Mandible with 3-articled palp. Uropod with 2 articles.

Slope (1220–2500 m). Temperate Australasia. SE Australia. 1 species (Just, 2003).

Haplomunna Richardson, 1908

Diagnosis. Pereonite 7 and pereopods 7 present. Pleotelson slightly expanded, half size of pereon. Head, pereonites and pleotelson spinose. Antennula and antenna attached directly to head. Antenna longer than body. Mandible with 3-articled palp. Uropod with 1 article.

Abyssal (3880–6450 m). GOODS bathyal provinces: Northern N Pacific, N Atlantic. Three species (Cunha and Wilson, 2003; Wilson, 1976).

Munella Bonnier, 1896

Diagnosis. Pereonite 7 and pereopods 7 absent. Pleotelson swollen, in line with axis of pereon. Head, pereonites and pleotelson with few spines. Antennula and antenna attached directly to head. Antenna as long as body. Mandible with 3-articled palp. Uropod with 2 articles.

Shelf–abyssal (100–4797 m). Temperate Northern Atlantic. GOODS bathyal provinces: N Atlantic, N Pacific. 2 species (Wilson and Hessler, 1974).

Thylakogaster Wilson and Hessler, 1974

Diagnosis. Pereonite 7 and pereopods 7 present. Pleotelson balloon-like, almost as large as pereon, acutely angled with axis of pereon. Pereonites, pleotelson lateral margins with spines. Antennula and antenna attached directly or on small projection to head. Antenna shorter than body. Mandible without palp. Uropod with 1 article.

Slope–abyssal (1141–5216 m). GOODS bathyal provinces: Northern N Atlantic, SE Pacific Ridges, Cocos Plate, S Atlantic. 4 species (Brenke and Buschmann, 2009; Wilson and Hessler, 1974).

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Haploniscidae Hansen, 1916

Figure 3.10

Haploniscids are common inhabitants of deep-water sediments, recognisable by their half-barrel-shaped body and spindly legs. Some species are able to conglobate (roll up like a pill bug; fig. 3.10). Lincoln (1985) reviewed the diversity of the family around New Zealand, adding two genera and providing a key to the seven then known. George (2004) added another genus,

Chandraniscus George, 2004, based on supposed differences in the degree of pereonite fusion. Brökeland (2005) considered these differences unreliable, later describing many species in existing genera (Brökeland, 2006; Brokeland and Brandt, 2006; Brökeland and Raupach, 2008; Brökeland and Wägele, 2004). *Chandraniscus* is treated as a synonym of *Haploniscus* here. Most species are in the size range 3–5 mm but specimens up to 11.3 mm have been recorded. The key to genera is based on that of George (2004).

Diagnosis. Body compact, oval, more or less flat; pereonites similar, wider than long. Coxal plates absent. Pleon without free pleonites, usually with posteriorly pointing posterolateral processes. Anus not covered by pleopodal operculum. Eyes absent. Antennal scale spine-like, fused to article 3. Maxillipedal palp articles 1–5 narrow, less than half as wide as endite. Pereopods 1–7 ambulatory. Uropod inserting posteroventrally, peduncle rod-like, uniramous.

Implicit generic attributes. Pereonites 2–4 without anterolateral processes; pereonite 7 in adult similar to pereonite 6. Female operculum fringed with simple short setae.

Key to genera of Haploniscidae

1.	Pleotelson tapering to point (fig. 3.10a, d)	2
–	Pleotelson truncate or broadly rounded (fig. 3.10b, e, g–h)	3
2.	Uropod not concealed, set close together, ventral to anal valves (fig. 3.10n). Female operculum fringed with long plumose distomarginal setae (fig. 3.10d)	*Aspidoniscus*
–	Uropod concealed (fig. 3.10m). Female operculum fringed with simple short setae (fig. 3.10a, p)	*Abyssoniscus*
3.	Antenna peduncle flat; article 3 longer than wide, grooved; article 4 short; articles 5 and 6 fused, apically prolonged; flagellum small, slender, subterminal (fig. 3.10b, j)	*Antennuloniscus*
–	Antenna peduncle not so modified (fig. 3.10k, i)	4
4.	Pereonites 5–7 fused with pleotelson. Head with large lobe-like rostrum (fig. 3.10h). Antenna article 3 without dorsal tooth	*Hydroniscus*
–	Pereonites 5–7 free or middorsally fused with pleotelson. Head without or with small rostrum. Antenna article 3 with dorsal tooth (fig. 3.10k)	5
5.	Pereonite 7 in adult shorter and narrower than pereonite 6 (fig. 3.10i)	*Mastigoniscus*
–	Pereonite 7 in adult similar to pereonite 6	6
6.	Some of pereonites 2–4 with anterolateral processes, more pronounced in male (fig. 3.10e, f)	*Chauliodoniscus*
–	Pereonites 2–4 without anterolateral processes (fig. 3.10g)	*Haploniscus*

Abyssoniscus Birstein, 1971

Diagnosis. Head with short rounded rostrum. Pereonites 6–7 free; pleotelson tapering to obtuse point. Antenna peduncle article 3 without dorsal tooth.

Abyssal (5005–5045 m). GOODS bathyal provinces: N Pacific. 1 species (Birstein, 1971; George, 2004).

Antennuloniscus Menzies, 1962

Diagnosis. Head with anteriorly prolonged clypeus. Pereonites 5–7 fused with pleotelson, sutures usually visible; pleotelson posterior margin truncate, with prominent posterolateral spines in male. Antenna peduncle article 1 small, concealed by article 2; article 3 longer than wide, with longitudinal groove, with small tooth; articles 5 and 6 fused; article 6 with terminal projection; flagellum small, slender, inserting subapically on peduncular article 6.

Slope–abyssal (1300–5800 m). GOODS bathyal provinces: Northern N Atlantic, N Atlantic, Antarctic, Subantarctic, S Atlantic. 12 species (Menzies and Schultz, 1967: key to 5 species; Brökeland, 2006: rediagnosis).

Aspidoniscus Menzies and Schultz, 1968

Diagnosis. Head with short rounded rostrum. Pereonite 7 fused to pleotelson; pleotelson tapering to obtuse point. Antenna peduncle article 3 without dorsal tooth. Female operculum fringed with long plumose distomarginal setae. Uropod not concealed, set close together, ventral to anal valves.

Bathyal (3071 m). GOODS bathyal provinces: N Atlantic. Caribbean. 1 species (Menzies and Schultz, 1967).

Chauliodoniscus Lincoln, 1985

Diagnosis. Head without rostrum. One or more of pereonites 2–4 with anterolateral processes, longer in male; pereonite 5 not fused to pereonite 6, enrolment possible; pleotelson posterior margin truncate, with small posterolateral angles. Antenna peduncle article 3 dorsal tooth as long as or longer

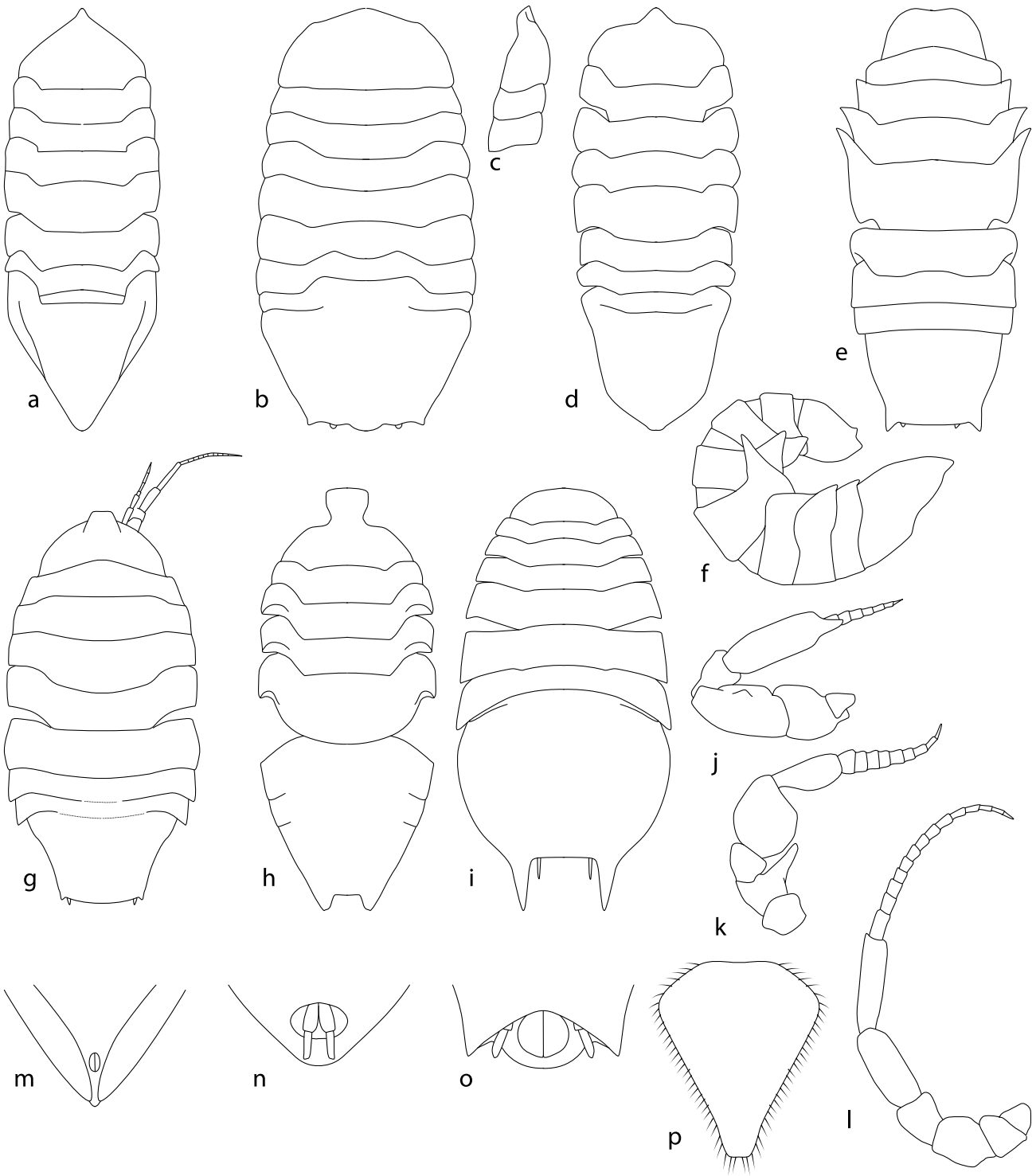


Figure 3.10. Haploniscidae. Dorsal views: a, *Abyssoniscus*; b, c, *Antennuloniscus* (with head, pereonites 1, 2, left, lateral); d, *Aspidoniscus*; e, f, *Chauliodoniscus* (with right lateral view); g, *Haploniscus*; h, *Hydroniscus*; i, *Mastigoniscus*. Antenna: j, *Antennuloniscus*; k, *Chauliodoniscus*; l, *Haploniscus*. Anus, uropods, ventral: m, *Abyssoniscus*; n, *Aspidoniscus*; o, *Haploniscus*. Female operculum: p, *Abyssoniscus*.

than width of article; article 5 inflated, with convex lateral margins.

Slope–abyssal (1300–5024 m). GOODS bathyal provinces: Northern N Atlantic, N Atlantic, New Zealand/Kermadec, Antarctic, Subantarctic, S Atlantic. 11 species (Lincoln, 1985: diagnosis, key to 9 species; Leese and Brenke, 2005).

Haploniscus Richardson, 1908

Diagnosis. Head with rostrum. Pereonites 5–7 at least laterally free, fused to pleotelson; pleotelson posterior margin truncate, with small posterolateral angles. Antenna peduncle article 3 little longer than wide, often with dorsal tooth; articles 5 and 6 not fused; flagellum distinct.

Slope (680–9043 m). Cosmopolitan. 77 species (Brökeland and Wägele, 2004: rediagnosis; Brökeland and Raupach, 2008: 7 new species; Brökeland, 2010: 4 new species; Knauber et al., 2025: *H. belyaevi* species complex).

Hydroniscus Hansen, 1916

Diagnosis. Head with large lobe-like rostrum. Pereonites 5–7 fused with pleotelson, lateral sutures faint, enrolment possible; pleotelson posterior margin convex, with broad triangular posterolateral angles. Antenna peduncle article 3 without dorsal tooth.

Bathyal–hadal (3200–7300 m). GOODS bathyal provinces: Northern N Atlantic, Northern N Pacific, N Atlantic, New Zealand/Kermadec, S Atlantic. 10 species (Lincoln, 1985: rediagnosis, key to 7 species; George, 2004: 3 new species).

Mastigoniscus Lincoln, 1985

Diagnosis. Head without rostrum. Pereonites 5–7 and pleotelson fused middorsally, sutures more or less distinct; pereonite 7 in adult shorter and narrower than pereonite 6; pleotelson posterior margin truncate, with prominent posterolateral spines in male. Antenna peduncle article 3 with dorsal tooth.

Abyssal, hadal (2476–8345 m). GOODS bathyal provinces: Northern N Pacific, SE Pacific Ridges, Cocos Plate, Nazca Plate, W Pacific. 13 species (Lincoln, 1985: diagnosis, key to 6 species; Park, 2000: rediagnosis, key to 10 species; Brokeland and Brandt, 2006).

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Ischnomesidae Hansen, 1916

Figure 3.11

Ischnomesids are cylindrical, blind, deep-water isopods with an elongate pereonite 5 (Kavanagh and Wilson, 2007). The family was rediagnosed by Merrin and Poore (2003) and again by Kavanagh and Sorbe (2006). The key to genera of Brandt et al. (2015), based on that of Wolff (1962), partly took into account the additional genera of Kavanagh and Wilson (2007) but not their comments on the enigmatic *Mixomesus*. Kussakin (1988) synonymised two of the genera erected by Wolff (1962) with *Stylomesus*. Maximum size recorded is 14.5 mm, but many species are much smaller.

Diagnosis. Body elongate, subcylindrical; head fused to pereonite 1; pereonite 5 elongate, cylindrical, much longer than pereonites 6, 7. Pleon without or with 1 or 2 free pleonites. Eyes absent. Pereopod 1 prehensile; pereopods 2–7 ambulatory; pereopod 4 coxa inserting on anterolateral margin; pereopodal 2–7 dactyli with 1 unguis. Uropod uniramous.

Key to genera of Ischnomesidae

1. Uropod of 2 articles (peduncle and ramus) (fig. 3.11a, e) 2
– Uropod of 1 article (*I. justi* excepted) (fig. 3.11g) 5
2. Head with projections supporting antennae (fig. 3.11g) ..... *Stylomesus*
– Head without projections supporting antennae 3
3. Pereonites and pleonites 1, 2 free, movable (fig. 3.11c, d) ..... *Ischnomesus*
– Pereonites and pleonites 1, 2 not movable 4
4. Pleotelson posterolateral margin produced at uropod insertion. Pereonite 4 about as long as wide (fig. 3.11a) ..... *Contrarimesus*
– Pleotelson evenly curved posterolaterally. Pereonite 4 1.5 times as long as wide (fig. 3.11m) ..... *Mixomesus*
5. Pereonite 5 free, pereonites 6, 7 and pleon fused (fig. 3.11c). Antennula article 2 inserting dorsally, strongly curved anteriorly at proximal insertion; following 1–3 articles less than 0.3 article 2 length (fig. 3.11d) ..... *Heteromesus*
– Pereonites 5–7 and pleon fused. Antennula with 5 or 6 articles, distal flagellar articles much longer than wide 6
6. Pleotelson axial ridge strongly vaulted, separated from lateral fields by distinct indented lines (fig. 3.11l) ..... *Haplomesus*
– Pleotelson axial ridge weakly vaulted, separated from lateral fields by shallow elongate concavities 7
7. Pleotelson posterolateral margin anterior to uropods without posterolateral spines or tubercles (fig. 3.11j) ..... *Fortimesus*
– Pleotelson posterolateral margin anterior to uropods with posterolateral spines or tubercles (fig. 3.11i, k) 8
8. Pereonite 4 at least 1.5 times as long as wide. Head with long, thin anterolateral projections supporting antennae (fig. 3.11i) ..... *Cornuamesus*
– Pereonite 4 as long as wide. Head without anterolateral projections supporting antennae (fig. 3.11k) ..... *Gracilimesus*

Contrarimesus Kavanagh and Wilson, 2007

Diagnosis. Pereonite 4 as long as wide; pereonites 5–7 articulation rudimentary, non-functional; pleotelson dorsal surface axial ridge weakly vaulted, separated from lateral fields by shallow elongate concavities; posterolateral margin anterior to uropods without spines; pleotelson posterolateral margin produced at uropod insertion. Antennula with 6 articles, distal flagellar articles much longer than wide. Maxillipedal palp narrower than endite, articles 2 and 3 scarcely expanded. Uropod of 2 articles, peduncle distinct.

Slope–abyssal (900–4149 m). Temperate Australasia, Southern Ocean. 19 species (Kavanagh and Wilson, 2007: diagnosis).

Cornuamesus Kavanagh and Wilson, 2007

Diagnosis. Head with long, thin anterolateral projections supporting antennae. Pereonite 4 at least 1.5 times as long as wide; pereonites 5–7, pleonite 1 and pleotelson not articulating; pleotelson dorsal surface axial ridge weakly vaulted, separated from lateral fields by shallow elongate concavities; pleotelson with distinct posterolateral spines. Antennula article 2 inserting on article 1 dorsally, straight, not curved at insertion. Maxillipedal palp narrower than endite, articles 2, 3 not expanded. Uropod of 1 long article.

Slope. Temperate Northern Atlantic. 2 species (Kavanagh and Sorbe, 2006: as *Haplomesus longiramus*, plus undescribed species; Kavanagh and Wilson, 2007: diagnosis, key to species).

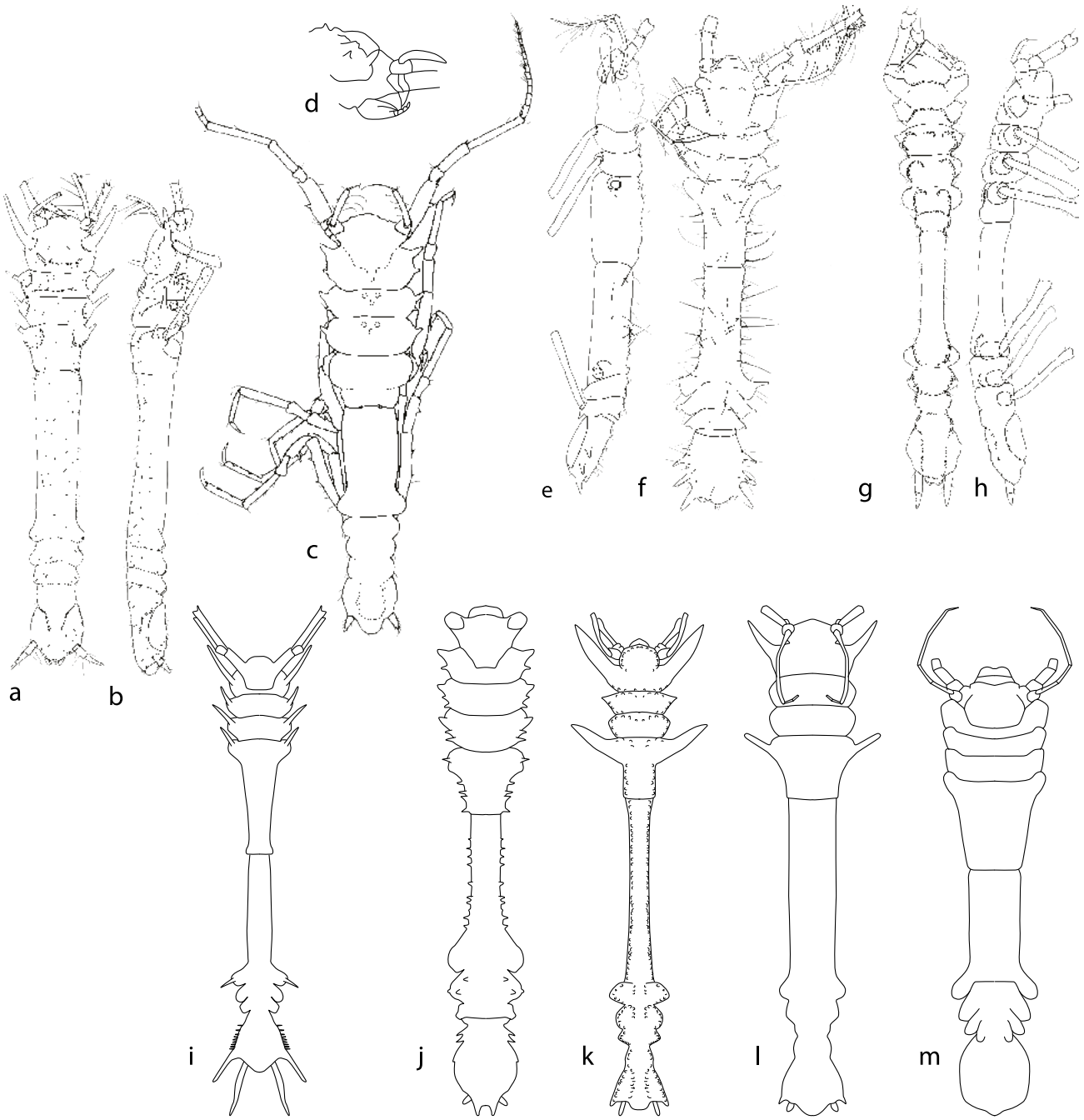


Figure 3.11. Ischnomesidae. Dorsal views: a, b, *Contrarimesus franklinae* (Merrin and Poore, 2003); c, d, *Heteromesus calcar* Cunha, 2006 (with lateral head, antennula, antenna); e, f, *Ischnomesus tasmanensis* Merrin and Poore, 2003; g, h, *Stylomesus sarsi* Merrin and Poore, 2003; i, *Cornuamesus*; j, *Fortimesus*; k, *Gracilimesus*; l, *Haplomesus*; m, *Mixomesus*.

Fortimesus Kavanagh and Wilson, 2007

Diagnosis. Pereonite 4 as long as wide; pereonites 5–7, pleonite 1 and pleotelson not articulating; pleotelson dorsal surface axial ridge weakly vaulted, smoothly arched; separated from lateral fields by shallow elongate concavities; pleotelson without posterolateral spines. Antennula with 5 or 6 articles, distal flagellar articles much longer than wide. Maxillipedal palp as wide as or wider than endite, articles 2 and 3 expanded. Uropod of 1 article.

Slope–hadal. Temperate Northern Pacific, Temperate Southern Africa. 12 species (Kavanagh and Wilson, 2007: diagnosis, key to 11 species).

Gracilimesus Kavanagh and Wilson, 2007

Diagnosis. Pereonite 4 as long as wide; pereonites 5–7, pleonite 1 and pleotelson not articulating; pleotelson dorsal surface axial ridge smoothly arched, not separated from lateral fields, or weakly vaulted, separated from lateral fields by shallow elongate concavities; pleotelson with distinct posterolateral spines. Antennula with 5 or 6 articles, distal flagellar articles much longer than wide. Maxillipedal palp narrower than endite, articles 2, 3 not expanded. Uropod of 1 long article.

Slope–abyssal. GOODS bathyal provinces: Northern N Atlantic, Northern N Pacific, Nazca Plate, Antarctic, W Pacific, S Atlantic. 12 species (Kavanagh et al., 2006: key to species without pereopod 7; Kavanagh and Wilson, 2007: diagnosis, key to 10 species).

Haplomesus Richardson, 1908

Diagnosis. Pereonites 5–7, pleonite 1 and pleotelson not articulating; pleotelson dorsal surface axial ridge strongly vaulted, separated from lateral fields by distinct indented line; pleotelson without posterolateral spines. Antennula with 5 or 6 articles, distal flagellar articles much longer than wide. Maxillipedal palp wider than endite, articles 2 and 3 expanded. Uropod of 1 article.

Slope–hadal. Temperate Australasia. GOODS bathyal provinces: Arctic, Northern N Atlantic, N Atlantic, Nazca Plate, S Atlantic, N Pacific. 4 species (Kavanagh and Wilson, 2007: rediagnosis, key to species).

Heteromesus Richardson, 1908

Diagnosis. Pereonite 4 wider than long; pereonite 5 articulating with pereonite 6; pereonites 6, 7, pleon not articulating; pleotelson dorsal surface axial ridge strongly vaulted, separated from lateral fields by distinct indented line; pleotelson posterolateral margin produced at uropod insertion. Antennula article 2 inserting dorsally, strongly curved anteriorly at proximal insertion; following 1–3 articles less than 0.3 article 2 length. Maxillipedal palp narrower than endite, articles 2, 3 not expanded. Uropod of 1 long article.

Slope–abyssal (364–4077 m). GOODS bathyal provinces: Northern N Atlantic, Northern N Pacific, N Atlantic, S Atlantic. 16 species (Cunha and Wilson, 2006: rediagnosis, key to 16 species, notes on undescribed species).

Ischnomesus Richardson, 1908

Diagnosis. Pereonite 4 at least 1.5 times as long as wide, or as long as wide; pereonites 5–7, pleonite 1 and pleotelson free, articulating; pleotelson dorsal surface axial ridge scarcely vaulted; pleotelson with distinct posterolateral spines. Antennula of 6 articles. Maxillipedal palp as wide as or wider than endite, articles 2 and 3 expanded. Uropod of 2 articles, peduncle distinct, or of 1 article (rare).

Rhabdomesus Richardson, 1908 is a junior subjective synonym without a type species. The type species is herein designated as: *Ischnosoma bacillus* Beddard, 1886.

Shelf–hadal. Cosmopolitan. 41 species (Merrin and Poore, 2003: rediagnosis; Kavanagh et al., 2015: key to European species).

Mixomesus Wolff, 1962

Diagnosis. Pereonite 4 at least 1.5 times as long as wide; pereonites 5–7 articulation rudimentary, non-functional; pleotelson dorsal surface axial ridge scarcely vaulted; pleotelson without posterolateral spines. Antennula article 2 short, articles 3–5 elongate. Maxillipedal palp wider than endite, articles 2 and 3 expanded. Uropod of 2 articles, peduncle distinct.

Slope (610 m). Central Indo-Pacific, Temperate Australasia (New Zealand, N Australia). 1 described species (Wolff, 1962: diagnosis, description of species; Kavanagh and Wilson, 2007: reassessment, undescribed species).

Stylomesus Wolff, 1956

Diagnosis. Head with projections supporting antennae. Pereonite 4 as long as wide; at least pereonite 7 fused with pleon; pleotelson dorsal surface axial ridge weakly vaulted, separated from lateral fields by shallow elongate concavities; pleotelson without posterolateral spines. Antennula of 6 articles. Maxillipedal palp narrower than endite, articles 2, 3 not expanded. Uropod of 2 articles, peduncle distinct.

Slope–abyssal (690–6079 m). Temperate Australasia. GOODS bathyal provinces: Northern N Pacific, Antarctic, Subantarctic, Indian, S Atlantic. 19 species (Wolff, 1962: key to 8 species; Merrin and Poore, 2003: rediagnosis; Brandt and Andres, 2008: list of 17 species with distributions).

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Janirellidae Menzies, 1956

Figure 3.12

The definition and composition of Janirellidae (originally erected as Ianirellidae) were disputed until settled by Just (2008). Janirellids are best recognised usually by the presence of lateral spines or plates, or by the combination of a covered anus, uniramous uropods and no free pleonites. Most species are found deeper than 500 m; half the species are abyssal or hadal. Maximum length is about 7.5 mm.

Diagnosis. Body subcylindrical or flattened; head frontal margin projecting forward; pereonites with or rarely without lateral spines. Pleon without free pleonites, lateral margins with spines or irregular denticles. Anus covered by pleopodal operculum. Eyes absent. Antennula much shorter than antenna. Maxillipedal palp articles 2 and 3 expanded medially. Pereopod 1 carposubchelate; pereopods 2–7 ambulatory; pereopod 4 coxa inserting on midlateral margin; pereopodal 2–7 dactyli with 1 unguis, sometimes with small secondary claw. Uropod inserting posterolaterally, uniramous, rodlike.

Key to genera and subgenera of Janirellidae

1. Head without rostrum or pseudorostrum. Front between antennulae as wide as antennula base. Posterior margin of pleotelson evenly convex curve between uropods. Uropod more than 0.7 pleotelson length (fig. 3.12a) ..... *Dactylostylis*

– Head with rostrum or pseudorostrum derived from frons/clypeus. Front between antennulae more than twice width of antennula base. Posterior margin of pleotelson projecting between uropods. Uropod about 0.2 pleotelson length 2

2. Head with pseudorostrum. Body flattened, margins parallel, pereonites laterally truncate without spines (fig. 3.12d) ..... *Triaina*

– Head with true simple or complex rostrum. Body fusiform, usually with lateral spines ..... *Janirella*

Dactylostylis Richardson, 1911

Diagnosis. Body fusiform, with lateral spines. Head without rostrum or pseudorostum; frontal margin between antennulae as wide as antennula base. Posterior margin of pleotelson evenly convex between uropods. Uropod greater than 0.7 pleotelson length.

Slope, bathyal (350–2970 m). Temperate Northern Atlantic, Tropical Atlantic, Temperate South America (Atlantic coast). 3 species (Hessler, 1968: rediagnosis, species description; Kensley and Heard, 1985: species description as *Spinianirella*).

Janirella Bonnier, 1896

Diagnosis. Body fusiform, usually with lateral spines. Head with rostrum; frontal margin between antennulae more than twice width of antennula base. Posterior margin of pleotelson projecting between uropods; uropod about 0.2 pleotelson length.

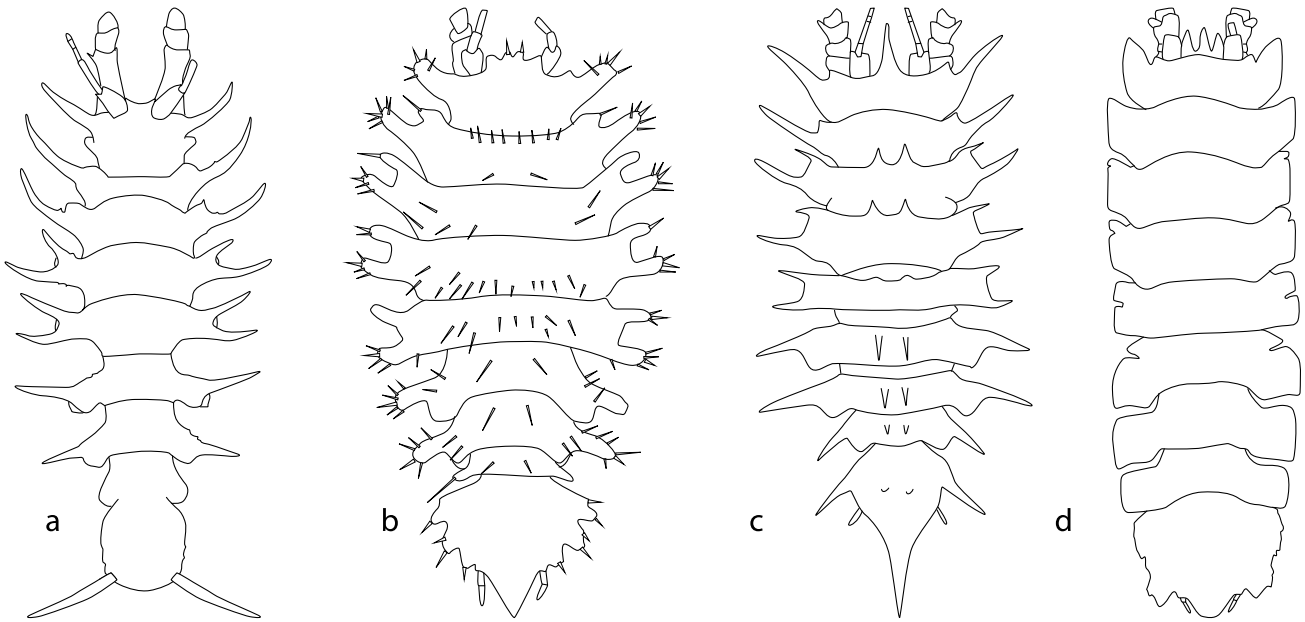


Figure 3.12. Janirellidae. Dorsal views: a, *Dactylostylis*; b, *Janirella bifida* Menzies, 1962; c, *J. diplospinosa* Birstein, 1971; d, *Triaina isodonte* Just, 2008.

Slope–hadal (946–9043 m). Temperate Northern and Tropical Atlantic, Temperate Northern W Pacific. GOODS bathyal provinces: New Zealand/Kermadec. 39 species. (Menzies, 1962: redignosis, key to 11 species; Kussakin, 1988: key to 33 species of N Pacific; George, 2004: diagnosis). Two subgenera, *Janirella* Bonnier, 1896, *Parjanirella* Birstein, 1971, are no longer recognised (Ohta et al., 2025).

Triaina Just, 2009

Diagnosis. Body flattened, margins parallel, truncate, without spines. Head with pseudorostrum derived from frons/clypeus; frontal margin between antennulae more than twice width of antennula base. Posterior margin of pleotelson projecting between uropods. Uropod about 0.2 pleotelson length.

Shelf, slope (80–2500 m). Temperate SE Australia. 2 species (Just, 2008).

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Janiridae G.O. Sars, 1897

Figures 3.13–3.15

Janiridae are archetypal janiroideans, the family that remains when other taxa are placed in more recognisable or better characterised families. Most are very small, usually less than 5 mm long, always longer than wide, with similar pereopods, although the first can be more or less prehensile. Most are marine, usually in shallow water, but a few are found exclusively in fresh water.

Of more than 50 genera placed at one time or another in Janiridae, many have been assigned to other smaller families, or synonymised (Wilson and Wägele, 1994). These authors reviewed and diagnosed the remaining genera, with many provisos, and their arrangement has been scarcely revisited. Their generic diagnoses have been simplified here and their key updated.

Diagnosis. Body oblong, depressed; head with or without rostrum; pereonites 1–7 free, wider than long, often with laminar lateral expansions. Pleon with 0, 1 or 2 free pleonites. Anus not covered by pleopodal operculum. Eyes usually present, dorsal. Maxillipedal palp articles 1–3 wider than distal articles. Pereopod 1 usually prehensile; pereopods 2–7 ambulatory; pereopod 4 coxa inserting on midlateral margin; pereopodal 2–7 dactyli with 2 or 3 claws. Uropod inserting laterally or terminally.

Key to genera of Janiridae

1. Uropod long, about as long as or longer than pleotelson; endopod longer than peduncle (figs 3.13b, f, k, l, 3.14b–d, k) 2
– Uropod shorter than pleotelson (even if narrow); endopod as long as or shorter than peduncle (figs 3.13a, c, g, h–j, 3.14a, e–j) 10
2. Eyes absent 3
– Eyes present 4
3. Body vermiform, more than 5 times as long as wide (fig. 3.13b) ..... *Caecianiropsis*
– Body broad, flat; pereonites 1–3 laterally bilobed (fig. 3.14d) ..... *Janthura*
4. Male pereopod 1 propodus and carpus enlarged, often swollen; carpus with strong marginal teeth (fig. 3.15a, g) 5
– Male pereopod 1 propodus and carpus similar to those of pereopods 2–7; if sexually dimorphic, carpus without strong marginal teeth (fig. 3.15b, c, e, f) 6
5. Front with rounded rostrum. Body flat, oval, twice as long as wide; coxa 1 and pereonites 2–4 projecting anteriorly (fig. 3.14k) ..... *Rostrobagatus*
– Front without rostrum. Body broad, pereonite 4 broadest, tergites of pereonites 2–4 laterally concave (fig. 3.13e, f) ..... *Carpias*
6. Pereonites often with large lateral lappets or spines (fig. 3.14c). Pereopod 1 propodus with proximal serration on lower margin (fig. 3.15c, d) ..... *Janiralata*
– Pereonites without lateral lappets or spines. Pereopod 1 propodus without proximal serration on lower margin, sometimes with distal palmar teeth 7
7. Head with small dorsally curved rostrum. Eyes large, often bulging laterally. Uropodal rami flattened (fig. 3.13l) ..... *Iathrippa*
– Head without rostrum. Eyes compact, not bulging laterally. Uropodal rami round in cross-section 8
8. Coxae 1–3 not visible dorsally (fig. 3.14b). Male pleopod 1 medial lobe convex, lateral lobe short, acute (fig. 3.15t) ..... *Janaira*
– Coxae 1–3 visible dorsally. Male pleopod 1 medial lobe lobed or convex, lateral lobe prominent (fig. 3.15r, s, u, v) 9
9. Male pleopod 1 distal tip with medial and lateral lobes posteriorly directed, separated by notch (fig. 3.15u). Maxillipedal palp as wide as endite (fig. 3.15o). Pereopod 2 elongate, longer than pereopods 1 and 3 (fig. 3.15f, i) ..... *Janira*

– Male pleopod 1 medial lobe convex, merging into acute prominent lateral lobe (fig. 3.15s). Maxillipedal palp wider than endite (fig. 3.15n). Pereopod 2 as long as pereopods 1 and 3 ..... *Ianiropsis*

10. Uropod with squat peduncle, wider than long, barely emerging from pleotelson margin; rami usually shorter than peduncle (figs 3.13c, h, 3.14a, h, i) 11

– Uropod with peduncle clearly emerging from pleotelson margin, especially in ventral view; rami longer than peduncle 14

11. Pereopods 2–7 with 3 claws, lower claw similar to upper claw, accessory seta enlarged as third claw (fig. 3.15k) (freshwater to marine) ..... *Jaera*

– Pereopods 2–7 with 2 dactylar claws (fig. 3.15h, j, m) (marine) 12

12. Pereopods 2–7 with lower dactylar claw subequal to upper claw (fig. 3.15j) ..... *Hawaianira*

– Pereopods 2–7 with lower dactylar claw distinctly smaller than upper claw 13

13. Pereopods 2–7 with lower dactylar claw minute (fig. 3.15h). Body flat, twice as long as wide, with setose margins (fig. 3.13c, d) ..... *Caecijaera*

– Pereopods 2–7 with lower dactylar claw slightly smaller than upper claw (fig. 3.15m). Body flat, at least 3.5 times as long as wide, without setose margins (fig. 3.14h, i) ..... *Neojaera*

14. Uropodal endopod longer than peduncle, longer than exopod (fig. 3.13a, g, j, 3.14f) 15

– Uropod with thin subequal rami and peduncle 18

15. Front of head with rostrum extending beyond anterior curved margin of head 16

– Front of head without rostrum extending beyond anterior curved margin of head 17

16. Eyes present. Pleotelson as wide as or wider than long (fig. 3.13a) ..... *Austrofilius*

– Eyes absent. Pleotelson longer than wide (fig. 3.14f) ..... *Microjaera*

17. Pereopod 1 gnathopod-like; carpus enlarged, with robust sensillate setae (fig. 3.15b) ..... *Ectias*

– Pereopod 1 leg-like; carpus slender, with few setae (fig. 3.15e) ..... *Iais*

18. Maxillipedal palp much narrower than endite (fig. 3.15q). Antennal articles 5–6 as long as articles 2–3 ..... *Protocharon*

– Maxillipedal palp wider than (fig. 3.15p) or subequal to endite. Antenna articles 5–6 longer than articles 1–4 19

19. Front broad, truncate, projecting between antennulae (fig. 3.14g) ..... *Microjanira*

– Front straight or convex, not projecting 20

20. Body more than 4 times as long as wide, pleotelson narrower than pereon (fig. 3.14e). Male pleopod 2 stylet shorter than peduncle, thin, with distinct angle in distal part (fig. 3.15x) (freshwater) ..... *Mackinia*

– Body about twice as long as wide, setose, broad, posterior pereonites and pleotelson wider than anterior pereonites (fig. 3.13i). Male pleopod 2 stylet much longer than peduncle, distally coiled (fig. 3.15w) (freshwater, estuarine) ..... *Heterias*

Austrofilius Hodgson, 1910

Diagnosis. Body broad, flattened. Front with broad, quadrate rostrum. Pleotelson wider than long. Antennula flagellum of 5 or 6 articles. Antennal flagellum proximal articles fused; with conspicuous scale. Maxillipedal palp wider than endite. Pereopod 1 ambulatory, carpus slender, with few setae. Pereopods 2–7 dactyli with lower claw smaller than upper claw. Male pleopod 1 medial lobes broad, rounded; lateral lobes curving, projecting posteriorly. Uropod shorter than pleotelson; endopod longer than peduncle, longer than exopod.

Shelf, slope. Temperate Northern Atlantic, Southern Ocean. 4 species (Winkler and Brandt, 1993: description of 2 species; Castelló, 2002).

Caecianiropsis Menzies and Pettit, 1956

Diagnosis. Body vermiform, more than 5 times as long as wide. Front with rounded rostrum, with acute anterolateral projections. Blind. Antennula flagellum of 2 or 3 articles. Antennal article 3 longer than articles 1, 2 and 4. Maxillipedal palp wider than endite. Pereopod 1 ambulatory, carpus slender, with few setae.

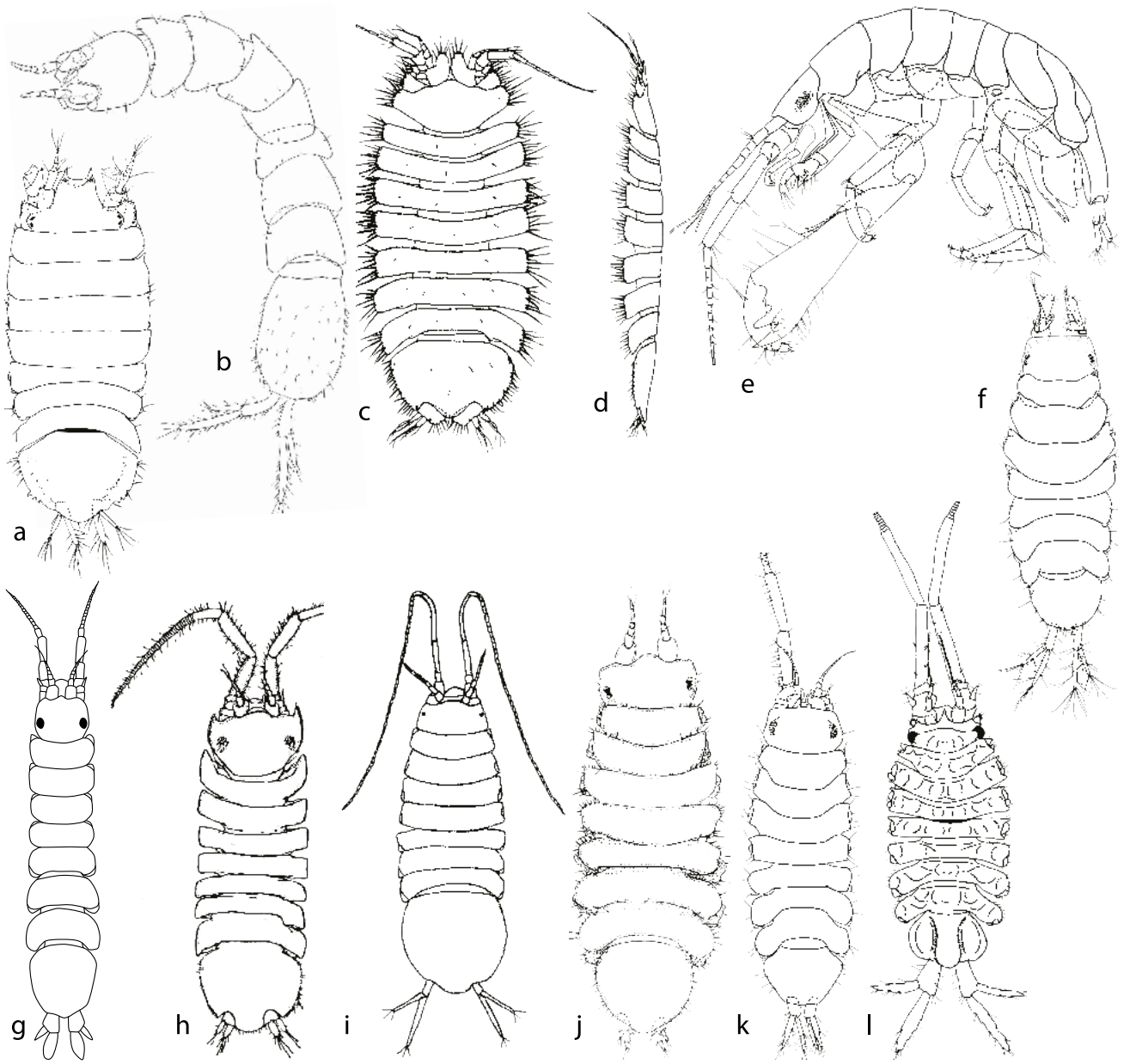


Figure 3.13. Janiridae. Dorsal views: a, *Austrofilius furcatus* Hodgson, 1910; b, *Caecianiropsis goseongensis* Kim, Lee and Karanovic, 2019; c, d, *Caecijaera kussakini* Malyutina, 1994 (dorsal, lateral); e, f, *Carpias montaguensis* Doti and Wilson, 2010 (lateral, dorsal); g, *Ectias turqueti* Richardson, 1906; h, *Hawaianira peleae* Miller, 1967; i, *Heterias exul* (F. Müller, 1892); j, *Iais pubescens* (Dana, 1853); k, *Ianiropsis alanmillari* Doti and Wilson, 2010; l, *Iathrippa sarsi* (Pfeffer, 1887).

Pereopods 2–7 dactyli with 2 similar claws. Male pleopod 1 medial lobes distally rounded; lateral lobes angular, projecting laterally. Male pleopod 2 stylet coiled. Uropod about as long as pleotelson; peduncle, elongate; endopod longer than endopod.

Intertidal (interstitial). Temperate Northern Pacific, Southern Ocean. 4 species (Menzies and Pettit, 1956; Kim et al., 2019: rediagnosis, key to species).

Caecijaera Menzies, 1951

Diagnosis. Body broad, about twice as long as wide, setose, lateral margins widening posteriorly. Front without rostrum. Blind. Antennula article 1 with medial lobe; flagellum of 2 or 3 articles. Antennal articles 5–6 as long as articles 1–4, with setose scale. Maxillipedal palp as wide as endite. Pereopod 1

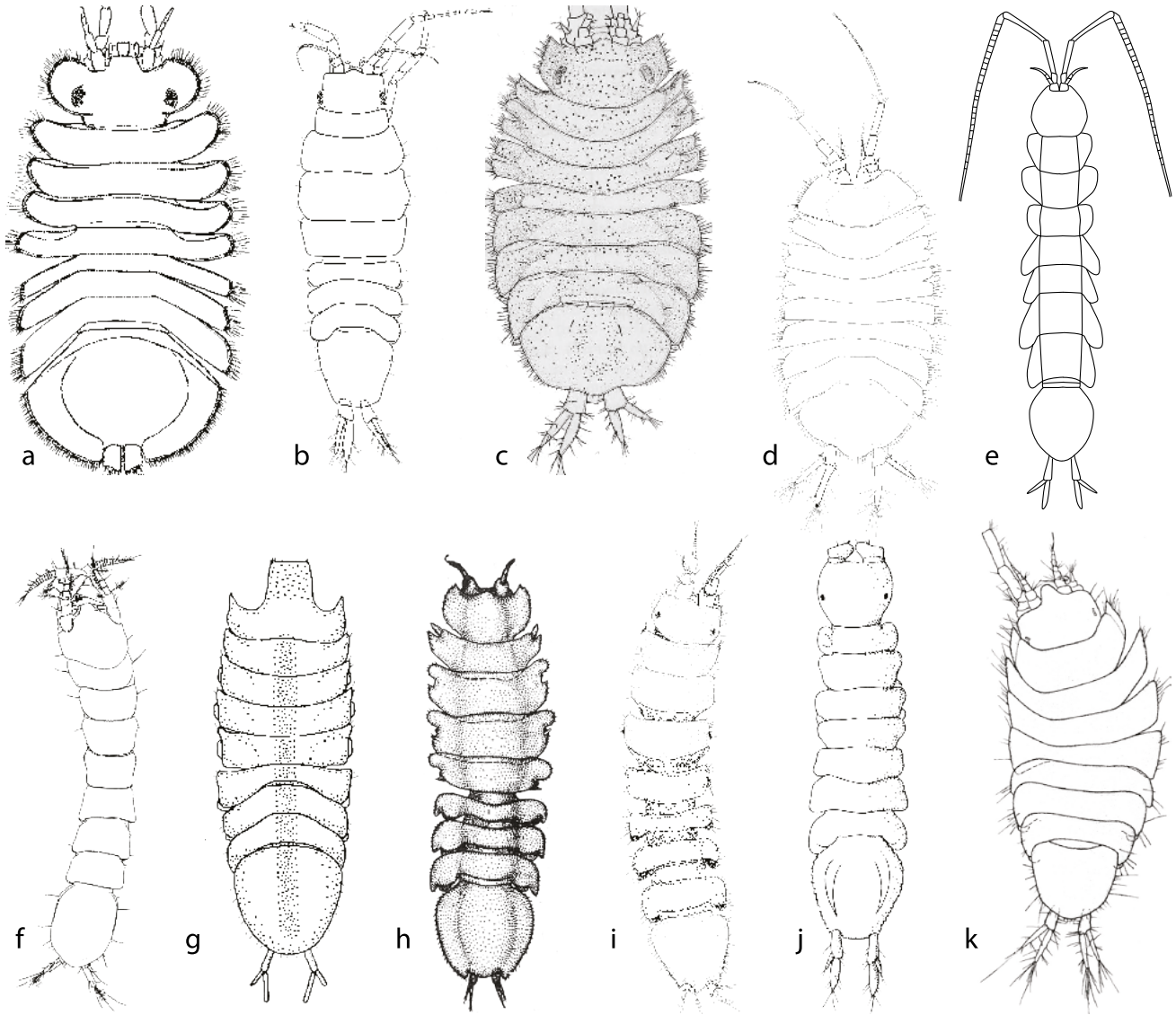


Figure 3.14. Janiridae. Dorsal views: a, *Jaera istri* Veuille, 1979; b, *Janaira platyoura* Doti and Wilson, 2010; c, *Janiralata davisi* Menzies, 1951; d, *Janthura abyssicola* Wolff, 1962; e, *Mackinia japonica* Matsumoto, 1956; f, *Microjaera morii* Shimomura, 2005; g, *Microjanira dentifrons* Schiecke and Fresi, 1970; h, *Neojaera caeca* Kussakin and Vasina, 1984; i, *Neojaera elongata* Menzies, 1962; j, *Protocharon arenicola* Chappuis, Delamare-Debouteville and Paulian, 1956; k, *Rostrobagatus microps* Müller, 1993.

ambulatory, carpus slender, with few setae. Pereopods 2–7 dactyli with 2 claws, lower claw minute. Male pleopod 1 medial lobe transverse, lateral lobes minute or prominent. Uropod with squat peduncle immersed in pleotelson margin, with setose mesial margin; rami short and narrow.

Intertidal (commensal with limnoriid isopods). Arctic, Temperate Northern Pacific, Central Indo-Pacific. 5 species (Kussakin, 1962: 3 species; 1988: key to 5 species; Malyutina, 1994).

Carpias Richardson, 1902

Diagnosis. Body broad, pereonite 4 broadest, tergites of pereonites 2–4 laterally concave. Front without rostrum. Antennula flagellum of 7–11 articles. Antennal articles 5–6 longer than articles 1–4; with scale. Maxillipedal palp wider than endite. Pereopod 1 carposubchelate, carpus oval in female, swollen with strong marginal spines in male; propodus elongate, curved. Pereopods 2–7 dactyli with 2 large subequal distal claws plus third large subdistal accessory seta. Male pleopod 1 distally V-shaped, with merging medial and posteriorly projecting lateral lobes. Uropod about as long as or longer than pleotelson; rami elongate, longer than peduncle.

Intertidal–shelf (coral and rocky reefs). Temperate Northern and Tropical W Atlantic, Indo West-Pacific, Temperate Australasia. 27 species (Doti and Wilson, 2010: rediagnosis, key to 19 species).

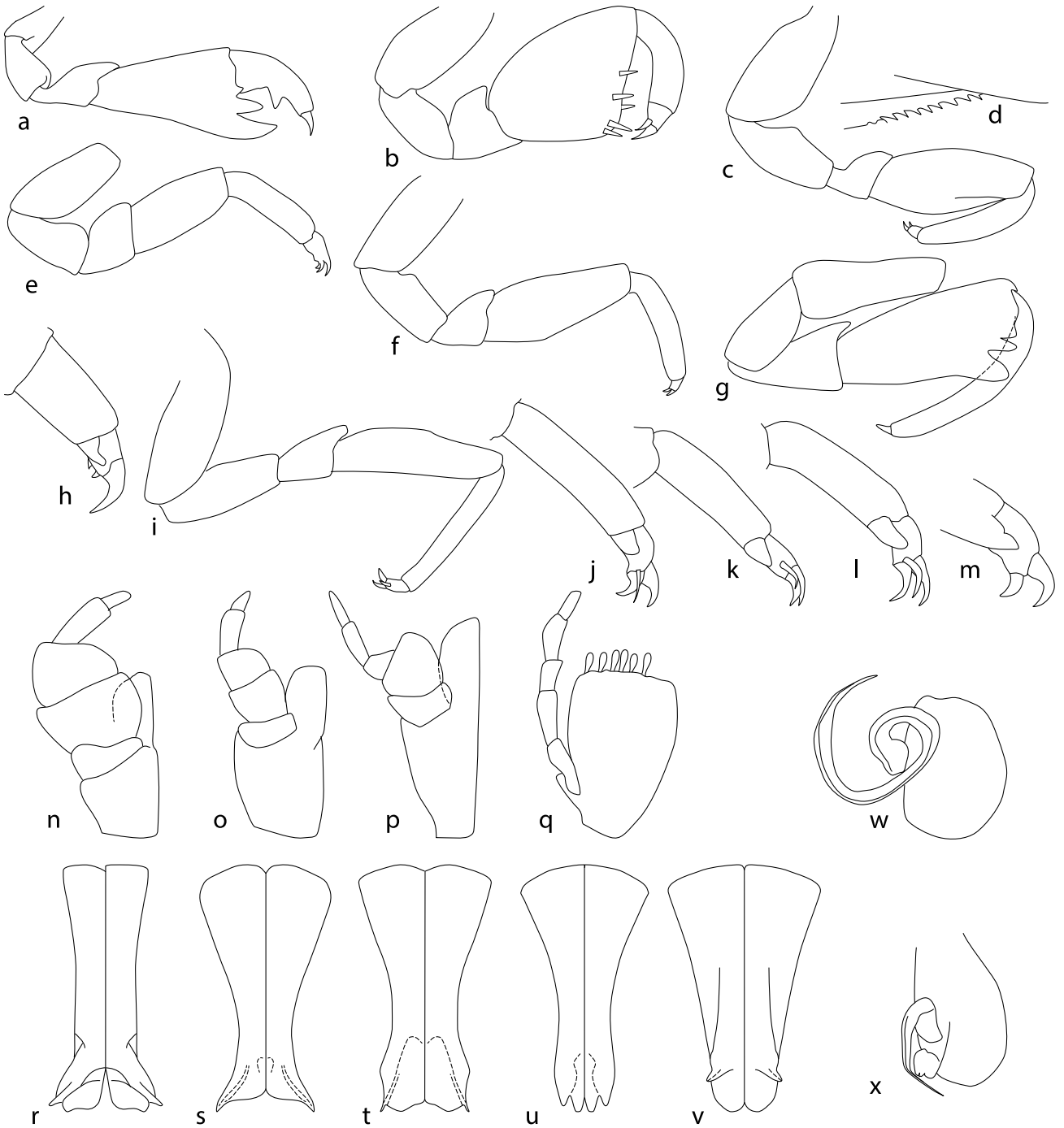


Figure 3.15. Janiridae. Pereopod 1; a, *Carpias*; b, *Ectias*; c, d, *Janiralata* (with detail of inner margin of dactylus); e, *Iais*; f, *Janira*; g, *Rostrobagatus*. Pereopod 2: h, *Caecijaera* (propodus, dactylus); i, *Janira*. Pereopod 4, propodus, dactylus: j, *Hawaianira*; k, *Jaera*. Pereopod 7: l, *Iais*; m, *Neojaera*. Maxilliped: n, *Ianiropsis*; o, *Jaera*; p, *Microjaera*; q, *Protocharon*. Male pleopods 1: r, *Heterias*; s, *Ianiropsis*; t, *Janaira*; u, *Janira*; v, *Mackinia*. Male pleopod 2: w, *Heterias*; x, *Mackinia*.

Ectias Richardson, 1906

Diagnosis. Body vermiform, about 6 times as wide as long. Front without rostrum. Antennula flagellum of 5 or 6 articles. Antennal articles 5–6 longer than articles 1–4; with scale. Maxillipedal palp as wide as endite. Pereopod 1 carposubchelate; carpus enlarged, subtriangular, with 2 rows of spiniform setae on transverse margin opposing propodus. Pereopods 2–7

dactyli with 2 large subequal distal claws plus third large subdistal accessory seta. Male pleopod 1 distally V-shaped, with medial and lateral lobes merged into elongate posterolateral projections. Male pleopod 2 stylet elongate, curved. Uropod shorter than pleotelson; endopod longer than peduncle, flat, ovoid, longer than exopod.

Subtidal, shelf. Temperate Southern Africa, Southern Ocean. 2 species (Barnard, 1920; Richardson, 1906).

Hawaianira Miller, 1967

Diagnosis. Body compact, flat, pereonites subequal. Front without rostrum, with acute anterolateral angles. Antennula flagellum of 3 articles. Antennal articles 5–6 longer than articles 1–4. Maxillipedal palp narrower than endite. Pereopod 1 ambulatory, carpus slender, with few setae. Pereopods 2–7 dactyli with 2 similar claws. Male pleopod 1 medial lobe short, setose, rounded; lateral lobe short, triangular. Uropod with squat peduncle immersed in pleotelson margin; rami short, adjacent.

Intertidal. Indo West-Pacific (Hawaii, Philippines, Réunion). 2 species (Miller, 1967).

Heterias Richardson, 1904

Diagnosis. Body broad, about twice as long as wide, setose, lateral margins widening posteriorly. Front without rostrum. Pleotelson wider than pereonite 7. Antennula flagellum of 3 or 4 articles. Antennal articles 5–6 longer than articles 1–4. Maxillipedal palp wider than endite. Pereopod 1 ambulatory, carpus slender, with few setae. Pereopods 2–7 dactyli with lower claw shorter than upper claw. Male pleopod 1 medial lobe broad, flattened; lateral lobe pointing laterally. Male pleopod 2 stylet much longer than peduncle, distally coiled. Uropod shorter than pleotelson, thin; endopod as long as peduncle, longer than exopod.

Estuarine, freshwater. Southern Australia, South America. 4 species (Bowman et al., 1987; Roberts, 1975). Two genera, *Heterias* for three species in fresh water and estuaries in southern Australia and *Fritzianira* Lemos de Castro and Brasil Lima, 1977 for *H. exul* (Müller, 1892) from fresh water in South America, are synonymous but sometimes treated as subgenera.

Iais Bovallius, 1886

Diagnosis. Body narrow, about 3 times as long as wide, broadest at pereonites 4–5. Front without rostrum. Eyes reduced to few ocelli. Antennula flagellum of 3 articles. Antennal articles 5–6 longer than articles 1–4. Pereopod 1 ambulatory, carpus slender, with few setae. Pereopods 2–7 dactyli with 2 similar claws and enlarged accessory seta. Male pleopod 1 medial and lateral lobes short, scarcely separated, projecting distally. Uropod shorter than pleotelson; endopod longer than peduncle, longer than exopod.

Estuarine, subtidal (commensal with sphaeromatid isopods). Tropical Atlantic, Indo West-Pacific, Temperate South America, Temperate Southern Africa, Temperate Australasia, Southern Ocean. 8 species (Kensley and Schotte, 1999; Menzies and Barnard, 1951).

Ianiropsis G. O. Sars, 1897

Diagnosis. Body narrow, 3 times as long as wide, anterior pereonites with visible coxae. Front without rostrum. Antennula flagellum of 5–25 articles. Antennal articles 5–6 longer than articles 1–4; with scale. Maxillipedal palp wider than endite. Pereopod 1 ambulatory, basis-merus of adult male elongate, distinctly longer than those on posterior pereopods; carpus elongate. Pereopods 2–7 dactyli with 2 large subequal distal claws plus third large subdistal accessory seta. Male pleopod 1 medial lobe convex, merging into acute prominent lateral lobe. Uropod about as long as pleotelson; rami longer than broad peduncle (rarely short).

Intertidal–slope. Cosmopolitan. 23 species (Kussakin, 1988: key to 27 species; Jang and Kwon, 1990; Doti and Wilson, 2010: rediagnosis, key to 22 species).

Iathrippa Bovallius, 1886

Diagnosis. Body broad, setose, pereonites 2–4 with small lappets. Front with small dorsally curved rostrum. Eyes bulging laterally. Antennula flagellum of more than 15 articles. Antennal articles 5–6 longer than articles 1–4; with scale. Maxillipedal palp wider than endite. Pereopod 1 ambulatory, basis-merus of adult male elongate, distinctly longer than those on posterior pereopods; carpus elongate. Pereopods 2–7 dactyli with 2 large subequal distal claws plus third large subdistal accessory seta. Male pleopod 1 medial lobe longer than acute lateral lobe. Male pleopod 2 stylet elongate, curved. Uropod longer than pleotelson; rami broad, flat, longer than peduncle, endopod longer than exopod.

Intertidal, subtidal. Temperate South America, Temperate Southern Africa, Temperate Australasia, Southern Ocean. 11 species (Winkler and Brandt, 1993: figures, some as *Notasellus* (junior synonym)).

Jaera Leach, 1814

Diagnosis. Body broad, setose, lateral margins often widening posteriorly. Front without or with small rostrum. Eyes present, or blind (rare). Antennula flagellum of 2 or 3 articles. Antennal articles 5–6 longer than articles 1–4. Pereopod 1 ambulatory, carpus slender, with few setae. Pereopods 2–7 dactyli with 3 claws, lower claw similar to upper claw, accessory seta enlarged as third claw. Male pleopod 1 broad, lateral lobe distinct from medial lobe, with projecting copulatory horns. Male pleopod 2 stylet elongate, curved. Uropod with squat peduncle immersed in pleotelson margin; rami short, adjacent.

Estuarine, intertidal, slope, freshwater (some commensal with sphaeromatid isopods). Arctic, Temperate Northern Atlantic, Southern Ocean. 18 species (Veuille, 1979: review of species; Kussakin, 1988: key to 21 species and subspecies; Linse et al., 2014: rediagnosis, distribution, discussion, phylogeny of Janiroidea).

Janaira Moreira and Pires, 1977

Diagnosis. Body narrow, 3 times as long as wide, anterior pereonites laterally rounded without visible coxae. Front without rostrum. Antennula flagellum of 9–12 articles. Antennal articles 5–6 longer than articles 1–4. Maxillipedal

palp wider than endite. Pereopod 1 of female ambulatory; carpus of male wider proximally than distally, with 2 rows of spiniform setae; dactylus with 2 claws. Pereopods 2–7 dactyli with 2 large subequal distal claws plus third large subdistal accessory seta. Male pleopod 1 medial lobe convex, lateral lobe short, acute. Uropod longer than pleotelson; peduncle broad; rami longer than peduncle.

Intertidal. Tropical W Atlantic, Temperate SE Australia. 2 species (Moreira and Pires, 1977a; b: biology of type species; Doti and Wilson, 2010).

Janira Leach, 1814

Diagnosis. Body narrow, 3 times as long as wide, anterior pereonites with visible coxae. Front without or with small rostrum. Antennula flagellum of more than 25 articles. Antennal articles 5–6 longer than articles 1–4; with scale. Maxillipedal palp as wide as endite. Pereopod 1 of female ambulatory; carpus of male wider proximally than distally, with 2 rows of spiniform setae; dactylus with 2 claws. Pereopod 2 of male elongate, longer than pereopods 1 and 3. Pereopods 2–7 dactyli with 2 large subequal distal claws plus third large subdistal accessory seta. Male pleopod 1 distal tip with medial and lateral lobes posteriorly directed, separated by notch. Uropod longer than pleotelson; peduncle and rami narrow.

Subtidal–bathyal. Temperate Northern and Tropical Atlantic, Temperate Northern W Pacific. 5 species (Menzies, 1951; Wolff, 1962: rediagnosis, key to 8 species, some now in other genera; Kussakin, 1988: 2 species).

Janiralata Menzies, 1951

Diagnosis. Body broad, flat; at least pereonites 2 and 3 (often other pereonites) with 2 lateral lappets. Front without rostrum, with acute anterolateral angles. Antennula flagellum of more than 15 articles. Antennal articles 5–6 longer than articles 1–4; with scale. Maxillipedal palp as wide as endite. Pereopod 1 carposubchelate, sexually dimorphic; carpus with marginal spiniform setae, propodus proximally serrate, dactylus short, with or without claws. Pereopods 2–7 dactyli with 2 similar claws and enlarged accessory seta. Male pleopod 1 with broad setose medial lobes merging into subtriangular lateral lobe. Male pleopod 2 stylet elongate, curved. Uropod longer than pleotelson; peduncle broad; rami longer than peduncle.

Subtidal–slope. Temperate Northern Pacific. 34 species (Kussakin and Mezhov, 1979: diagnoses of 15 species; Kussakin, 1988: key to 53 species, some now in other genera; Wilson and Wägele, 1994: divided genus in several groups and subgroups; Kim and Yoon, 2021). Ohta et al. (2023) reviewed species attached to other invertebrates such as asteroids and sponges.

Janthura Wolff, 1962

Diagnosis. Body broad, flat; pereonites 1–3 laterally bilobed. Front without rostrum. Blind. Antennula flagellum of 3 articles. Antennal articles 5–6 longer than articles 1–4; with scale. Maxillipedal palp wider than endite. Pereopod 1 ambulatory, carpus slender, with few setae. Pereopods 2–7 dactyli with lower claw smaller than upper claw (on anterior pereopods). Male pleopod 1 medial lobe expanded; lateral lobe pointing laterally. Male pleopod 2 stylet elongate, curved. Uropod longer than pleotelson; rami elongate, longer than thick peduncle.

Bathyal–hadal (2250–9034 m). Tropical Atlantic, Central Indo-Pacific. 2 species (Birstein, 1963; Wolff, 1962).

Mackinia Matsumoto, 1956

Diagnosis. Body elongate, more than 4 times as long as wide. Front without rostrum. Blind. Antennula flagellum of 4 articles. Antennal articles 5–6 longer than articles 1–4; with scale. Maxillipedal palp wider than endite. Pereopod 1 ambulatory, carpus slender, with few setae. Pereopods 2–7 dactyli with lower claw smaller than upper claw. Male pleopod 1 medial lobe semicircular; lateral lobe reduced. Male pleopod 2 stylet shorter than peduncle, thin, with distal angle. Uropod shorter than pleotelson, thin; endopod as long as peduncle, much longer than exopod.

Freshwater. Japan, Korea, far east of Russia. 7 species (Birstein and Ljovuschkin, 1965; Matsumoto, 1956, 1967).

Microjaera Bocquet and Levi, 1955

Diagnosis. Body vermiform, about 6 times as wide as long. Front with broad, truncate rostrum projecting between antennulae. Pleotelson longer than wide. Blind. Antennula flagellum of 2 articles. Antennal articles 5–6 longer than articles 1–4. Maxillipedal palp wider than endite. Pereopod 1 ambulatory but stouter than pereopods 2–7; carpus with few spiniform setae; dactylus short, with 2 unequal claws, distal claw as long as dactylus. Pereopods 2–7 dactyli with 2 similar claws. Male pleopod 1 medial lobe distally flat, merging into lateral lobe elongated into copulatory horns. Male pleopod 2 stylet elongate, curved. Uropod shorter than pleotelson; exopod longer than peduncle; endopod 3 times as long as exopod.

Intertidal (interstitial). Temperate Northern Atlantic, Temperate Northern W Pacific (Mediterranean, Japan). 2 species (Bocquet and Lévi, 1955; Shimomura, 2005).

Microjanira Schiecke and Fresi, 1970

Diagnosis. Body flat, less than 3 times as long as wide. Front with broad, truncate rostrum projecting between antennulae. Blind, or eyes reduced to few ocelli. Antennula flagellum of 3 or 4 articles. Antennal articles 5–6 longer than articles 1–4; with scale. Maxillipedal palp wider than endite. Pereopod 1 ambulatory, carpus slender, with few setae. Pereopods 2–7 dactyli with lower claw smaller than upper claw. Male pleopod 1 not distolaterally expanded, tip bilobed. Uropod shorter than pleotelson, thin; endopod as long as peduncle, longer than exopod.

Intertidal, shelf (interstitial). Temperate Northern and Tropical Atlantic. 3 species (Hooker, 1985; Jaume, 1995; Schiecke and Fresi, 1970). *Trogloianiropsis* Jaume, 1995 is treated as a synonym of *Microjanira* here. Its only species has similar male pleopods and a similar rostrum.

Neojaera Nordenstam, 1933

Diagnosis. Body flat, at least 3.5 times as long as wide. Front without rostrum. Blind, or eyes reduced to few ocelli. Antennula flagellum of 2 or 3 articles. Antennal articles 5–6 longer than

articles 1–4. Maxillipedal palp narrower than endite, or as wide as endite. Pereopod 1 ambulatory, carpus slender, with few setae. Pereopods 2–7 dactyli with lower claw smaller than upper claw. Male pleopod 1 medial lobe rounded; lateral lobe sometimes prolonged; proximal region broad, rounded. Male pleopod 2 stylet much longer than peduncle, distally coiled. Uropod with squat peduncle immersed in pleotelson margin; rami narrow, longer than peduncle.

Intertidal–slope. Temperate South America, Temperate Southern Africa, Southern Ocean. 10 species (Kussakin and Vasina, 1984; Menzies, 1962; Wilson and Wägele, 1994).

Protocharon Chappuis, Delamare-Deboutteville and Paulian, 1956

Diagnosis. Body flat, 4 times as long as wide. Front without rostrum. Eyes reduced to few ocelli. Antennula flagellum of 3 or 4 articles. Antennal articles 5–6 as long as articles 2–3. Maxillipedal palp narrower than endite. Pereopod 1 ambulatory, carpus slender, with few setae. Pereopods 2–7 dactyli with 2 similar claws. Male pleopod 1 medial lobe rounded; lateral lobe slightly rounded. Uropod shorter than pleotelson, thin; endopod as long as peduncle, longer than exopod.

Intertidal marine, freshwater (interstitial). Tropical Atlantic, Western Indo-Pacific (Domincan Republic, Réunion). 2 species (Chappuis et al., 1956; Wagner, 1990: second species as Jehaia, junior synonym).

Rostrobagatus Müller, 1993

Diagnosis. Body flat, oval, twice as long as wide; coxa 1 and pereonites 2–4 projecting anteriorly. Front with rounded rostrum. Eyes reduced to few ocelli. Antennula flagellum of 4 articles. Antennal articles 5–6 longer than articles 1–4; with scale. Maxillipedal palp wider than endite. Pereopod 1 carposubchelate, carpus oval in female, swollen with strong marginal spines in male; propodus elongate, curved. Pereopods 2–7 dactyli with 2 similar claws. Male pleopod 1 medial lobe rounded; lateral lobe digitiform. Uropod about as long as or longer than pleotelson; rami elongate, longer than peduncle.

Subtidal (coral rubble). Tropical Atlantic (French Antilles). 1 species (Müller, 1993).

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Joeropsididae Nordenstam, 1933

Figure 3.16

The family Joeropsididae, particularly the genus *Joeropsis*, is distributed globally except in polar waters (Bruce, 2015; Just, 2001). *Joeropsis* is well represented in tropical coral reefs worldwide but has been reported from slope depths. The family is readily recognised, even in the field, by the compact body shape, with a characteristically robust and reflexed antenna (fig. 3.16d), and small, ventrolaterally inserted uropods with a large peduncle and tiny rami (fig. 3.16g). Many species are coloured with brown patches. Most individuals are less than 2 mm long and few species reach more than 5 mm long.

A single genus was known until Just (2001) erected two more for just three species from the continental slope of southeastern Australia.

Diagnosis. Body flat, longer than wide, robust; head with rostrum; anterior pereonites with sternal keels. Coxal plates absent. Pleon of 1 evenly-rounded segment. Anus not covered by pleopodal operculum. Antenna geniculate, peduncular article 6 and flagellum folding laterally and backwards under lateral expansion of peduncular article 5. Mandibular molar spiniform. Maxillipedal palp articles 1–5 narrow, less than half as wide as endite. Uropod inserted in terminal incision of pleotelson; rami minute.

Key to genera of Joeropsididae

1. Body lateral margins converging posteriorly (fig. 3.16c). Maxillipedal palp articles 2 and 3 widest distally, each with distomesial lobe (fig. 3.16f) ..... *Scaphojoeropsis*

– Body lateral margins straight (fig. 3.16a, b). Maxillipedal palp article 2 with distomesial lobe, not widest distally (fig. 3.16e) 2

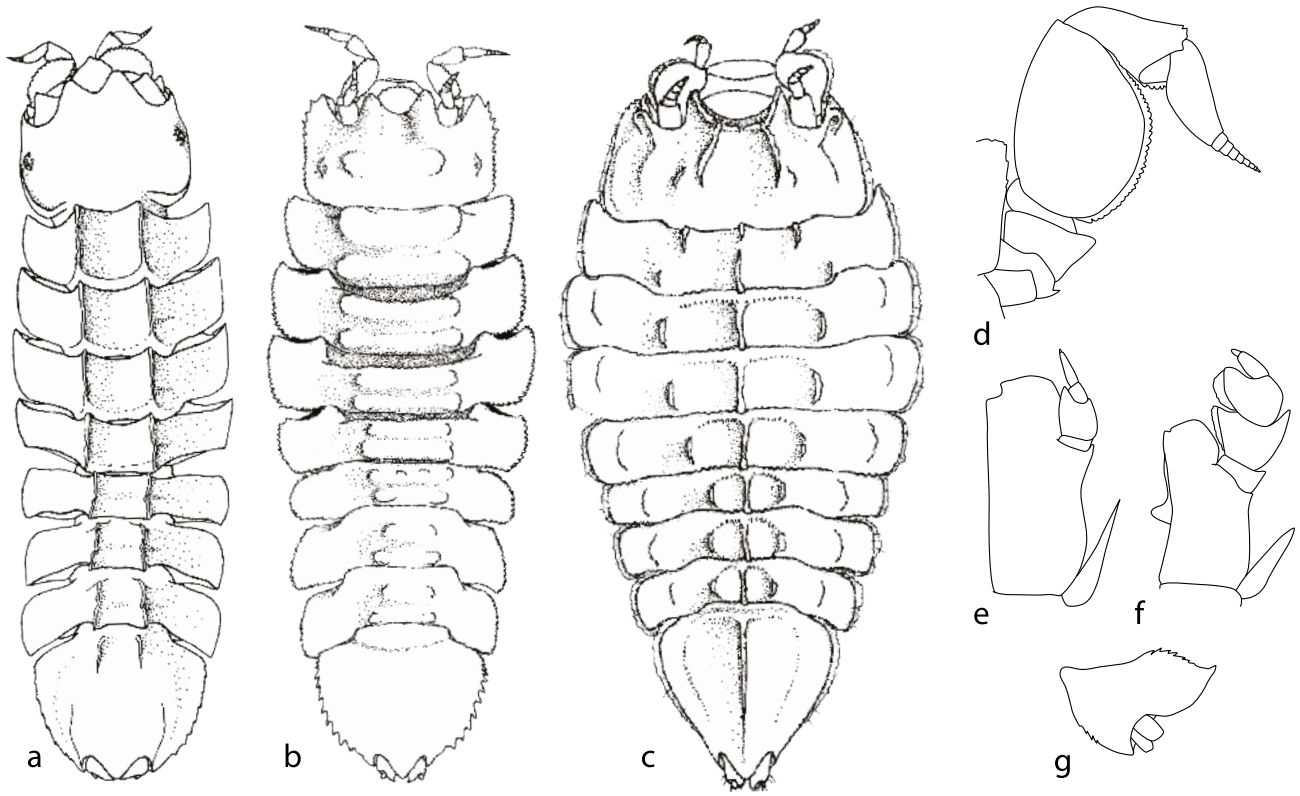


Figure 3.16. Joeropsididae. Dorsal views: a, *Joeropsis bicarinata* Just, 2001; b, *Rugojoeropsis rugosa* Just, 2001; c, *Scaphojoeropsis multicarinata* Just, 2001. Antenna: d, *Joeropsis*. Maxilliped: e, *Joeropsis*; f, *Scaphojoeropsis*. Uropod: g, *Joeropsis*.

2. Body dorsal surface coarsely granular and nodulose (fig. 3.16b) ..... *Rugojoeropsis*
– Body dorsal surfaces smooth or finely granular, with or without longitudinal carinae (fig. 3.16b) ..... *Joeropsis*

Joeropsis Koehler, 1885

Diagnosis. Body with subparallel margins, one or more of pereonites 2–4 occasionally slightly wider than pereonite 1, particularly in ovigerous females; cuticle smooth. Head without dorsal ornaments. Anterior margin between antennae not depressed; pseudorostrum in lateral view with apical projection. Eyes dorsolateral on bulges. Maxillipedal palp article 2 only with distomesial lobe, not widest distally.

Intertidal–slope (0–1408 m). Cosmopolitan. 81 species (Just, 2001: rediagnosis, list of species; Kensley and Schotte, 2002: key to 22 species from Indian Ocean; Bruce, 2015: rediagnosis, key to 10 species from Great Barrier Reef).

Rugojoeropsis Just, 2001

Diagnosis. Body with subparallel margins, one or more of pereonites 2–4 occasionally slightly wider than pereonite 1, particularly in ovigerous females; cuticle roughly calcified. Head with middorsal humps. Anterior margin between antennae not depressed; pseudorostrum in lateral view without lateral projection. Eyes dorsolateral on bulges. Maxillipedal palp article 2 only with distomesial lobe, not widest distally.

Slope (400–600 m). Temperate SE Australia. 1 species (Just, 2001).

Scaphojoeropsis Just, 2001

Diagnosis. Body fusiform, tapering from pereonites 2 or 3 to posterior of pleotelson; cuticle roughly calcified. Head with anterior and dorsal ridges. Anterior margin between antennae strongly depressed relative to dorsal face of head; pseudorostrum attached to depressed anterior margin of head, nearly vertical. Eyes absent. Maxillipedal palp articles 2 and 3 widest distally, each with distomesial lobe.

Shelf, slope (124–363 m). Temperate SE Australia. 2 species (Just, 2001).

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Katianiridae Svavarsson, 1987

Figure 3.17

Katianirids can be recognised by lateral pereonal lappets, the structure of the maxillipedal palp, by the chelate structure of pereopod 1, and by the antennula being larger than the antenna (Svavarsson, 1987). There are two genera whose few species occur in cold waters in polar regions or the moderately deep sea. The maximum length is around 2.5–3.0 mm.

Diagnosis. Body broad, flat; head frontal margin projecting forward; pereonites 2–4 with lateral projections. Pleon of 1 swollen segment angled dorsally to pereon. Anus covered by pleopodal operculum. Eyes absent. Antennula basal article directed anterodorsally; much shorter than head width. Antennal scale absent. Maxillipedal palp of 4 articles, 3 and 4 little narrower than article 2. Pereopod 1 chelate between dactylus and spine; pereopods 2–7 ambulatory; pereopod 4 coxa inserting on midlateral margin; pereopodal 2–7 dactyli with 1 unguis. Uropod inserting posterolaterally, comprising single long article.

Katianira Hansen, 1916

Diagnosis. Body without dorsal bumps. Pleotelson evenly rounded laterally (fig. 3.17a). Antennula article 1 linear, without lateral robust setae (fig. 3.17c).

Shelf, slope (74–1050 m). Arctic, Temperate Northern Atlantic, Temperate Northern W Pacific, Southern Ocean. 4 species, perhaps associated with sponges (Svavarsson, 1987: key to 4 species; Shimomura and Akiyama, 2006).

Natalianira Kensley, 1984

Diagnosis. Body dorsal surface with rows of bumps. Pleotelson with rounded lateral lobes (fig. 3.17b). Antennula article 1 enlarged, with lateral robust setae (fig. 3.17d).

Slope (550–850 m). Temperate Southern Africa. 1 species (Kensley, 1984).

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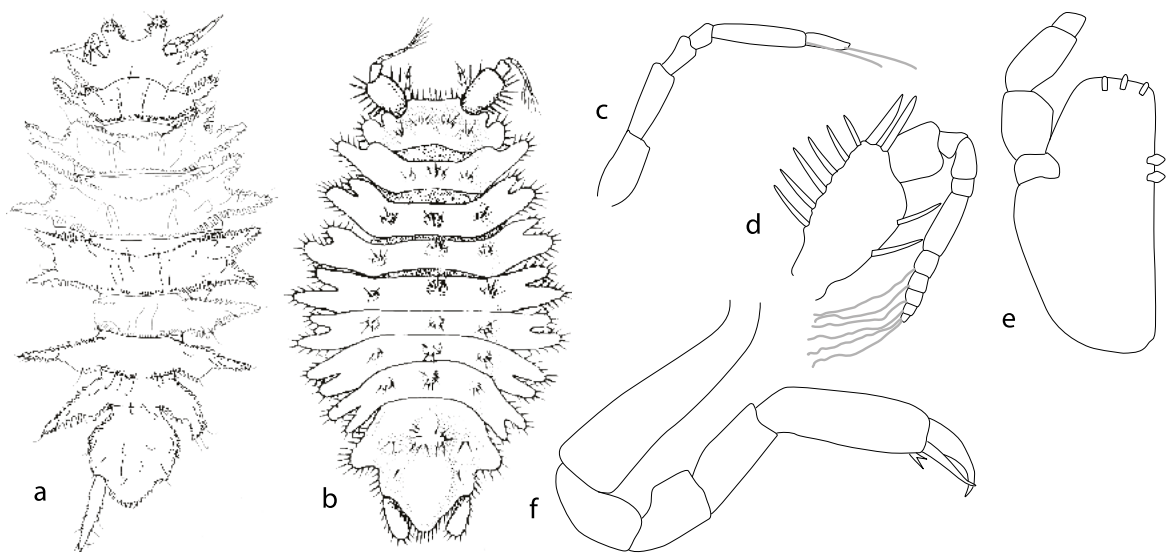


Figure 3.17. Katianiridae. Dorsal views: a, *Katianira bilobata* Gurjanova, 1930; b, *Natalianira spinosa* Kensley, 1984. Antennula: c, *Katianira*; d, *Natalianira*. Maxilliped: e, *Katianira*. Pereopod 1: f, *Katianira*.

Lepidocharontidae Galassi and Bruce *in* Galassi, Bruce, Fiasca and Dole-Olivier, 2016

Figure 3.18

Lepidocharontids include three genera of slender blind isopods from interstitial environments. While two genera are fully marine, the largest genus *Microcharon* comprises mostly species from fresh or brackish water in wells or caves, often far from the sea. Unlike other interstitial asellotes, they have large biramous uropods (Galassi et al., 2016).

Diagnosis. Body flat, slender, up to 10 times as long as wide; head without or with small rostrum; pereonites similar, rectangular, with subparallel margins. Pleon of 1 free pleonite plus pleotelson. Anus not covered by pleopodal operculum. Eyes absent. Antenna flagellum longer than peduncle; antennal scale present. Maxillipedal palp about as wide as endite. Pereopods 2–7 ambulatory, articulating dorsolaterally or laterally; pereopodal 2–7 dactyli with 2 claws. Uropod inserting ventrally, with long peduncle, with exopod articulating anteriorly and separately from endopod.

Key to genera of Lepidocharontidae

1. Pereonites 1–7 cylindrical. Pleonite 1 as wide as pereonite 7 (fig. 3.18c) ..... *Microcharon*
– Pereonites 1–7 dorsally flat, trapezoidal, except pereonite 4. Pleonite 1 narrower than pereonite 7 (fig. 3.18a, b) 2
2. Male pleopod 1 with transverse stylet-guiding grooves, unfolded; proximal posterolateral margins without scale-like elements (fig. 3.18d) ..... *Janinella*
– Male pleopod 1 with distal stylet-guiding grooves parallel to lateral margins, folded by hyaline lamella posteriorly; proximal lateral margins with scale-like elements (fig. 3.18e) ..... *Lepidocharon*

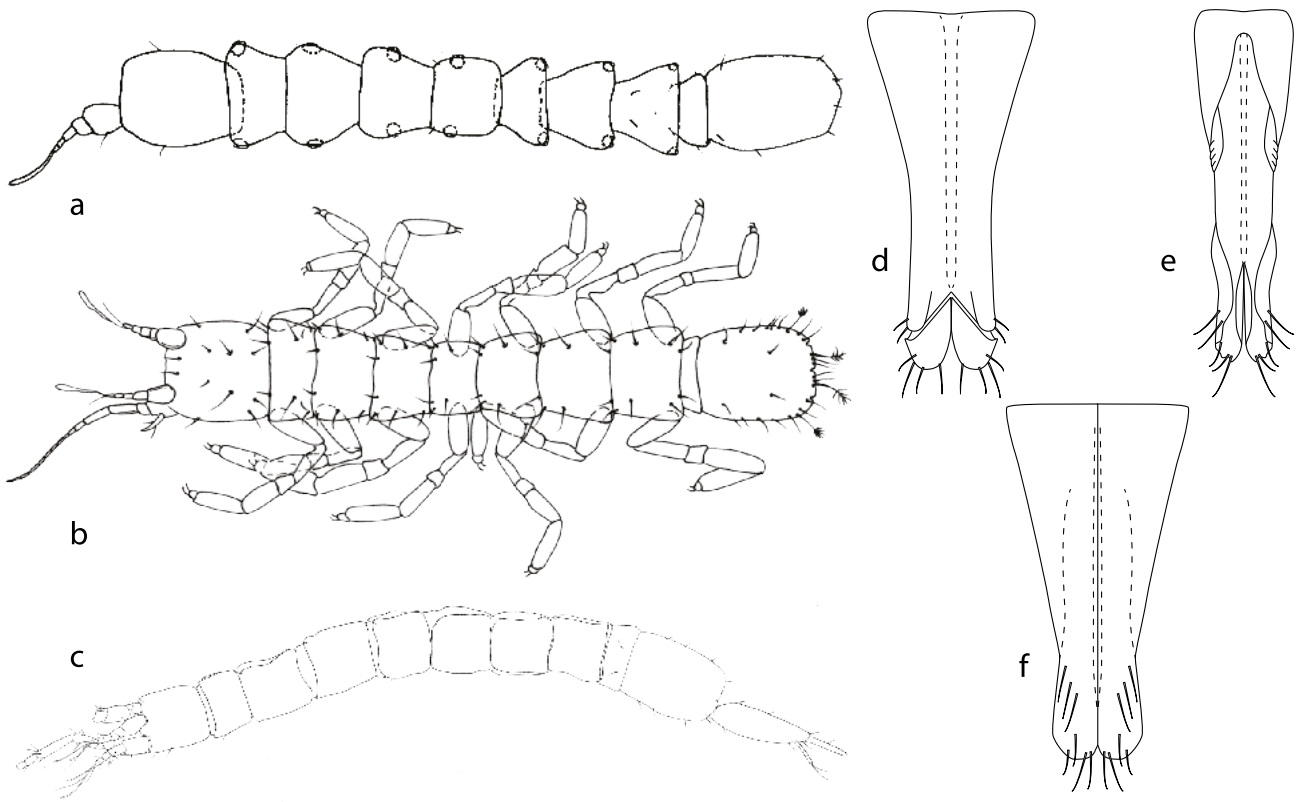


Figure 3.18. Lepidocharontidae. a, *Janinella brasiliensis* Albuquerque, Boulanouar and Coineau, 2014; b, *Lepidocharon lizardensis* Galassi and Bruce *in* Galassi, Bruce, Fiasca and Dole-Olivier, 2016; c, *Microcharon tanakai* Kim, Lee, and Karanovic, 2017. Male pleopod 1: d, *Janinella*; e, *Lepidocharon*; f, *Microcharon*.

Janinella Albuquerque, Boulanouar and Coineau, 2014

Diagnosis. Pereonites 1–7 dorsally flat, trapezoidal, except pereonite 4. Pleonite 1 narrower than pereonite 7. Male pleopod 1 with transverse stylet-guiding grooves, unfolded; proximal posterolateral margins without scale-like elements.

Intertidal, subtidal (interstitial). Tropical Atlantic (Brazil), Central Indo-Pacific (New Caledonia). 2 species (Albuquerque et al., 2014; Coineau, 1968). The genus name replaces *Paracharon* Coineau, 1970.

Lepidocharon Galassi and Bruce *in* Galassi, Bruce, Fiasca and Dole-Olivier, 2016

Diagnosis. Pereonites 1–7 dorsally flat, trapezoidal, except pereonite 4. Pleonite 1 narrower than pereonite 7. Male pleopod 1 with distal stylet-guiding grooves parallel to lateral margins, folded by hyaline lamella posteriorly; proximal lateral margins armed with scale-like elements.

Subtidal (4 m). Central Indo-Pacific (Great Barrier Reef, Australia). 2 species (Galassi et al., 2016).

Microcharon Boyko, 2024

Diagnosis. Pereonites 1–7 cylindrical. Pleonite 1 as wide as pereonite 7. Male pleopod 1 with distal stylet-guiding grooves parallel to lateral margins.

Freshwater and brackish wells, interstitial on beaches, in Europe, North Africa, Iran, New Caledonia and Caribbean. 66 species (Coineau, 1986: list of species with localities; Kim et al., 2017: rediagnosis, 1 marine species from Japan). Kensley (1984) characterised marine species of *Microcharon*. *Microcharon* Karaman, 1934 is an unavailable name (Boyko, 2024).

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Macrostylidae Hansen, 1916

Figure 3.19

Macrostylids are one of the commonest deep-water asellotes that emerge into shallower water in the Arctic and Antarctica. The only genus has many species, recognisable by the pereonites 1–3 forming a rectangular block, sometimes called a "fossosome", and the long uniramous uropods. Maximum length range 2.0–5.4 mm (Riehl and Brandt, 2013).

Diagnosis. Body slender, cylindrical; pereonites 1–3 more or less fused forming subrectangular section. Pleon of 1 segment. Anus not covered by pleopodal operculum. Eyes absent. Antennal scale absent. Mandible without palp. Maxillipedal palp articles 1–3 wider than distal articles, as wide or wider than endite. Pereopods 1–4 fossorial, with marginal robust setae; pereopod 4 coxa inserting on midlateral margin. Uropod uniramous, long.

Macrostylis G.O. Sars, 1864

Shelf–hadal (27–10730 m). Cosmopolitan in all ocean basins. 87 species (Menzies, 1962: key to 18 species; Riehl and Brandt, 2010: rediagnosis, synonymy of *Desmostylis* Brandt, 1992; Riehl and Brandt, 2013: key to 9 species from Southern Ocean; Bober et al., 2018: distributions of 86 species, key to 9 species of NW Pacific).

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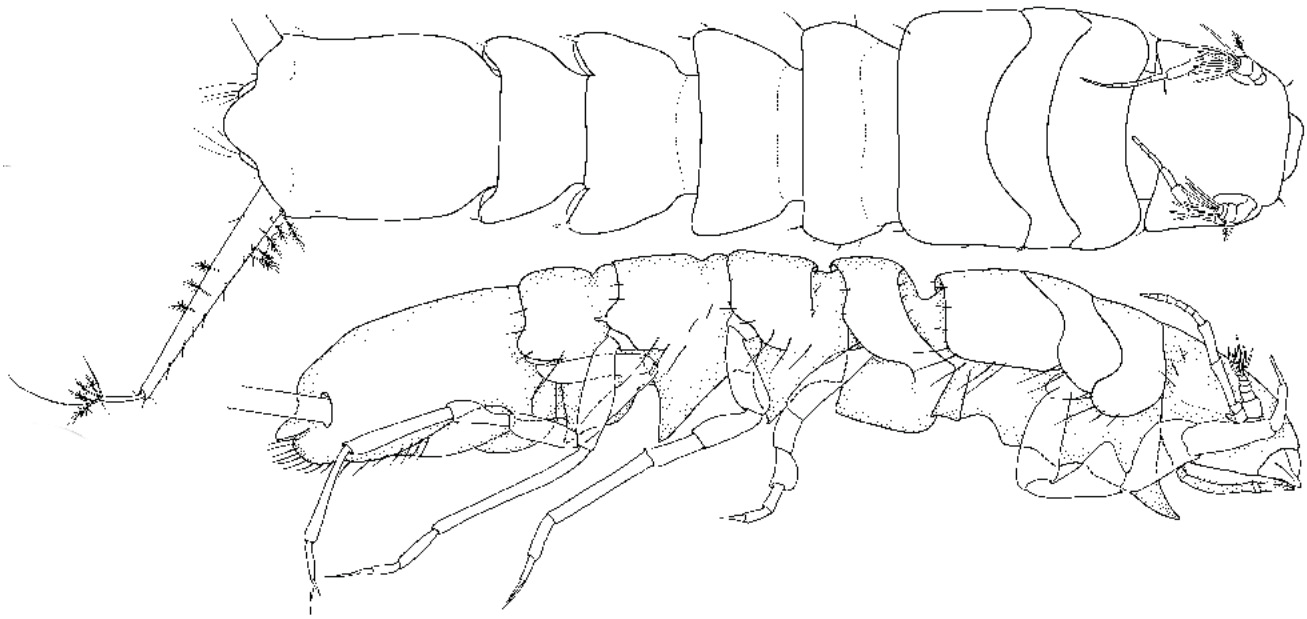


Figure 3.19. Macrostylidae, *Macrostylis scotti* Riehl and Brandt, 2013 (dorsal, lateral views).

Mesosignidae Schultz, 1969

Figure 3.20

Mesosignids are a family of highly decorated asellotes from deep oceanic basins and trenches but occur in shallower water in polar seas. The family comprised a single genus, *Mesosignum* (Menzies, 1962; Menzies and Frankenberg, 1967; Schultz, 1969) until George (2003) divided it into five genera based on the segmental pattern of lateral spines or lappets. Since then only two species have been described but neither was allocated to George's new genera (Choudhury and Brandt, 2004, 2006). Choudhury and Brandt (2004) listed all species as *Mesosignum* with distributions and depth ranges. Specimens range from 1.6 to 3.5 mm long.

Diagnosis. Body oval; pereonites 2–6 with 1 or 2 pairs of prominent lateral projections, often spinose. Pleon of 1 segment. Eyes absent. Antennula as long or longer than head width. Pereopods 1–7 ambulatory. Uropod uniramous, short.

Key to genera of Mesosignidae

1	Pleotelson without lateral spines and with spine or extension at posterolateral angles	2
–	Pleotelson with pronounced lateral spines or extensions plus spine or extension at posterolateral angles	4
2.	Pereonite 7 with prominent lateral spines or extensions (fig. 3.20b)	*Costasignum*
–	Pereonite 7 without lateral spine or extensions (fig. 3.20a, c–e)	3
3.	Head not more than twice as wide as long (fig. 3.20e)	*Mesosignum*
–	Head about 5 times as wide as long (fig. 3.20d)	*Kurilosignum*
4.	Pereonite 7 without prominent lateral extensions (fig. 3.20a)	*Bermudasignum*
–	Pereonite 7 with prominent lateral extensions (fig. 3.20c)	*Japanosignum*

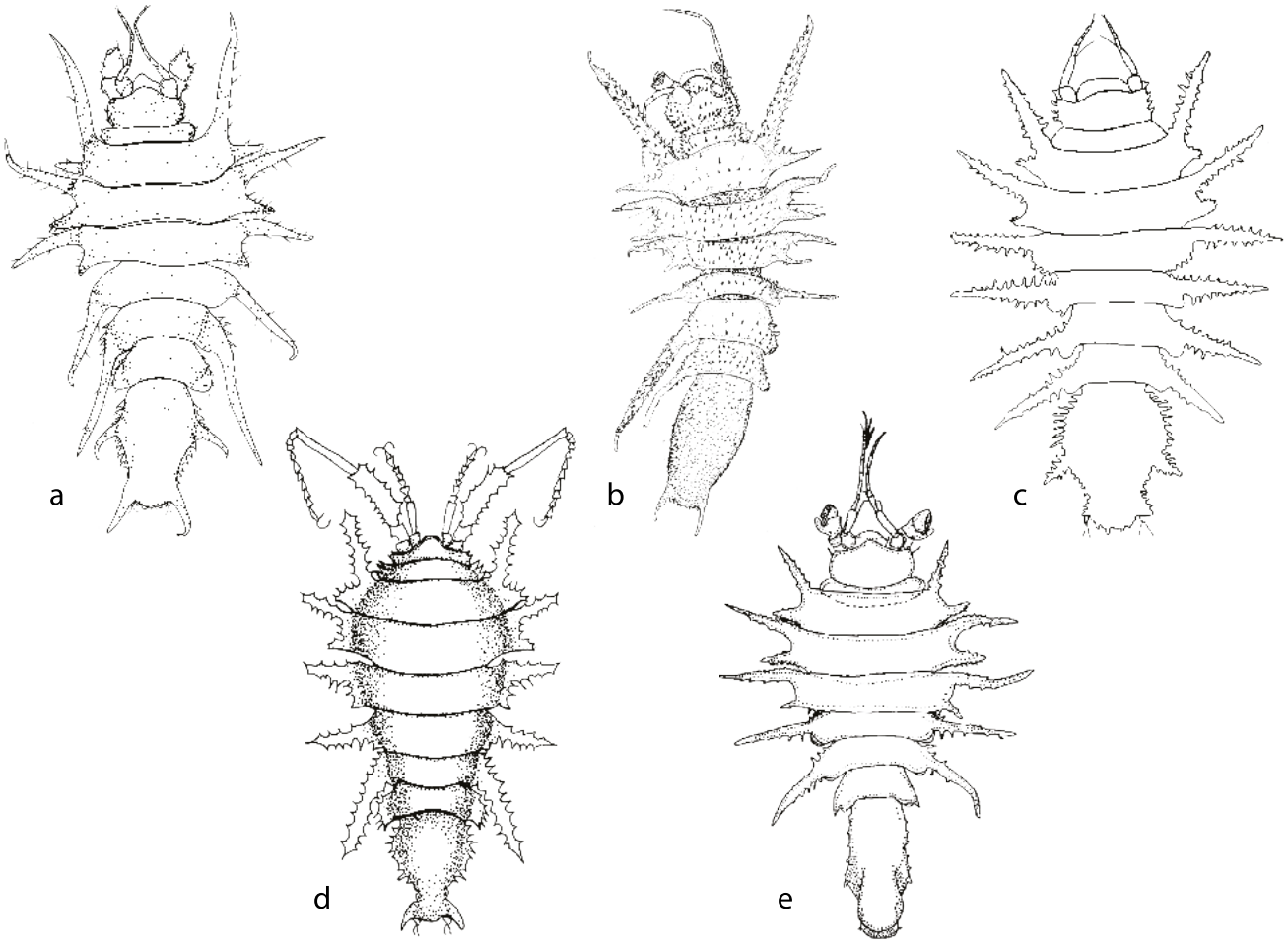


Figure 3.20. Mesosignidae. Dorsal views of type species: a, *Bermudasignum frankenbergi* George, 2003; b, *Costasignum macrum* (Menzies and Frankenberg, 1967); c, *Japanosignum elegantulum* (Birstein, 1963); d, *Kurilosignum latum* (Birstein, 1970); e, *Mesosignum kohleri* Menzies, 1962.

Bermudasignum George, 2003

Diagnosis. Head as wide as or twice as wide as long. Pereonite 7 without lateral spines or extensions. Pleotelson with pronounced lateral spine or extension plus spine or extension at posterolateral angle.

Slope–abyssal (1174–6354 m). GOODS bathyal provinces: N Atlantic, Cocos Plate, Nazca Plate. 4 species (George, 2003: diagnosis and description of type species).

Costasignum George, 2003

Diagnosis. Head as wide as or twice as wide as long. Pereonite 7 with prominent lateral spines or extensions. Pleotelson without lateral spine and with spine or extension at posterolateral angle.

Bathyal–hadal (3260–7954 m). GOODS bathyal provinces: Cocos Plate, W Pacific. 2 species (Menzies and Frankenberg, 1967: description and figure of type species; George, 2003: diagnosis).

Japanosignum George, 2003

Diagnosis. Head as wide as or twice as wide as long, with serrated lateral margin. Pereonite 7 with prominent lateral spines or extensions. Pleotelson with pronounced lateral spine or extension plus spine or extension at posterolateral angle.

Abyssal (4000–5670 m). GOODS bathyal provinces: Northern N Pacific, Antarctic, W Pacific. 3 species (Menzies and Frankenberg, 1967: description of type species; George, 2003: diagnosis)

Kurilosignum George, 2003

Diagnosis. Head about 5 times as wide as long, with convex front. Pereonite 7 without lateral spines or extensions. Pleotelson without lateral spine and with spine or extension at posterolateral angle.

Abyssal (5005–6135 m). GOODS bathyal provinces: Northern N Pacific. 1 species (Birstein, 1970: description of type species; George, 2003: diagnosis).

Mesosignum Menzies, 1962

Diagnosis. Head as wide as long. Pereonite 7 without lateral spines or extensions. Pleotelson without lateral spine and with spine or extension at posterolateral angle.

Slope–abyssal (1530–4925 m). GOODS bathyal provinces: Nazca Plate, Antarctic, Subantarctic. 7 species (Menzies and Frankenberg, 1967: diagnosis of genus s.l.; key to 11 species).

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Microparasellidae Karaman, 1934

Galassi et al. (2016) restricted Microparasellidae to a single genus of four tiny (< 2 mm long) interstitial species distinguished from similar families by the prominent acute or narrowly rounded rostrum and the unique uniramous and short uropods. All species are from freshwater caves and wells (Argano and Pesce, 1979).

Diagnosis. Body flat, slender, almost parallel-sided; head with rostrum; pereonites similar, margins with scales. Pleon of 1 free pleonite plus pleotelson. Anus not covered by pleopodal operculum. Eyes absent. Antenna flagellum shorter than peduncle; antennal scale absent. Maxillipedal palp about as wide as endite. Pereopods 2–7 ambulatory, articulating ventrally; pereopodal 2–7 dactlyi with 2 claws. Uropod uniramous, short.

Microparasellus Karaman, 1934

Freshwater wells and caves. Europe, Mediterranean coasts. 4 species (Coineau, 1986: list of species with distributions).

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Mictosomatidae Wolff, 1965

Figure 3.21

The tiny specimen of the only species of Mictosomatidae has been taken only once, on the slope south of Iceland. The narrow anterior "stalk" on pereonite 5 is diagnostic. Hansen's (1916) genus name *Schistosoma* was replaced by *Mictosoma* by Wolff (1965).

Diagnosis. Body slender, cylindrical; head frontal margin projecting forward; pereonites 1–4 with anterolateral projections; pereonite 5 narrowed anteriorly as short stalk. Pleon of 1 free pleonite plus pleotelson. Anus covered by pleopodal operculum. Eyes absent. Maxillipedal palp article 3 half as wide as article 2. Pereopods 2–7 ambulatory; pereopod 4 coxa inserting on midlateral margin; pereopodal 2–7 dactyli with 1 unguis. Uropod inserting posterolaterally, uniramous, rodlike. Maximum length 1.4 mm.

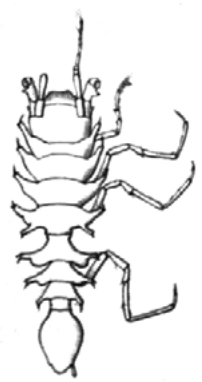


Figure 3.21. Mictosomatidae, *Mictosoma ramosum* (Hansen, 1916).

Mictosoma Wolff, 1965

Slope (1900 m). Temperate Northern Atlantic. 1 species (Hansen, 1916: description and figure of only species as *Schistosoma ramosum* Hansen, 1916; Wolff, 1965: family and genus names).

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Munnidae G.O. Sars, 1897

Figures 3.22, 3.23

Munnids are tiny asellotes, around 2 mm long, recognised by the pear-shaped pleotelson and the long spindly legs. Some genera are common inhabitants of shallow reefs and algal beds in temperate and polar waters, but others occur at much greater depths.

Diagnosis. Body subpyriform; head with prominent lateral processes. Pleon of 1 free pleonite plus pear-shaped pleotelson. Anus not covered by pleopodal operculum. Eyes on lateral process (if present). Maxillipedal palp articles 1–3 wider than distal articles. Pereopod 1 prehensile, subchelate or carpochelate in male; pereopods 2–7 ambulatory. Uropod absent or minute, without peduncle.

Key to genera of Munnidae

1. Front with pair of horns. Coxal plates not visible dorsally on pereonites 2–7, obscured by lateral pereonal spikes (fig. 3.22a–c) 2
– Front rounded or truncate. Coxal plates visible dorsally on pereonites 2–7 (fig. 3.22d–f) 3
2. Eyes present (fig. 3.22a, c). Pereopod 1 of male carpochelate, carpus produced distally (fig. 3.23a). Antennular flagellum last article elongate, with 1 aesthetasc ..... *Astrurus*
– Eyes absent (fig. 3.22c). Pereopod 1 of male subchelate, carpus not produced distally. Antennular flagellum last article minute, penultimate article, both with 1 aesthetasc (fig. 3.23e) ..... *Echinomunna*
3. Body with numerous dorsal setae and often with articulating robust setae on head, pleon, pleopods 1 and 2 (fig. 3.22d). Antennular flagellum last article minute, last and penultimate article both with 1 aesthetasc (fig. 3.23e) ..... *Munna*
– Body smooth, with few setae, without articulating robust setae (fig. 3.22e–g). Antennular flagellum last article elongate, with 1 aesthetasc, or of 6 articles (fig. 3.23f, g) 4
4. Eyes absent (fig. 3.22g). Antennular flagellum of 6 articles (fig. 3.23g). Mandibular palp reaching beyond incisor (fig. 3.23j) ..... *Zoromunna*
– Eyes present (fig. 3.22e, f). Antennular flagellum last article last article elongate, with 1 aesthetasc (fig. 3.23f). Mandibular palp not reaching incisor (fig. 3.23h) 5
5. Pereopod 1 of male short, robust; carpus triangular; propodus oval, bearing strong distal horn-like process; palm with row of many sharp teeth; dactylus long, slender, pointed (fig. 3.23c). Mandibular molar elongate, with several small teeth in distal half (fig. 3.23i) ..... *Salvatiella*
– Pereopod 1 not sexually dimorphic, symmetrical, small (fig. 3.23d). Mandibular molar strong, subcylindrical, truncate ..... *Uromunna*

Astrurus Beddard, 1886

Diagnosis. Body with dorsal scattered or clustered robust setae; coxal plates not visible dorsally, obscured by lateral spikes on pereonites 1–7; front with pair of horns; eyes present. Antennular flagellum last article elongate, with 1 aesthetasc. Mandibular molar subcylindrical; palp reaching beyond incisor. Pereopod 1 of male carpochelate; carpus produced distally.

Shelf, slope (141–385 m). Southern Ocean (Kergulen I., Davis Strait). 2 species (Beddard, 1886; Vanhöffen, 1914). The two species differ remarkably.

Echinomunna Vanhöffen, 1914

Diagnosis. Pereonites 1–6 with transverse rows of long spines; all pereonites, pleotelson with lateral spines; coxal plates not

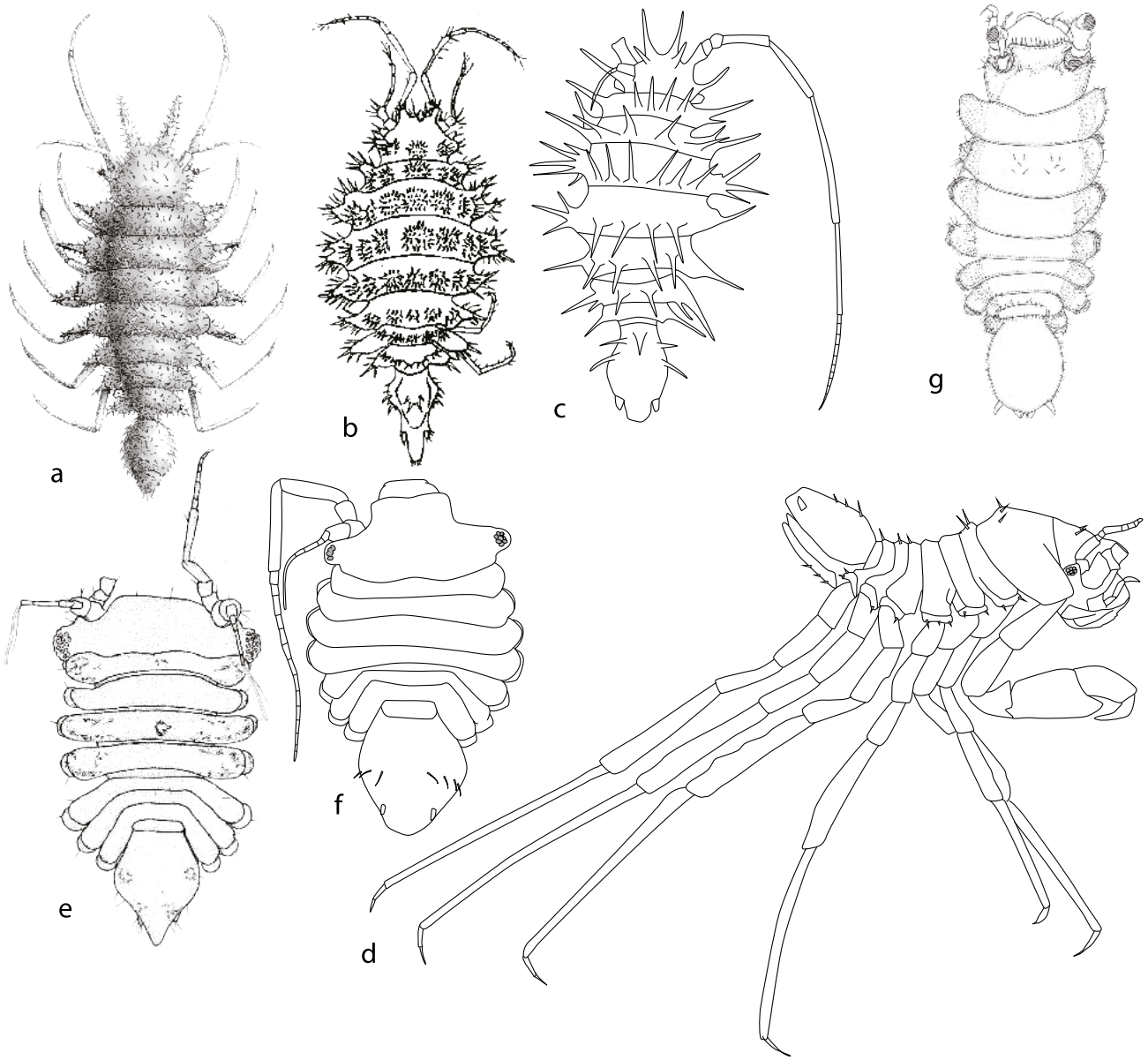


Figure 3.22. Munnidae. a, *Astrurus crucicauda* Beddard, 1886; b, *Astrurus ornatus* Vanhöffen, 1914; c, *Echinomunna horrida* Vanhöffen, 1914; d, *Munna spicata* Teodorczyk and Wägele, 1994; e, *Salvatiella polynesica* Müller, 1990; f, *Uromunna humei* Poore, 1984; g, *Zoromunna setifrons* Menzies and George, 1972.

visible dorsally, obscured by lateral spikes on pereonites 1–7; front with pair of horns; eyes absent. Antennular flagellum last article minute, penultimate article, both with 1 aesthetasc. Mandibular molar subcylindrical; palp reaching beyond incisor. Pereopod 1 subchelate, carpus not produced.

Slope (385 m). Southern Ocean. 2 species (Kensley, 1976; Vanhöffen, 1914).

Munna Krøyer, 1839

Diagnosis. Body with numerous dorsal setae and often with articulating robust setae on head, pleon, pleopods 1 and 2; coxal plates visible dorsally on pereonites 2–7; front rounded; eyes present. Antennular flagellum last article minute, penultimate article, both with 1 aesthetasc. Mandibular molar strong, subcylindrical, truncate, with accessory seta; palp reaching beyond incisor. Pereopod 1 sexually dimorphic; of male usually enlarged, sometimes massive, sometimes carpochelate, or subchelate, carpus not produced. Pereopod 2 not or barely sexually dimorphic.

Intertidal, subtidal. Arctic, Temperate Northern Atlantic, Temperate Northern Pacific, Temperate Northern W Pacific, Western Indo-Pacific, Temperate South America, Temperate Southern Africa, Temperate Australasia, Southern Ocean. 80

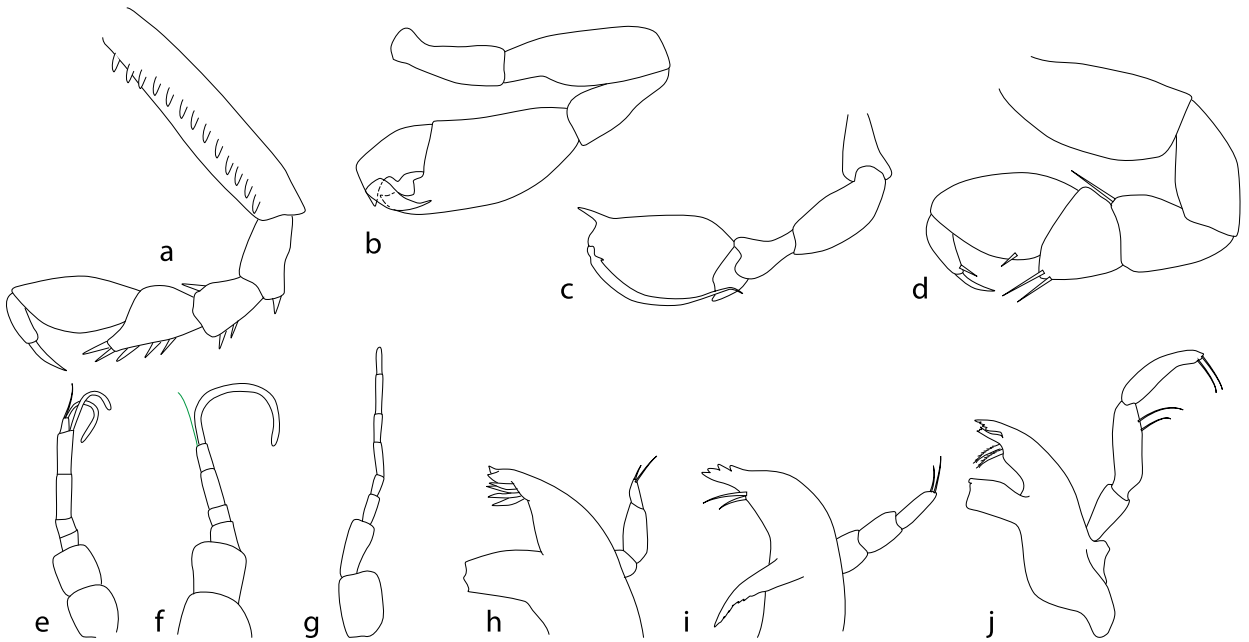


Figure 3.23. Munnidae. Male pereopod 1: a, *Astrurus*; b, *Munna*; c, *Salvatiella*; d, *Uromunna*. Antennula: e, *Munna*; f, *Uromunna*; g, *Zoromunna*. Mandible: h, *Uromunna*; i, *Salvatiella*; j, *Zoromunna*.

species (Kussakin, 1962: key to 63 species [in Russian]; Kussakin, 1972: notes on 9 species; Poore, 1984: rediagnosis, list of species, key to 2 Australian species; Teodorczyk and Wägele, 1994: key to 33 Antarctic and subantarctic species, descriptions of several species, discussion of genus).

Salvatiella Müller, 1990

Diagnosis. Body smooth, with few setae, without articulating robust setae; coxal plates visible dorsally on pereonites 2–7; front rounded; eyes present. Antennular flagellum last article elongate, with 1 aesthetasc. Mandibular molar elongate, with several small teeth in distal half; palp not exceeding incisor. Pereopod 1 of male short, robust; carpus triangular; propodus oval, bearing strong distal horn-like process; palm with row of many sharp teeth; dactylus long, slender, pointed.

Subtidal (dead coral, sponges). Western Indo-Pacific (French Polynesia, Easter I.) 2 species (Kensley, 2003; Müller, 1990).

Uromunna Menzies, 1962

Diagnosis. Body smooth, with few setae, without articulating robust setae; coxal plates visible dorsally on pereonites 2–7; front rounded; eyes present. Antennular flagellum last article elongate, with 1 aesthetasc. Mandibular molar strong, subcylindrical, truncate, without accessory seta; palp not exceeding incisor. Pereopod 1 not sexually dimorphic, symmetrical, small. Pereopod 2 sexually dimorphic; carpus and propodus of male broadened.

Intertidal, subtidal. Tropical Atlantic, Temperate Northern Pacific, Western Indo-Pacific, Temperate South America, Temperate Southern Africa, Temperate Australasia. 29 species (Poore, 1984: rediagnosis, list of species, key to 3 Australian species).

Zoromunna Menzies and George, 1972

Diagnosis. Body smooth, with few setae, without articulating robust setae; coxal plates visible dorsally on pereonites 2–7; front truncate, with row of short setae; eyes absent. Antennular flagellum of 6 articles. Mandibular molar subcylindrical; palp reaching beyond incisor.

Abyssal (5986–6134 m). GOODS bathyal provinces: Nazca Plate (Peru-Chile Trench). 1 species (Menzies and George, 1972).

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Munnopsidae Lilljeborg, 1864

Figures 3.24–3.32

Munnopsidae (or less frequently Munnopsididae) are a diverse group of asellote isopods important in the deep sea (Wilson and Hessler, 1987). Munnopsidae is the largest family of Asellota but many species remain undescribed (e.g. Malyutina and Brandt, 2015, 2018). Munnopsids live digging below the seafloor surface (e.g. *Ilyarachna*), epibenthic on the seafloor (e.g., *Munnopsurus*, *Vanhoeffenura*), holopelagic in the water column (e.g. *Acanthamunnopsis*, *Paramunnopsis* and some species of *Munneurycope*), or benthopelagic both on the seafloor and in the water column (e.g. *Munnopsoides*, *Paropsurus*, *Rectisura*) (Hessler and Strömberg, 1989; Jamieson et al., 2012; Osborn, 2009). Munnopsids may be benthic scavengers or predators on foraminiferans (Gudmundsson et al., 2000; Svavarsson et al., 1993). This ecological diversity is reflected in high levels of morphological variation. They have in common, unlike other asellotes, paddle-like posterior pereopods specialised for swimming, but a small number of genera are not modified in this way. Few are associated with hydrothermal vents (Malyutina and Golovan, 2022). The maximum size of munnopsids varies; many species are typically a few millimetres (3–10 mm) long but *Eurycope magna* Birstein, 1963 reaches 40 mm long.

The taxonomy of Munnopsidae was established by Kussakin (2003) in a large work in Russian. His substantial revision and key to subfamilies, genera and species concentrated on the Northern Hemisphere fauna. Relationships between the many genera and subfamilies was attempted using morphological characters (Merrin, 2007) but her suggestion that the family could be divided into smaller families has not been followed. A hypothetical tree of the Munnopsidae compiled from previous phylogenetic analyses and suggested relationships based on morphological similarity was summarised by Osborn (2009). Munnopsidae are certainly monophyletic on morphological and molecular grounds (Osborn, 2009). Her finding that not all subfamilies are monophyletic and not all genera can be placed confidently corroborated earlier opinions (Kussakin, 2003; Malyutina and Brandt, 2007).

This family diagnosis is abbreviated from earlier diagnoses (Kussakin, 2003; Wilson et al., 1989; Wolff, 1962). Nine subfamilies are recognised, but four genera appear not to fall into any of them. Keys are provided for subfamilies with more than two genera.

Diagnosis. Body oval; pereonites 1–4 (ambulosome) differentiated from pereonites 5–7 and pleon (collectively natasome). Pleon more or less semicircular, without free pleonites. Eyes absent. Maxillipedal palp articles 1–3 wider than distal articles. Pereopods 5, 6, sometimes 7, usually oar-shaped, carpus and propodus expanded, with margins bearing long plumose setae.

Key to subfamilies and unaligned genera of Munnopsidae

1.	Rostrum present (fig. 3.24d–k)	Eurycopinae
–	Rostrum absent	2
2.	Pereopods 5–7 without dactyli (fig. 3.31i, m). Uropod terminal or slightly ventral, uniramous (fig. 3.27)	Munnopsinae
–	Pereopods 5–7 with dactyli (rarely rudimentary on pereopod 5) (fig. 3.31b, d, e, k, l). Uropod ventral, uniramous or biramous	3
3.	Body smooth or setose dorsally and laterally, without spines	4
–	Body with strong dorsal and lateral spines	12
4.	Head hidden dorsally by anterior flange of pereonite 1 (fig. 3.29c, d)	*Microcope*
–	Head visible dorsally	5
5.	Mandible short, thick, with blunt incisor, with reduced molar process (fig. 3.30l, n). Head usually wider than anterior pereonites. Pereopods 3, 4 bases much shorter than pereopod 2 basis (figs 3.24a–d, 3.25)	Ilyarachninae

– Mandible typical, rarely reduced. Head usually about as wide as already anterior pereonites. Pereopods 3, 4 bases elongate, rarely slightly shorter than pereopod 2 basis 6

6. Antennula inserted on anterior margin; article 1 cylindrical, shorter than article 2. Pleotelson elongate, 1.3 or more times as long as wide (fig. 3.28n–q). Pereopods 5–7 natatory, but with narrow carpi- and propodi; dactyli strong, long, more than half as long as propodi, with apical setae and 1 or 2 claws (fig. 3.31t) ..... Syneurycopinae

– Antennula dorsal; article 1 wide, much larger than article 2. Pleotelson swollen or typical, less than 1.5 times as long as wide. Pereopods 5, 6 and usually 7 natatory, with broad carpi and propodi; dactyli small, less than half as long as propodi, without apical setae and claws 7

7. Pereonites 5–7 and pleotelson large, swollen, as high as wide. Antennulae inserted between antennae. Pereopod 1 slender, basis 3 times as long as those of pereopods 2–4 ..... Bathyopsurinae

– Pereonites 5–7 and pleotelson more or less flattened, not as high as wide. Antennulae inserted above/behind antennae. Pereopods 1–4 bases of similar lengths; first not especially elongate 8

8. Pereonite 7 strongly reduced, much shorter than more anterior natasome pereonites, or absent. Pereopod 7 simple walking leg or absent (fig. 3.26e–l) ..... Lipomerinae

– Pereonite 7 shorter or longer than more anterior natasome pereonites. Pereopod 7 natatory 9

9. Mandibular molar strong, rounded, with 1 or 2 bundles of small setae (fig. 3.30m) ..... *Munnopsurus*

– Mandibular molar cylindrical, truncate 10

10. Pleotelson more or less triangular, strongly tapering posteriorly (fig. 3.24c). Uropod peduncle strong, not cylindrical, tapering; biramous, rami attached laterally (fig. 3.32a) ..... Betamorphinae

– Pleotelson posterior margin rounded or truncate. Uropod peduncle cylindrical, biramous, rami attached distally 11

11. Pleotelson posterior margin rounded. Pereopod 1 basis little longer than bases of pereopods 2–4 (fig. 3.29e, f) ..... *Munneurycope*

– Pleotelson posterior margin truncate with medial notch including anus and uropods. Pereopod 1 basis twice as long as bases of pereopods 2–4 (fig. 3.29a, b) ..... *Gurjanopsis*

12. Pereopods 5–7 bases shorter than pereopod 4 basis (fig. 3.24a, b). Uropod usually uniramous, rarely with rudimentary exopod ..... Acanthocopinae ... *Acanthocope*

– Pereopods 5–7 bases of similar lengths. Uropod biramous (fig. 3.28a–m) ..... Storthyngurinae

Subfamily Acanthocopinae Wolff, 1962

The subfamily was introduced by Wolff (1962) and its only genus reviewed by Malyutina et al. (2018).

Diagnosis. Body with natasome differentiated, with strong dorsal and lateral spines; rostrum absent. Pereonites 5–7 dorsally fused; pleotelson suboval, fused to all natasome segments, with 2 pairs of lateral and 1 long terminal spine. Antennulae dorsal; article 1 wide, much larger than article 2. Pereopods 3, 4 bases elongate, about as long as pereopod 2 basis; pereopods 5–7 natatory, with broad carpi and propodi; bases shorter than pereopod 4 basis; dactyli small, less than half as long as propodi, without apical setae and claws. Uropod ventral, usually uniramous, rarely with rudimentary exopod (fig. 3.24a, b).

Acanthocope Beddard, 1885

Bathyal, abyssal (2149–5778 m). GOODS bathyal provinces: Northern N Atlantic, Northern N Pacific, N Atlantic, SE Pacific Ridges, Cocos Plate, Nazca Plate, Antarctic, Indian, W Pacific, S Atlantic (almost cosmopolitan). 18 species (Malyutina et al., 2018: rediagnosis, key to species, distributions).

Subfamily Bathyopsurinae Wolff, 1962

The subfamily was introduced by Wolff (1962).

Diagnosis. Body with enlarged natasome, 3 times as long as anterior segments; rostrum absent. Pereonites 5–7 with complete dorsal articulation; pleotelson huge. Antennulae dorsal, inserted between antennae; article 1 broad. Mandibular molar absent or vestigial. Pereopods 2–4 bases similar; pereopod 1 slender, basis 3 times as long as more posterior pereopods; pereopods 5, 6 natatory, with broad carpi and propodi; pereopod 7 smaller than 5 and 6. Uropod ventrolateral, minute, biramous, or absent.

Bathyopsurus Nordenstam, 1955

Diagnosis. Maxilliped palp article 3 with mesial margin as long as lateral margin; article 4 elongate, much narrower than article 3; epipod short, rounded (fig. 3.32p). Pereopod 7 basis less than half as long and wide as pereopods 5, 6 bases.

Abyssal, hadal (4400–7900 m). GOODS bathyal provinces: N Atlantic, New Zealand Kermadec. 3 species (Nordenstam, 1955; Wolff, 1962: rediagnosis, key to 2 species; Brandt et al., 2025).

Paropsurus Wolff, 1962

Diagnosis. Maxilliped palp article 3 with mesial margin longer than lateral margin; article 4 oval or triangular, at least half as wide as article 3; epipod diamond-shaped (fig. 3.32q). Pereopod 7 basis almost as long and wide as pereopods 5, 6 bases.

Bathyal, abyssal (1957–3570 m). GOODS bathyal provinces: Cocos Plate, W Pacific. 2 species (Wolff, 1962: rediagnosis, key to 2 species).

Subfamily Betamorphinae Kussakin, 2003

Wilson and Thistle (1985) reviewed the subfamily.

Diagnosis. Body smooth or setose dorsally and laterally, without spines; natasome segments free; head narrower than anterior pereonites; rostrum absent. Pereonites 5–7 with complete dorsal articulation; pleotelson less than 1.5 times as long as wide. Antennulae dorsal; article 1 wide, much larger than article 2. Pereopods 3, 4 bases elongate, about as long as pereopod 2 basis; pereopods 5–7 natatory, with broad carpi and propodi; dactyli small, less than half as long as propodi, without apical setae and claws. Uropod ventral, strong, not cylindrical, tapering; biramous, rami attached proximolaterally (fig. 3.24c).

Amuletta Wilson and Thistle, 1985

Diagnosis. Mandibular palp absent (fig. 3.30f). Uropod peduncle with distomesial lobe, with 2 subdistal similar rami (fig. 3.32a).

Bathyal, abyssal (2397–4829 m). GOODS bathyal provinces: Northern N Atlantic. 1 species (Wilson and Thistle, 1985).

Betamorpha Hessler and Thistle, 1975

Diagnosis. Mandibular palp present (fig. 3.30i). Uropod peduncle narrow, with 2 proximal rami, endopod longer than exopod (fig. 3.32e).

Slope–hadal (587–8400 m). GOODS bathyal provinces: Northern N Pacific, N Atlantic, S Atlantic. 10 species (Hessler and Thistle, 1975; Thistle and Hessler, 1977: rediagnosis, key to 7 species).

Subfamily Eurycopinae Hansen, 1916

Eurycope, type genus of Eurycopinae (formerly Eurycopidae) was reviewed by several authors including Wilson and Hessler (1980, 1981), who erected three new genera, and Malyutina and Brandt (2006), who erected another. Malyutina and Brandt (2006) compared in a table and by illustration features of six genera and groups of *Eurycope*. This subfamily diagnosis and key are based on their table and key to six genera.

Diagnosis. Body smooth or setose dorsally and laterally, without spines; rostrum present. Pereonites 5–7 free or fused dorsally; pleotelson less than 1.5 times as long as wide. Antennulae dorsal; article 1 wide, much larger than article 2. Mandibular palp 3-articulate, article 3 twisted. Pereopods 3, 4 bases elongate, about as long as pereopod 2 basis; pereopods 5–7 natatory, with broad carpi and propodi; dactyli small, less than half as long as propodi, without apical setae and claws. Uropod ventral, biramous, with short peduncle, exopod usually shorter than endopod (fig. 3.24d–k).

Key to the genera of Eurycopinae

1. Pereopod 2 ischium longer than basis (fig. 3.31j) ..... *Pirinectes*
– Pereopod 2 ischium shorter than basis 2
2. Pleotelson posterior margin with outer rim projecting dorsally and ventrally. Uropod peduncle bent at midlength, both margins angled (fig. 3.32u). Cuticle strongly calcified, mat. Body highest at head ..... *Dubinectes*
– Pleotelson posterior margin simple, projecting ventrally only. Uropod peduncle with straight lateral margin (fig. 3.32d, g, h). Cuticle thin, glossy. Body highest at natasome 3
3. Pereonites 5 and 6 with complete dorsal articulation (fig. 3.24d, e). Antennula article 1 with produced distomesial lobe (fig. 3.30a) 4
– Pereonites 5 and 6 without complete dorsal articulation (fig. 3.24f–k). Antennula article 1 with reduced distomesial lobe (fig. 3.30b, c) 5

4. Male pleopod 2 stylet reflexed, overreaching distal margin of endopod (fig. 3.32s) ..... *Eurycope*

– Male pleopod 2 stylet barely emerging from endopod margin (fig. 3.32t) ..... *Munnicope*

5. Pereonite 6 dorsally fused with pereonite 7. Rostrum without distinct margins (fig. 3.24f, g). Mandibular molar thick, condyle longer than molar (fig. 3.30h). Maxilliped epipod truncate (fig. 3.32o) ..... *Baeonectes*

– Pereonite 7 separated from pereonite 6 by dorsal suture. Rostrum with lateral margins (fig. 3.24h–k). Mandibular molar narrow, condyle shorter than molar. Maxilliped epipod elongate, with acute tip (fig. 3.30p) 6

6. Pereonite 7 much shorter than pereonite 6. Pereonites 5–7 compressed dorsally. Pereonite 6 bulging ventrally (fig. 3.24j, k) ..... *Tytthocope*

– Pereonite 7 subequal to pereonite 6 in lateral length. Pereonites 5–7 convex dorsally. Pereonite 5 bulging ventrally 7

7. Body broad (fig. 3.24i). Pereonite 5 bulging anteroventrally. Uropodal exopod as long as or longer than endopod (fig. 3.32g) ..... *Disconectes*

– Body elongate (fig. 3.24h). Pereonite 5 bulging posteroventrally. Uropod exopod much smaller than endopod (fig. 3.32d) ..... *Belonectes*

Baeonectes Wilson, 1982

Diagnosis. Body broad, highest at natasome; cuticle thin, glossy; rostrum without distinct margins. Pereonites 5–7 convex dorsally, not bulging ventrally; 5–7 dorsally fused. Antennular article 1 without mesial spine, distolateral lobe subrectangular, distally truncate. Mandibular molar thick, condyle longer than molar. Maxilliped epipod truncate, broad. Pereopod 2 ischium shorter than basis. Uropod peduncle with straight lateral margin.

Shelf, slope (9–787 m). Temperate Northern Atlantic, Temperate Northern Pacific. 7 species (Wilson, 1982b; Malyutina and Golovan, 2010: rediagnosis, species list; Malyutina et al., 2013).

Belonectes Wilson and Hessler, 1981

Diagnosis. Body elongate, highest at natasome; cuticle thin, glossy; rostrum with lateral margins. Pereonites 5–7 convex dorsally; pereonite 5 bulging posteroventrally; pereonite 7 lateral length as long as pereonite 6; 5, 6 without complete dorsal articulation; pereonite 7 separated by dorsal suture from pereonite 6. Antennular article 1 without mesial spine, distolateral lobe subrectangular, distally truncate. Mandibular molar narrow, condyle shorter than molar. Maxilliped epipod narrow, with acute tip. Pereopod 2 ischium shorter than basis. Uropod peduncle with straight lateral margin; exopod much smaller than endopod.

Slope–abyssal (1227–4382 m). GOODS bathyal provinces: Northern N Atlantic, Antarctic, W Pacific. 5 species (Wilson and Hessler, 1981; Malyutina and Brandt, 2009: rediagnosis, key to species).

Disconectes Wilson and Hessler, 1981

Diagnosis. Body broad, highest at natasome; cuticle thin, glossy; rostrum with lateral margins. Pereonites 5–7 convex dorsally; pereonite 5 bulging anteroventrally; pereonite 7 lateral length as long as pereonite 6; 5, 6 without complete dorsal articulation; pereonite 7 separated by dorsal suture from pereonite 6. Antennular article 1 without mesial spine, distolateral lobe subrectangular, distally truncate. Mandibular molar narrow, condyle shorter than molar. Maxilliped epipod narrow, with acute tip. Pereopod 2 ischium shorter than basis. Uropod peduncle with straight lateral margin; exopod as long or longer than endopod.

Shelf–hadal (15–7934 m). Temperate Northern Atlantic. GOODS bathyal provinces: Northern N Atlantic, Northern N Pacific, New Zealand/Kermadec, Nazca Plate, Antarctic, S Atlantic. 13 species (Wilson and Hessler, 1981: species list).

Dubinectes Malyutina and Brandt, 2006

Diagnosis. Body highest at head; cuticle strongly calcified, mat; rostrum long, robust. Pereonites 5–7 with complete dorsal articulation; pleotelson posterior margin with outer rim projecting dorsally and ventrally. Antennular article 1 triangular. Mandibular molar thick, condyle longer than molar. Maxilliped epipod truncate, broad. Pereopod 2 ischium shorter than basis. Uropod peduncle bent at midlength, both margins angled.

Slope–abyssal (1121–4960 m). GOODS bathyal provinces: Antarctic, S Atlantic. 5 species (Malyutina and Brandt, 2006: tabulation of generic characters).

Eurycope G.O. Sars, 1864

Diagnosis. Body broad, highest at natasome; cuticle thin, glossy; rostrum with lateral margins. Pereonites 5–7 convex dorsally, not bulging ventrally; 5–7 with complete dorsal articulation. Antennular article 1 with produced distomesial lobe. Mandibular molar thick, condyle longer than molar. Maxilliped epipod produced distally, laterally convex. Pereopod 2 ischium shorter than basis. Male pleopod 2 stylet reflexed, overreaching distal margin of endopod. Uropod peduncle with straight lateral margin.

Shelf–hadal (46–7230 m). Cosmopolitan. 53 species (Wilson and Hessler, 1981: list of species; Wilson, 1982a: rediagnosis, revison of *E. complanata* species complex)

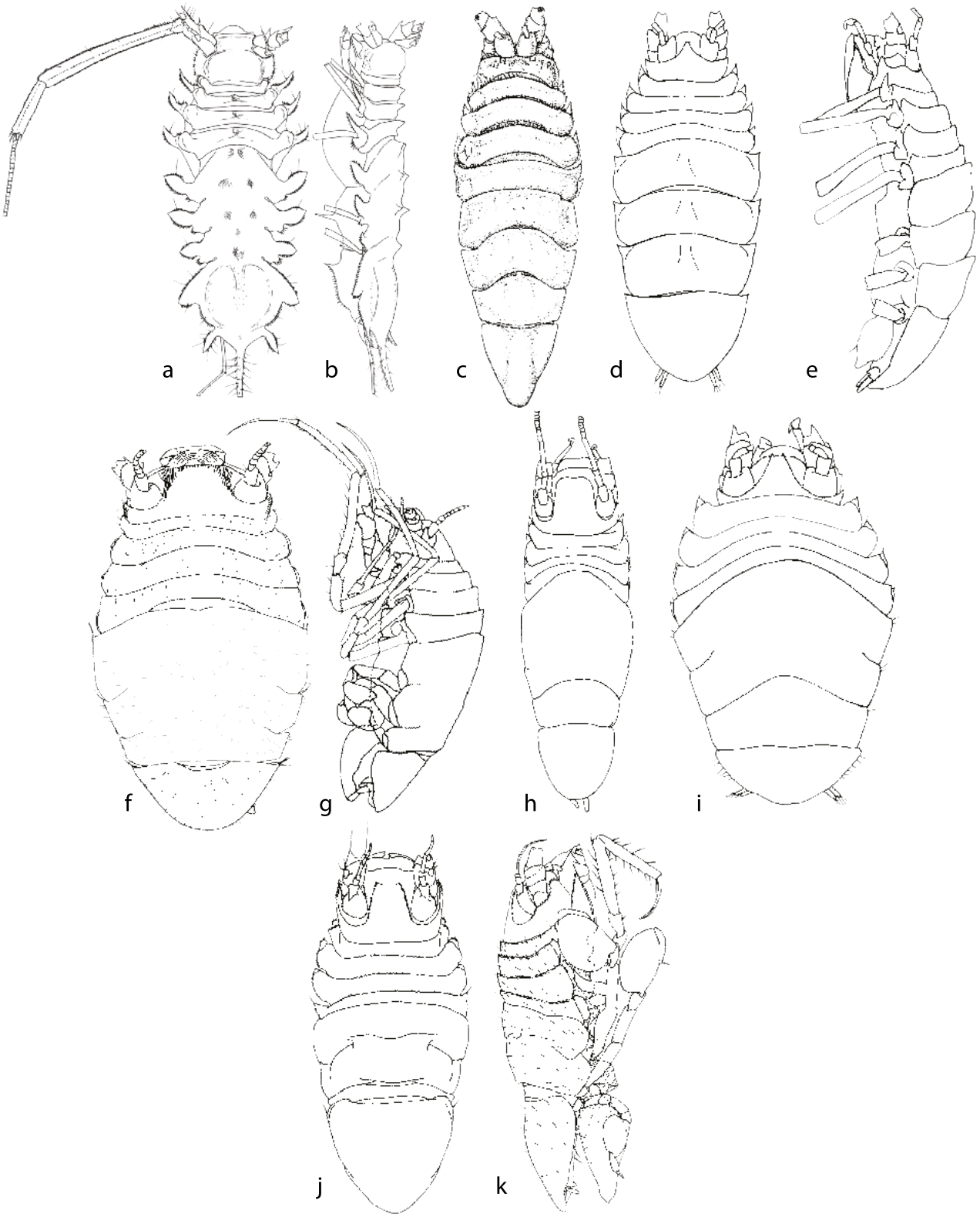


Figure 3.24. Munnopsidae. Dorsal and lateral views. Acanthocopinae: a, b, *Acanthocope puertoricana* Malyutina, Frutos and Brandt, 2018. Betamorphinae: c, *Amuletta abyssorum* (Richardson, 1911). Eurycopinae: d, e, *Eurycope cornuta* G.O Sars, 1864; f, g, *Baeonectes improvisus* Wilson, 1982; h, *Belonectes* sp.; i, *Disconectes* sp.; j, k, *Tytthocope megalura* (G.O. Sars, 1872).

Munnicope Menzies and George, 1972

Diagnosis. Body broad, highest at natasome; cuticle thin, glossy; rostrum with lateral margins. Pereonites 5–7 convex dorsally, not bulging ventrally; 5–7 with complete dorsal articulation. Antennular article 1 with produced distomesial lobe. Mandibular molar thick, condyle longer than molar. Maxilliped epipod produced distally, laterally convex. Pereopod 2 ischium shorter than basis. Male pleopod 2 stylet barely emerging from endopod margin.

Bathyal–hadal (2486–8100 m). GOODS bathyal provinces: Northern N Pacific, Cocos Plate, Nazca Plate. 6 species (Menzies and George, 1972; Malyutina, 2025).

Pirinectes Malyutina and Brix *in* Malyutina, Kihara and Brix, 2020

Diagnosis. Body broad, highest at natasome; cuticle thin, glossy; rostrum with rounded margin. Pereonites 5–7 convex dorsally, not bulging ventrally; 5, 6 without complete dorsal articulation; pereonite 7 separated by dorsal suture from pereonite 6. Antennular article 1 without distomesial lobe, article 3 not shorter than article 2. Mandibular molar thick, condyle longer than molar. Maxilliped oval. Pereopod 2 ischium longer than basis. Uropod peduncle with straight lateral margin; exopod much smaller than endopod.

Abyssal (4122–5019m). GOODS bathyal provinces: N Pacific. 2 species (Malyutina et al., 2020: key to species).

Tytthocope Wilson and Hessler, 1981

Diagnosis. Body broad, highest at natasome; cuticle thin, glossy; rostrum with lateral margins. Pereonites 5–7 compressed dorsally; pereonite 6 bulging ventrally; pereonite 7 much shorter than pereonite 6; pereonites 5, 6 without complete dorsal articulation; pereonite 7 separated by dorsal suture from pereonite 6. Antennular article 1 without mesial spine, distolateral lobe subrectangular, distally truncate. Mandibular molar narrow, condyle shorter than molar. Maxilliped epipod narrow, with acute tip. Pereopod 2 ischium shorter than basis. Uropod peduncle with straight lateral margin.

Slope–abyssal (267–4605 m). Arctic, Temperate Northern Atlantic, Tropical Atlantic, Temperate South America, Temperate Southern Africa, Southern Ocean. 8 species (Wilson and Hessler, 1981; Malyutina and Brandt, 2014: rediagnosis, key to 3 S Atlantic species).

Subfamily Ilyarachninae Hansen, 1916

Ilyarachines are recognised by the bases of pereopods 3, 4 being much shorter than that of pereopod 2, short, thick mandibles with a blunt incisor and reduced molar process, and a head usually wider than anterior pereonites. Merrin's (2007) thesis addressed the taxonomy of Ilyarachninae and was the basis of revision of existing genera and addition of two new genera (Merrin, 2004, 2006, 2009, 2011, 2016; Merrin et al., 2009).

Diagnosis. Body elongate, articulating, anterior margins smooth or with robust setae, without lateral spines; head usually wider than anterior pereonites; rostrum absent. Pereonites 5–7 with complete dorsal articulation; pleotelson oval-elongate. Antennulae inserted close together on frons; article 1 laminar. Antenna much longer than body. Mandible short, thick, with blunt incisor, with reduced molar process. Pereopods 3, 4 bases much shorter than bases of prehensile pereopods 1, 2; pereopods 5–7 natatory, propodi narrower than carpi; dactyli strong, long, more than half as long as propodi, with apical setae and 1 or 2 claws. Uropod ventral; uniramous or if biramous exopod minute (figs 3.25, 3.26a–d).

Key to genera of Ilyarachninae

1. Mandibular palp present (fig. 3.30g, l) 2
– Mandibular palp absent (fig. 3.30n) 5
2. Natasome outline streamlined, pereonites not laterally separate (fig. 3.25a, b, h, i) 3
– Natasome outline with pereonites laterally separate (figs 3.25c, d, 3.26a, b) 4
3. Uropod exopod reduced to small bump (fig. 3.32j) or absent. Pereonites 1–4 anterior margins with or without spines (fig. 3.25h, i) ..... *Ilyarachna*
– Uropod exopod small (fig. 3.32b). Pereonites 1–4 anterior margins without spines (fig. 3.25a, b) ..... *Aspidarachna*
4. Pereonites 1–4 anterior margins with spines, each without apical seta; pereonites 5–7 without lateral extensions (fig. 3.26a, b) ..... *Nyctobadistes*
– Pereonites 1–4 anterior margins with spines, each topped with apical seta; pereonites 5–7 lateral margins narrow and distinct from each other, either with elongate spine-like extensions or jagged (fig. 3.25c, d) ..... *Bathybadistes*
5. Pereonite 2 and pereopod 2 much larger than preceding pereonites and pereopods. Antennulae minute, placed far apart; article 1 laterally expanded (fig. 3.26c, d) ..... *Pseudarachna*

– Pereonite 2 and pereopod 2 not much larger than preceding pereonites and pereopods. Antennulae well developed, adjacent; article 1 rectangular or with lateral flange 6

6. Antenna article 1 distolateral angle with prominent horn-like spine and terminal robust seta (fig. 3.30e). Frons of head narrow, allowing maxillipeds to lie horizontally (fig. 3.25j, k) ..... *Notopais*

– Antenna article 1 rectangular, without prominent distolateral angle (fig. 3.30d). Frons of head wide, maxillipeds lying obliquely in lateral view 7

7. Pereonites 1–4 with simple setae, without spines (fig. 3.25f, g) ..... *Epikopais*

– Pereonites 1–4 anterior margins with spines, each without apical robust seta (fig. 3.25e) ..... *Echinozone*

Aspidarachna G.O. Sars, 1897

Diagnosis. Frons of head wide, rectangular. Pereonites 1–4 anterior margins without spines. Natasome outline streamlined, pereonites not laterally separate; pereonites 5–7 without lateral extensions. Antennulae well developed, adjacent; article 1 rectangular. Mandibular palp present. Pereopods 5, 6 carpi flat, subcircular; propodi expanded, oar-like; pereopod 7 carpus and propodus slender, with margin of plumose setae. Uropod foliaceous; exopod smaller than endopod.

Slope–abyssal (220–5495 m). GOODS bathyal provinces: Arctic, Northern N Pacific, N Atlantic. 4 species (Sars, 1896–1899: type species; Kussakin, 2003: rediagnosis, key to 3 species).

Bathybadistes Hessler and Thistle, 1975

Diagnosis. Frons of head wide, rectangular; cephalic anterior flanges absent. Pereonites 1–4 anterior margins with spines, each topped with apical robust seta. Natasome outline with pereonites laterally separate; pereonites 5–7 lateral margins narrow and distinct from each other, with either elongate spine-like extensions or jagged. Antennulae well developed, adjacent; article 1 rectangular. Mandibular palp present. Pereopods 5, 6 carpi flat, subcircular; propodi expanded, oar-like; pereopod 7 carpus and propodus slender, with margin of plumose setae. Uropod foliaceous; exopod reduced to bump or absent.

Bathyal, abyssal (2700–5024 m). GOODS bathyal provinces: Northern N Pacific, N Atlantic, Antarctic, Subantarctic, S Atlantic. 11 species (Merrin et al., 2009: key to 6 species).

Echinozone G.O. Sars, 1897

Diagnosis. Frons of head wide, rectangular. Pereonites 1–4 anterior margins with spines, each without apical robust seta. Natasome outline streamlined, pereonites not laterally separate; pereonites 5–7 without lateral extensions. Antennulae well developed, adjacent; article 1 rectangular. Mandibular palp absent. Pereopods 5, 6 carpi flat, subcircular; propodi expanded, oar-like; pereopod 7 carpus and propodus slender, with margin of plumose setae. Uropod foliaceous; exopod smaller than endopod.

Shelf, slope (100–1100 m). Arctic, Temperate Northern Atlantic, Temperate Northern W Pacific, Southern Ocean. 4 species (Brandt, 1990; Sars, 1896–1899; Kussakin and Vasina, 1982: all species dealt with belong to *Notopais*; Kussakin and Vasina, 1993).

Epikopais Merrin, 2009

Diagnosis. Frons of head laterally rounded; anterior flanges present. Pereonites 1–4 anterior margins with simple setae, dorsal spines absent. Natasome outline streamlined, pereonites not laterally separate; pereonites 5–7 without lateral extensions. Antennulae well developed, adjacent; article 1 rectangular. Mandibular palp absent. Pereopods 5, 6 carpi flat, subcircular; propodi expanded, oar-like; pereopod 7 carpus and propodus slender, with margin of plumose setae. Uropod foliaceous; exopod smaller than endopod.

Slope (385–1586 m). Temperate Australasia, Southern Ocean. 4 species (Merrin, 2009: key to 4 species).

Ilyarachna G.O. Sars, 1869

Diagnosis. Frons of head wide, rectangular; cephalic anterior flanges present, small. Pereonites 1–4 anterior margins with or without spines. Natasome outline streamlined, pereonites not laterally separate; pereonites 5–7 without lateral extensions. Antennulae well developed, adjacent; article 1 rectangular. Mandibular palp present. Pereopods 5, 6 carpi flat, subcircular; propodi expanded, oar-like; pereopod 7 carpus and propodus slender, with margin of plumose setae. Uropod foliaceous; exopod reduced to bump or absent.

Shelf–hadal (8–7230 m). Cosmopolitan. 45 species (Thistle, 1980: key to 10 Atlantic species; Kussakin, 2003: rediagnosis, key to 19 N Pacific species; Merrin, 2016: rediagnosis, key to 5 Australian species; Merrin, 2024: descriptions, and key to 12 species from SW Pacific).

Notopais Hodgson, 1910

Diagnosis. Frons of head narrow, allowing maxillipeds to lie horizontally. Pereonites 1–4 anterior margins usually with spines, if not, margins with robust setae; all spines tipped with robust setae. Natasome outline streamlined, pereonites not laterally separate; pereonites 5–7 without lateral extensions. Antennulae well developed, adjacent; article 1 rectangular. Antenna article 1 distolateral angle with prominent horn-like spine and terminal robust seta. Mandibular palp absent. Pereopods 5, 6 carpi flat, subcircular; propodi expanded, oar-like; pereopod 7 carpus and propodus slender, with margin of plumose setae. Uropod foliaceous; exopod smaller than endopod.

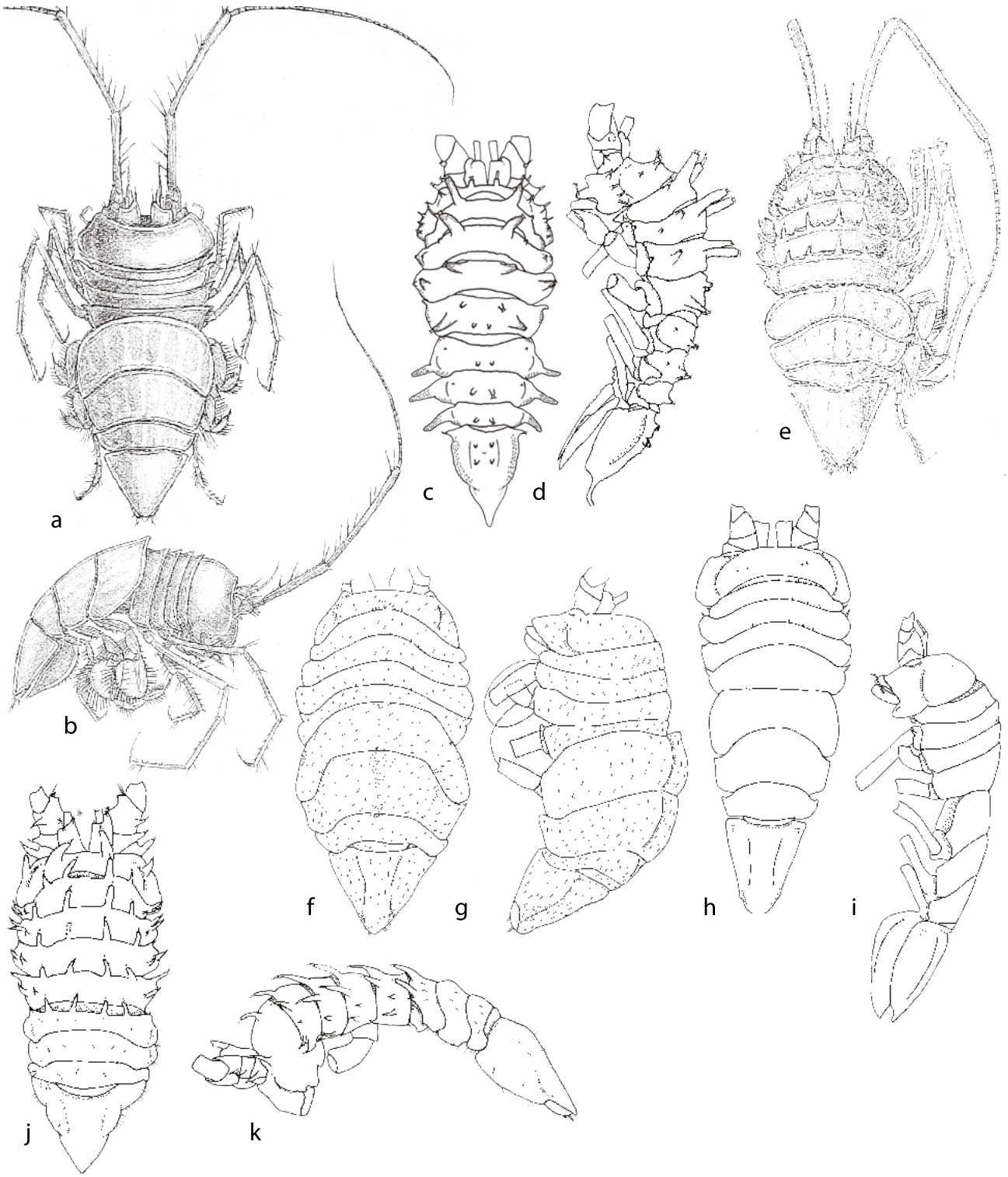


Figure 3.25. Munnopsidae, Ilyarachninae. Dorsal and lateral views: a, b, *Aspidarachna clypeata* (G.O. Sars, 1870); c, d, *Bathybadistes andrewsi* Merrin, 2009; e, *Echinozone coronata* (Sars, 1870); f, g, *Epikopais poorei* Merrin, 2009; h, i, *Ilyarachna ellae* Merrin, 2016; j, k, *Notopais spicatus* Hodgson, 1910.

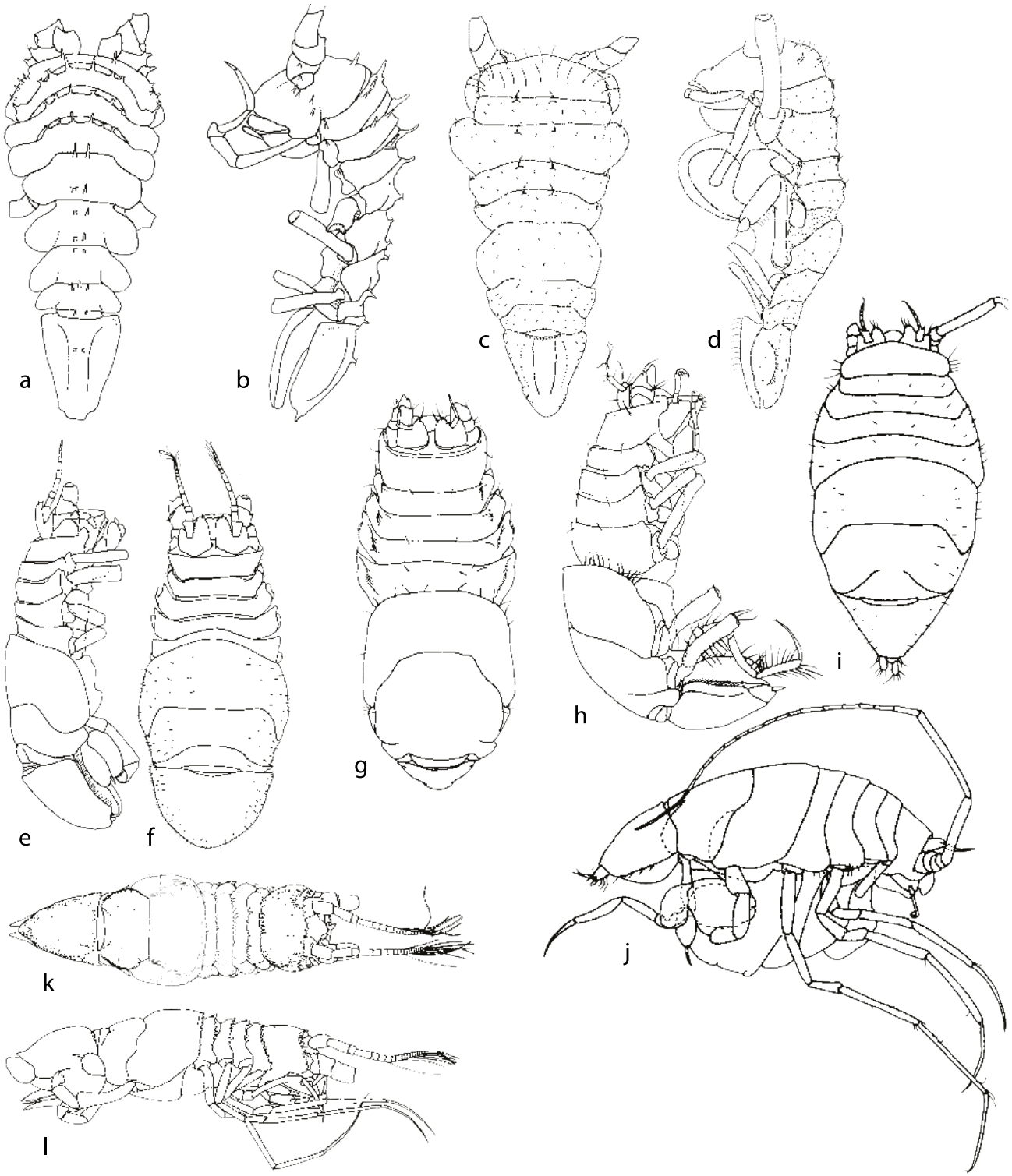


Figure 3.26. Munnopsidae, Ilyarachninae (cont.). Dorsal and lateral views: a, b, *Nyctobadistes hamatus* Merrin, 2011; c, d, *Pseudarachna nohinohi* Merrin, 2006. Lipomerinae: e, f, *Coperonus comptus* Wilson, 1989; g, h, *Hapsidohedra ochlera* Wilson, 1989; i, j, *Lionectes humicephalotus* Wilson, 1989; k, l, *Lipomera knorrae* Wilson,1989.

Shelf, slope (36–1640 m). Temperate Australasia, Southern Ocean. 11 species (Brandt, 1990: list of species as *Echinozone*; Merrin, 2004: rediagnosis, key to 7 species; Merrin and Bruce, 2006: 2 species; Merrin, 2024: descriptions, and key to 5 species of SW Pacific).

Nyctobadistes Merrin, 2011

Diagnosis. Frons of head wide, rectangular; cephalic anterior flanges absent. Pereonites 1–4 anterior margins with spines, each without apical robust seta. Natasome outline with pereonites laterally separate; pereonites 5–7 without lateral extensions. Antennulae well developed, adjacent; article 1 with lateral flange. Mandibular palp present. Pereopods 5–7 carpi and propodi narrow, elongate, not expanded and oar-like.

Slope (720–800 m). Temperate Australasia (SE Australia). 1 species (Merrin, 2011).

Pseudarachna G.O. Sars, 1897

Diagnosis. Frons of head wide, enlarged, semicircular; anterior flanges absent. Pereonites 1–4 anterior margins with spines, each topped with apical robust seta; pereonite 2 and pereopod 2 much larger than preceding pereonites and pereopods. Natasome outline streamlined, pereonites not laterally separate; pereonites 5–7 without lateral extensions. Antennulae minute, placed far apart; article 1 laterally expanded. Mandibular palp absent. Pereopods 5, 6 carpi flat, subcircular; propodi expanded, oar-like; pereopod 7 carpus and propodus slender, with margin of plumose setae. Uropod flat; exopod absent.

Shelf, slope (50–1463 m). Temperate Northern Atlantic, Temperate Australasia. 2 species (Merrin, 2006: rediagnosis).

Subfamily Lipomerinae Tattersall, 1905

Wilson (1989) revised the subfamily, adding three genera to the one existing. Members of Lipomerinae are recognised by the reduced or absent pereonite 7, a neotenous feature.

Diagnosis. Body smooth or setose dorsally and laterally, without spines; natasome wider than ambulosome; rostrum absent. Pereonites 5, 6 free or fused; pereonite 7 strongly reduced, much shorter than more anterior natasomites, or absent; pleotelson less than 1.5 times as long as wide. Antennulae dorsal; article 1 wide, much larger than article 2. Pereopods 3, 4 bases elongate, about as long as pereopod 2 basis; only pereopod 1 prehensile; pereopods 5, 6 natatory, with broad carpi and propodi; dactyli small, less than half as long as propodi, without apical setae and claws; pereopod 7 simple walking leg or absent. Uropod ventral, linear or expanded (fig. 3.26e–l).

Key to genera of Lipomerinae

1. Pereopod 7 large, similar to walking legs but with plumose setae on carpus and propodus (fig. 3.31d, e). Antennula article 1 with pronounced mesial lobe (fig. 3.26i) 2
– Pereopod 7 rudimentary or absent. Antennula article 1 without or with obsolete mesial lobe 4
2. Pereonite 7 of adult recessed into pleotelson (fig. 3.26i, j) ..... *Lionectes*
– Pereonite 7 of adult reaching lateral margin of pereon 3
3. Uropod small, with thick peduncle having pronounced mesial projection (fig. 3.32f). Natasome rounded posteriorly, not strongly reflexed ventrally (fig. 3.26e, f). Mandibular molar cylindrical, truncate (fig. 3.30j) ..... *Coperonus*
– Uropod large, with leaf-like peduncle (fig. 3.32i). Natasome angular posteriorly, strongly reflexed ventrally (fig. 3.26g, h). Mandible with massive molar process and blunt incisor process (fig. 3.30k) ..... *Hapsidohedra*
4. Uropod large, flat, rami absent, reaching end of pleotelson (fig. 3.32k). Pereopod 5 merus short; dactylus distinct (fig. 3.31f) ..... *Lipomera*
– Uropod small, sometimes with rudimentary exopod, not reaching end of pleotelson (fig. 3.32l). Pereopod 5 merus elongate; dactylus rudimentary (fig. 3.31h) ..... *Mimocopelates*

Coperonus Wilson, 1989

Diagnosis. Natasome rounded posteriorly, not strongly reflexed ventrally; pereonites 5--7 articulated; pereonite 7 strip-like, reaching lateral margin of pereon. Antennular article 1 with produced distomesial lobe. Pereopod 5 dactylus small, lenticular; pereopod 7 large, similar to walking legs but with plumose setae on carpus and propodus. Uropod small, with thick peduncle having pronounced mesial projection.

Shelf, slope (139–2012 m). Temperate South America, Southern Ocean. 8 species (Wilson, 1989; Brandt, 1992a: rediagnosis, key to 7 species; 1992b).

Hapsidohedra Wilson, 1989

Diagnosis. Natasome angular posteriorly, strongly reflexed ventrally; pereonite 7 strip-like, reaching lateral margin of pereon. Antennular article 1 with produced distomesial lobe. Mandible with massive molar process and blunt incisor process. Pereopod 7 large, similar to walking legs but with plumose setae on carpus and propodus. Uropod large, with leaf-like peduncle.

Slope (213–1022 m). Tropical Atlantic, Temperate Australasia. 2 species (Wilson, 1989).

Lionectes Wilson, 1989

Diagnosis. Natasome compact, conical in dorsal view; pereonites 5–7 articulated laterally, indistinctly articulated medially between pereonites 5 and 6, fused medially between pereonites 6 and 7; pereonite 7 recessed into pleotelson, not reaching lateral margin of natasome. Antennular article 1 with mesial and lateral lobes. Pereopod 5 dactylus rudimentary; pereopod 7 large, similar to walking legs but with plumose setae on carpus and propodus. Uropod peduncle flat, oval; endopod larger than small exopod.

Slope (282 m). Southern Ocean. 1 species (Wilson, 1989).

Lipomera Tattersall, 1905

Diagnosis. Natasome triangular in dorsal view; pereonites 5 and 6 large, dorsally articulated; pereonite 7 reduced, fused to pereonite 6. Antennular article 1 without mesial lobe, with lateral lobe. Pereopod 5 merus short; dactylus distinct; pereopod 7 rudimentary. Uropod peduncle leaf-like, flat, rami absent, reaching end of pleotelson.

Slope, bathyal (364–3264 m). Temperate Northern and Tropical SW Atlantic, Temperate South America. 3 species (Kussakin, 2003; Wilson, 1989: key and descriptions of 3 species, each in own subgenus).

Mimocopelates Wilson, 1989

Diagnosis. Natasome triangular in dorsal view; pereonites 5 and 6 large, dorsally articulated; pereonite 7 strip-like, reaching lateral margin of pereon. Antennular article 1 with obsolete mesial lobe, with lateral lobe. Mandible with molar process distally convex, heavily sclerotized. Pereopod 5 merus elongate; dactylus rudimentary; pereopod 7 absent in adult. Uropod small, exopod absent or rudimentary, not reaching end of pleotelson.

Slope, bathyal (587–2890 m). Temperate Northern Atlantic, Temperate South America. Atlantic. 2 species (Wilson, 1989).

Subfamily Munnopsinae Lilljeborg, 1864

Munnopsines are noted for the absence of dactyli on pereopods 5–7 and the terminal or slightly ventral uniramous uropod. Systematics of the subfamily has not been addressed since Kussakin's (2003) diagnosis and key to genera. In some genera the natasome is much narrower than the ambulosome.

Diagnosis. Body with natasome (pereonites 1–4) clearly differentiated from ambulosome (pereonites 5–7), with or without spines; rostrum absent. Pereonites 5–7 free, partly or completely fused dorsally; pleotelson oval-elongate. Antennulae dorsal; article 1 wide, much larger than article 2. Antenna much longer than body. Mandibular molar absent or narrowly conical, reduced; palp present, or absent. Pereopods 3, 4 bases much shorter than bases of prehensile pereopods 1, 2; pereopods 5–7 natatory, with broad carpi and propodi; without dactyli. Uropod terminal or slightly ventral; cylindrical, uniramous (rarely exopod indicated by setae) (fig. 3.27).

Key to genera of Munnopsinae

1. Natasome and pereonite 5 with few dorsal spines in midline (fig. 3.27a, b) ..... *Acanthamunnopsis*
– Natasome dorsal surface smooth 2
2. Natasome and ambulosome widths slightly different. Pereopods 5–7 carpi much wider than propodi (fig. 3.27e). Mandibles with molar process thin, conical (fig. 3.30o) ..... *Paramunnopsis*
– Natasome and ambulosome widths usually considerably different. Pereopods 5–7 carpi not wider than propodi (fig. 3.27c, d). Mandibles with molar process reduced or absent 4
4. Pereopods 5–7 carpi with sparse, spaced setae (fig. 3.31m) ..... *Pseudomunnopsis*
– Pereopods 5–7 carpi with many adjacent long setae (fig. 3.27c, d) 5

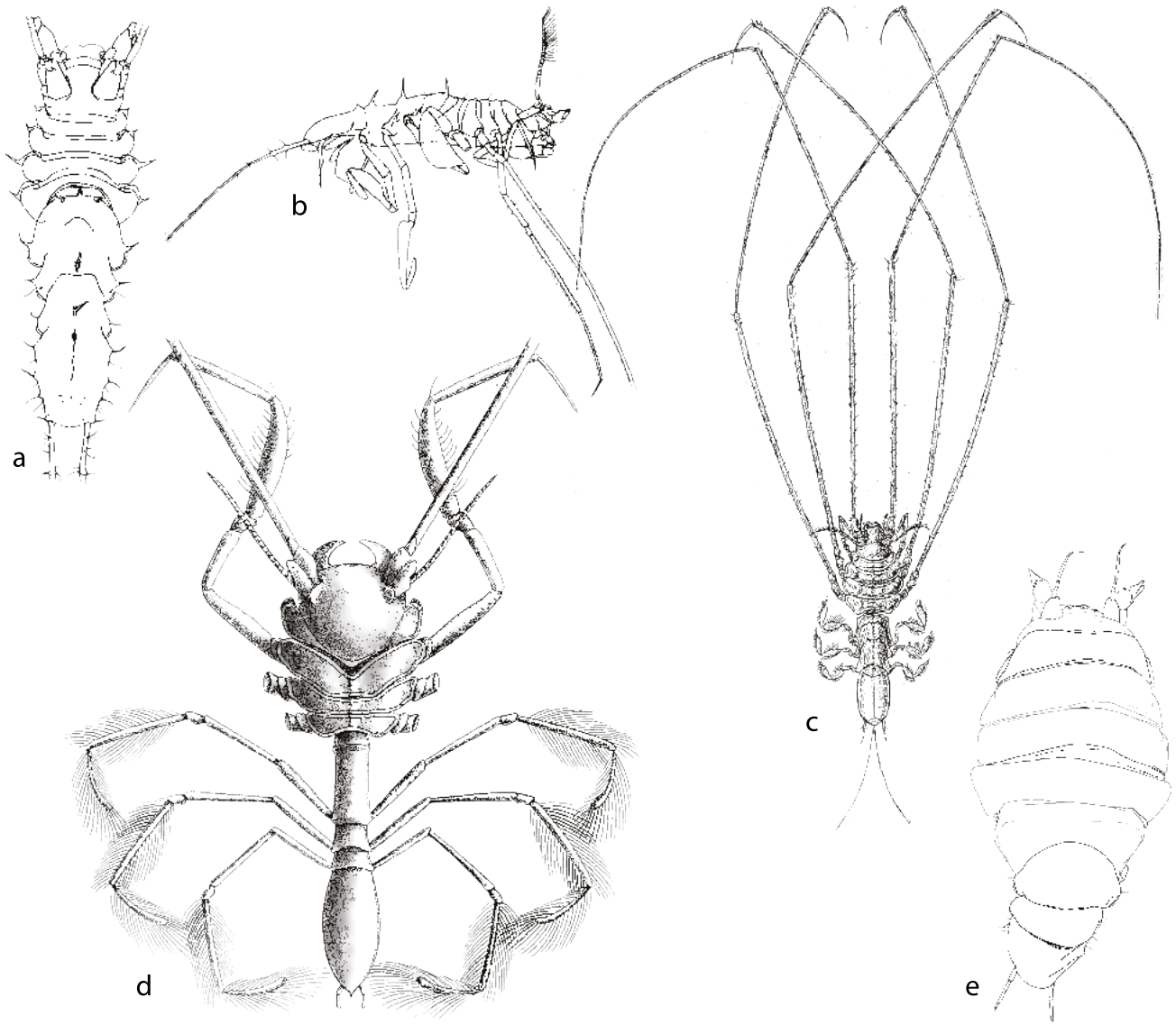


Figure 3.27. Munnopsidae, Munnopsinae. Dorsal and lateral views: a, b, *Acanthamunnopsis milleri* Wilson, 1982; c, *Munnopsis typica* M. Sars, 1861; d, *Munnopsoides australis* (Beddard, 1885); e, *Paramunnopsis justi* Svavarsson, 1988.

5. Natasome width less than 0.4 width of ambulosome. Pereonite 5 not longer along midline than each of pereonites 6 and 7 (fig. 3.27c). Mandibular palp well developed ..... *Munnopsis*

– Natasome width more than 0.4 width of ambulosome. Pereonite 5 longer along midline than each of pereonites 6 and 7 (fig. 3.27d). Mandibular palp absent ..... *Munnopsoides*

Acanthamunnopsis Schultz, 1978

Diagnosis. Natasome and pereonite 5 with middorsal spines; natasome slightly narrower than ambulosome, segments fused. Mandible with molar process thin, conical; mandibular palp present. Pereopods 5–7 carpi much wider than propodi, both with setose margins.

Bathypelagic (0–2893 m). Tropical Atlantic, Temperate Northern Pacific, Southern Ocean. 4 species (Schultz, 1978; Wilson, 1982b: rediagnosis, species composition, 2 species described).

Munnopsis M. Sars, 1861

Diagnosis. Natasome width less than 0.4 width of ambulosome, smooth; pereonite 5 not longer along midline than each of pereonites 6 and 7. Mandible with molar process reduced or absent; mandibular palp present. Pereopods 5–7 carpi not wider than propodi; carpi with setose margins.

Shelf–abyssal, mesopelagic, bathypelagic (4–4506 m). Temperate Northern Atlantic, Temperate Northern W Pacific, Temperate Southern Africa, Temperate Australasia. GOODS bathyal provinces: Northern N Pacific, Cocos Plate, Nazca Plate, Indian, W Pacific. 10 species (Sars, 1896–1899: figures of type species; Kussakin, 2003: rediagnosis, 2 species described).

Munnopsoides Tattersall, 1905

Diagnosis. Natasome width more than 0.4 width of ambulosome, smooth; pereonite 5 longer along midline than each of pereonites 6 and 7. Mandible with molar process reduced or absent; mandibular palp absent. Pereopods 5–7 carpi not wider than propodi; carpi with setose margins.

Slope–abyssal (400–4925m). GOODS bathyal provinces: Arctic, Northern N Pacific, Nazca Plate, Indian. 5 species (Beddard, 1886: figures of type species; Menzies and George, 1972: rediagnosis, 2 species).

Paramunnopsis Hansen, 1916

Diagnosis. Natasome and ambulosome widths slightly different, smooth. Mandible with molar process thin, conical; mandibular palp present. Pereopods 5–7 carpi much wider than propodi, both with setose margins.

Slope, bathyal, abyssal (1273–3909 m). GOODS bathyal provinces: Arctic, Northern N Atlantic. 2 species (Hansen, 1916; Svavarsson, 1988: second species).

Pseudomunnopsis Hansen, 1916

Diagnosis. Natasome width about half width of ambulosome, setose; pereonite 5 longer along midline than length of pereonites 6 and 7 together. Mandible with molar process reduced or absent; mandibular palp absent. Pereopods 5–7 carpi not wider than propodi; carpi with sparse setae.

Bathyal (2626 m). GOODS bathyal provinces: Northern N Atlantic. 1 species (Hansen, 1916; Tattersall, 1905).

Subfamily Storthyngurinae Kussakin, 2003

Storthyngurines have a body with strong dorsal and lateral spines, also with spines on the coxae of pereopods 2–4. They differ from acanthocopines in that the bases of pereopods 4–7 are of similar lengths and the uropod is biramous (Kussakin, 2003; Malyutina, 2003; Malyutina and Brandt, 2004a).

Diagnosis. Body with natasome differentiated, with strong dorsal and lateral spines; rostrum absent. Pereonites 5–7 dorsally fused; pleotelson suboval, fused to all natasome segments, with lateral spines. Antennulae dorsal; article 1 wide, much larger than article 2. Pereopods 3, 4 bases elongate, about as long as pereopod 2 basis; pereopods 5–7 natatory, with broad carpi and propodi; dactyli small, less than half as long as propodi, or ambulatory, with cylindrical carpi and propodi. Uropod ventral, biramous, with elongate peduncle and rami (fig. 3.28a–m).

Key to genera of Storthyngurinae

1.	Head with pair of dorsal spines (fig. 3.28i–k)	2
–	Head without pair of dorsal spines (tubercles at most) (fig. 3.28a–h, l, m)	3
2.	Pleotelson terminal process acute, bent dorsally (fig. 3.28k)	*Sursumura*
–	Pleotelson apex prolonged (fig. 3.28i, j)	*Storthyngurella*
3.	Pereopods 5–7 ambulatory, carpi and propodi elongate, cylindrical, without marginal plumose setae (fig. 3.31g, k, l)	4
–	Pereopods 5–7 natatory, carpi and propodi flat, with setose margins (fig. 3.31q–s)	5
4.	Body flat, with lateral spines on pereonites 3, 4. Pleotelson flat, wider than flat natasome, terminally truncate (fig. 3.28c, d)	*Platyprotus*
–	Body subcylindrical, with sublateral spines on pereonites 2–4 and lateral spines on pereonites 5–7 pleotelson. Pleotelson tapering to bifid apex (fig. 3.28a, b)	*Microprotus*
5.	Pereopods 2–4 of similar lengths (fig. 3.31a–c)	*Storthyngura*
–	Pereopods 3 and 4 significantly longer than pereopod 2	6
6.	Body stout, vaulted, with lateral spines on pereonites 4–7 and pleotelson. Head with pair of dorsal anterior tubercles. Pleotelson terminal process bent ventrally (fig. 3.28l, m)	*Vanhoeffenura*
–	Body subcylindrical, with lateral spines on pereonites 3–7 and pleotelson. Head without pair of tubercles. Pleotelson terminal process rounded, not bent ventrally (fig. 3.28e, f)	*Rectisura*

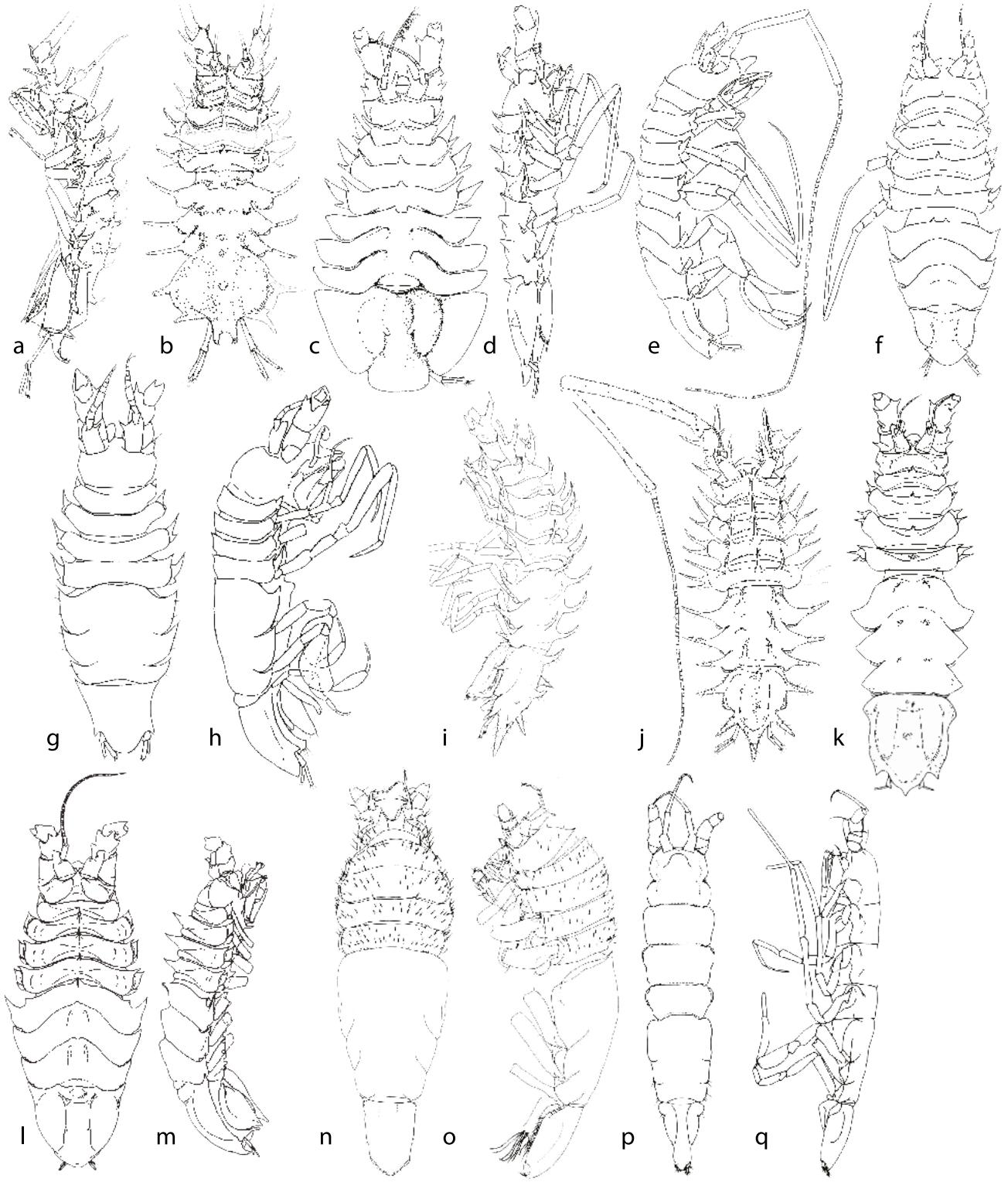


Figure 3.28. Munnopsidae, Storthyngurinae. Dorsal and lateral views: a, b, *Microprotus caecus* Richardson, 1910; c, d, *Platyprotus phyllosoma* Just, 2001; e, f, *Rectisura slavai* Malyutina, 2011; g, h, *Storthyngura yuzhmorgeo* Malyutina, 2011; i, j, *Storthyngurella andeepae* Malyutina and Brandt, 2004; k, *Sursumura aberrata* Malyutina, 2003; l, m, *Vanhoeffenura georgei* Malyutina, 2003. Syneurycopinae: n, o, *Bellibos buzwilsoni* Haugsness and Hessler, 1979; p, q, *Syneurycope parallela* Hansen, 1916.

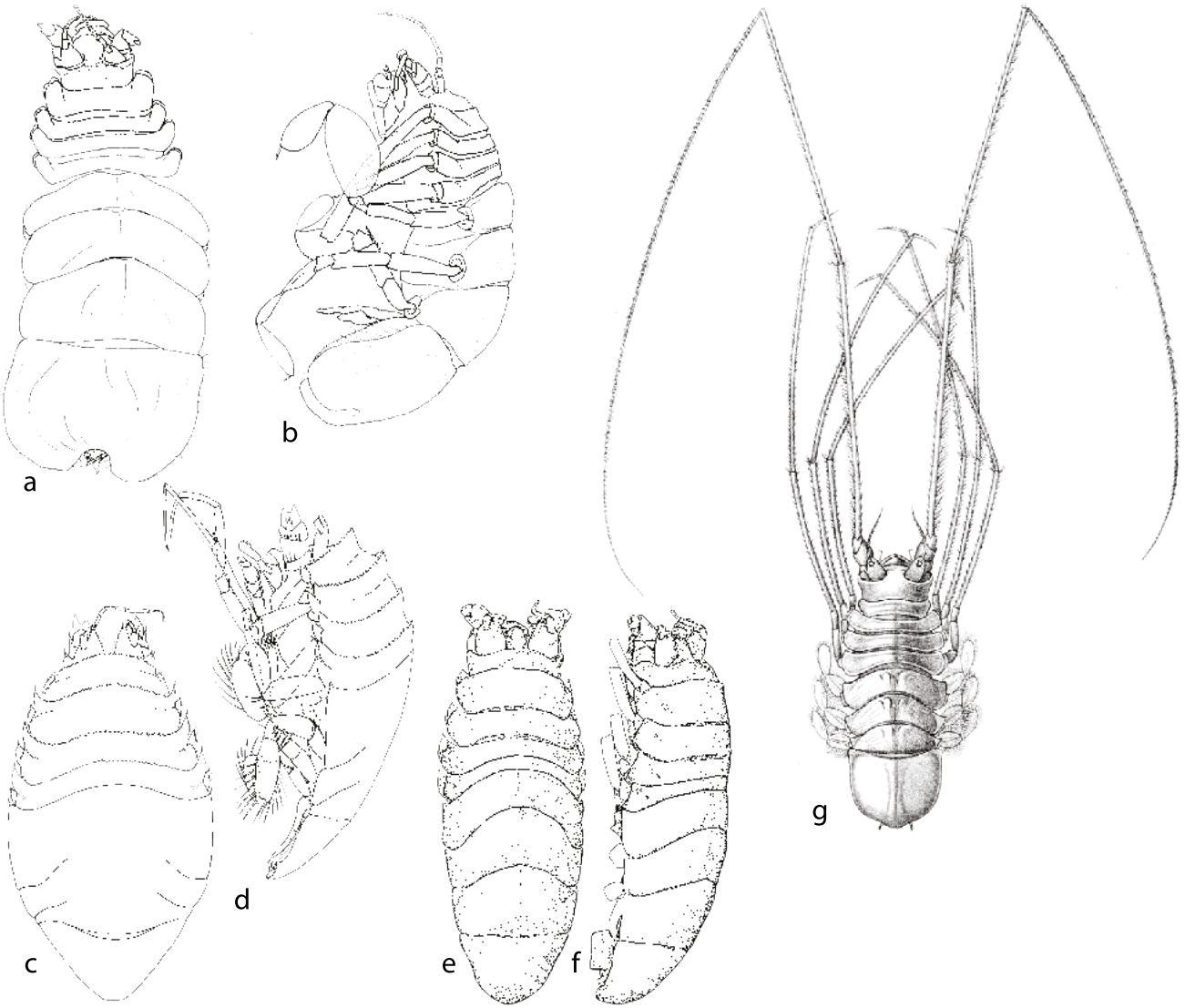


Figure 3.29. Munnopsidae. Dorsal and lateral views. Unaligned genera: a, b, *Gurjanopsis australis* Malyutina, 2007; c, d, *Microcope denticulata* Malyutina, 2008; e, f, *Munneurycope persephone* Mursch, Brenke and Wägele, 2008; g, *Munnopsurus giganteus* (G.O. Sars, 1877).

Microprotus Richardson, 1909

Diagnosis. Body subcylindrical, with sublateral spines on pereonites 2–4 and lateral spines on pereonites 5–7 pleotelson; head without dorsal spines. Pleotelson bifid. Antennular article 1 without mesial spine. Pereopods 5–7 ambulatory, carpi and propodi elongate, cylindrical, without plumose setae.

Slope, bathyal (550–3400 m). Temperate Northern Pacific, Southern Ocean. 5 species (Wilson et al., 1989: rediagnosis, key to species).

Platyprotus Just, 2001

Diagnosis. Body flat, with lateral spines on pereonites 3, 4; head without dorsal spines. Pleotelson flat, wider than flat natasome, terminally truncate. Antennular article 1 with long mesial spine. Pereopods 5–7 ambulatory, carpi and propodi elongate, cylindrical, without plumose setae.

Slope (540 m). Southern Ocean. 1 species (Just, 2001). Malyutina and Brandt (2004c) treated *Platyprotus* as a junior synonym of *Storthyngura*, but it is resurrected here for the time being on basis of its ambulatory pereopods 5–7.

***Rectisura* Malyutina, 2003**

Diagnosis. Body stout, vaulted, with lateral spines on pereonites 4–7 and pleotelson; head vaulted, without dorsal spines. Pleotelson tip broad, truncate or rounded. Antennular article 1 without mesial spine. Pereopods 3 and 4 significantly longer than pereopod 2; 5–7 natatory, carpi and propodi broad, oval, propodi longer than carpi.

Bathyal–hadal (2084–9345 m). GOODS bathyal provinces: Northern N Pacific, SE Pacific Ridges, New Zealand/ Kermadec, Cocos Plate, Antarctic. 12 species (Malyutina and Brandt, 2004b: species list with distributions; Malyutina, 2011).

***Storthyngura* Vanhöffen, 1914**

Diagnosis. Body subcylindrical, with lateral spines on some pereonites and pleotelson; head without dorsal spines, tubercles at most. Pleotelson not acute. Antennular article 1 without or with small mesial spine. Pereopods 2–4 of similar lengths; 5–7 natatory, carpi and propodi broad, oval, propodi longer than carpi.

Slope–abyssal (181–5166 m). GOODS bathyal provinces: Northern N Pacific, N Atlantic, Nazca Plate, Antarctic. 13 species (Malyutina, 2003: rediagnosis; Malyutina, 2011; Malyutina and Brandt, 2004c).

***Storthyngurella* Malyutina, 1999**

Diagnosis. Body subcylindrical, with lateral spines on pereonites 4–7 and pleotelson; head with pair of dorsal spines. Pleotelson apex prolonged. Antennular article 1 with long mesial spine. Pereopods 5–7 narrow, carpi and propodi tubular, without marginal setae, or barely natatory, with marginal setae.

Bathyal–hadal (2856–7200 m). GOODS bathyal provinces: New Zealand/Kermadec, Cocos Plate, Antarctic, Subantarctic, Indian, S Atlantic. 9 species (Malyutina, 1999; Malyutina and Brandt, 2004a: table of differences from *Sursumara*).

***Sursumura* Malyutina, 2003**

Diagnosis. Body subcylindrical, with lateral spines on pereonites 5–7 and pleotelson; head with pair of dorsal spines. Pleotelson terminal process acute, bent dorsally. Antennular article 1 with long mesial spine. Pereopods 5–7 carpi and especially propodi narrow, more than 3 times as long as wide.

Slope– (400–7216 m). GOODS bathyal provinces: N Atlantic, New Zealand/Kermadec, Antarctic, Subantarctic, Indian, W Pacific, S Atlantic. 12 species (Malyutina, 2003; Malyutina and Brandt, 2004a: differences from *Storthyngurella*, species list).

***Vanhoeffenura* Malyutina, 2004**

Diagnosis. Body subcylindrical, with lateral spines on pereonites 3–7 and pleotelson; head with pair of tubercles near anterior margin. Pleotelson terminal process rounded, bent ventrally. Antennular article 1 without mesial spine. Pereopods 3 and 4 significantly longer than pereopod 2; 5–7 natatory, carpi and propodi broad, oval, propodi longer than carpi.

Slope–hadal (1257–8045 m). GOODS bathyal provinces: Northern N Pacific, N Atlantic, New Zealand/Kermadec, Cocos Plate, Subantarctic, S Atlantic. 18 species (Malyutina, 2003: as Vanhoeffenella; 2004: correction of name; Malyutina and Brandt, 2004a).

Subfamily Syneurycopinae Wolff, 1962

Syneurycopinae are more elongate than most other munnopsids and unique in the terminal position of the antennulae and the subcylindrical shape of the first article, in denticles on the maxillipedal palp and in short pleopods. Although Haugsness and Hessler (1979) noted considerable morphological variation in this subfamily, they did rediagnosise it and provided a key to two genera and all seven species.

Diagnosis. Body elongate, more than 3 times as long as wide, smooth or setose dorsally and laterally, without spines; pereonites 5–7 usually fused; rostrum absent. Pereonites 5–7 dorsally fused; pleotelson elongate, 1.3 or more times as long as wide. Antennulae inserted on anterior margin; article 1 cylindrical, shorter than article 2. Pereopods 3, 4 bases elongate, about as long as pereopod 2 basis; pereopods 5–7 natatory, but with narrow carpi and propodi; dactyli strong, long, more than half as long as propodi, with apical setae and 1 or 2 claws. Uropod ventral, small, flat, biramous (fig. 28n–q).

***Bellibos* Haugsness and Hessler, 1979**

Diagnosis. Body usually less than 4 times as long as wide; pereonites 1–4 usually shorter than pereonites 5–7; head free from pereonite 1, with pair of dorsal spines. Pleotelson tapers simply. Antennular flagellum of female multiarticulate. Uropod exopod at least two thirds length of endopod (fig. 3.32c).

Bathyal, abyssal (2379–4980 m). GOODS bathyal provinces: N Atlantic, S Atlantic. 4 species (Haugsness and Hessler, 1979: two subgenera, key to species).

***Syneurycope* Hansen, 1916**

Diagnosis. Body greater than 4 times as long as wide; pereonites 1–4 longer than pereonites 5–7; head fused to pereonite 1, without dorsal spines. Pleotelson complexly contoured. Antennular flagellum of female of 1 article. Uropod exopod less than one third length of endopod (fig. 3.32n).

Slope–abyssal (1280–5122 m). GOODS bathyal provinces: Northern N Pacific, N Atlantic, S Atlantic. 3 species (Haugsness and Hessler, 1979: key to species).

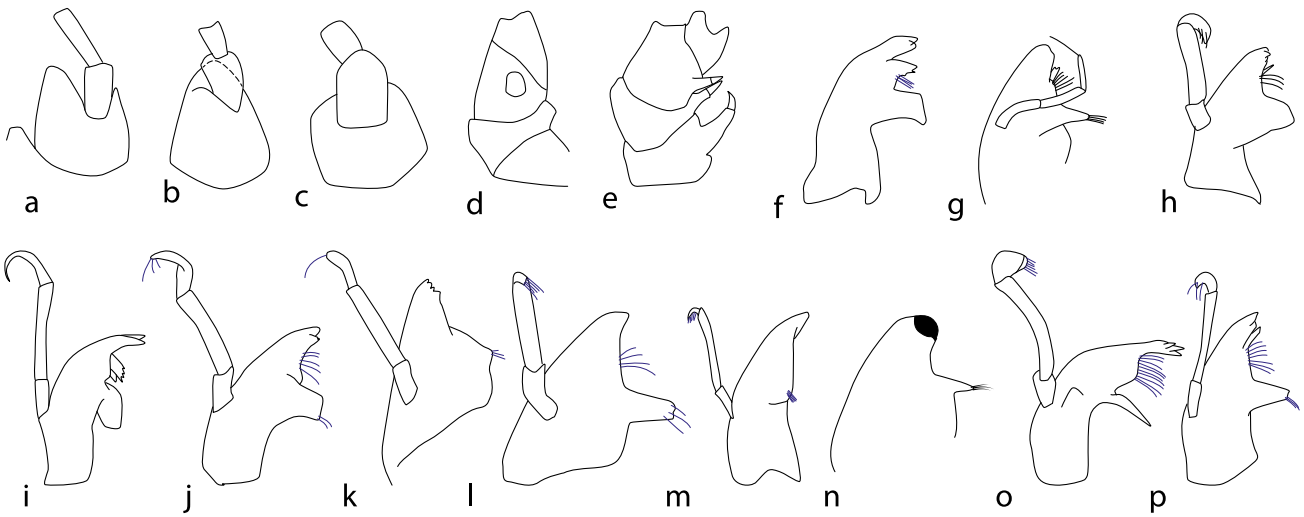


Figure 3.30. Munnopsidae. Right antennula, articles 1–3: a, *Eurycope*; b, *Baeonectes*; c, *Disconectes*. Right antenna, proximal articles: d, *Epikopais*; e, *Notopais*. Mandible: f, *Amuletta*; g, *Aspidarachna*: h, *Baeonectes*; i, *Betamorpha*; j, *Coperonus*; k, *Hapsidohedra*; l, *Ilyarachna*; m, *Munnopsurus*; n, *Notopais*; o, *Paramunnopsis*; p, *Tytthocope*.

Subfamily incertae sedis

Gurjanopsis Malyutina and Brandt, 2007

Diagnosis. Body smooth or setose dorsally and laterally, without spines; rostrum absent. Pereonites 5–7 with complete dorsal articulation; pleotelson broader than long, subrectangular, swollen dorsally, flattened ventrally, posteromedial area pleotelson compressed, with deep notch including anus and uropods. Antennulae dorsal; article 1 wide, much larger than article 2. Pereopods 2–4 bases similar; pereopod 1 slender, basis twice as long as that of more posterior pereopods; pereopods 5–7 natatory, with broad carpi and propodi; dactyli small, less than half as long as propodi, without apical setae and claws. Uropod ventral, peduncle cylindrical, biramous, rami attached distally (fig. 3.29a, b).

Bathyal, abyssal (2380–3709 m). GOODS bathyal provinces: Arctic, Northern N Pacific, Antarctic. 3 species. Malyutina and Brandt (2007) argued the genus was close to *Munneurycope* but later did not include it in a subfamily (Malyutina and Brandt, 2018).

Microcope Malyutina, 2008

Diagnosis. Body broad, highest at natasome; cuticle thin, glossy; frons of head high; head hidden under anterior flange of pereonite 1; rostrum absent. Pereonites 5–7 dorsally fused; pleotelson wider than long, subtriangular. Antennulae inserted close together on frons; article 1 with anteromesial lobe; antennular article 1 with produced distomesial lobe. Mandibular molar thick, condyle longer than molar. Maxilliped epipod produced distally, laterally convex. Pereopods 1–4 bases subequal in length; pereopods 2–4 with conspicuous difference between bulky basis–ischium part and slender carpus–dactylus part; pereopods 5–7 natatory, propodi narrower than carpi; dactyli almost as long as propodi. Uropod peduncle with mesial extension; rami inserted at midlength of lateral margin (fig. 3.29c, d).

Slope, bathyal, abyssal (349–5780 m). GOODS bathyal provinces: Northern N Pacific, Antarctic, W Pacific, S Atlantic. 5 species (Malyutina, 2008; 2015: rediagnosis, key to species). Malyutina (2008) compared *Microcope* with six other munnopsid genera and argued that the genus combined characters common to some genera of Eurycopinae, Betamorphinae and Syneurycopinae.

Munneurycope Stephensen, 1912

Diagnosis. Body smooth or setose dorsally and laterally, without spines; rostrum absent. Pereonites 5–7 with complete dorsal articulation; pleotelson posterior margin more or less rounded. Antennulae dorsal; article 1 wide, much larger than article 2. Pereopods 2–4 bases similar; pereopod 1 slender, basis little longer than that of more posterior pereopods; pereopods 5–7 natatory, with broad carpi and propodi; dactyli small, less than half as long as propodi, without apical setae and claws. Uropod ventral, peduncle cylindrical, biramous, rami attached distally (fig. 3.29e, f).

Slope–hadal (530–7800 m). Arctic, Temperate Northern Atlantic, Tropical Atlantic, Temperate South America, Temperate Australasia, Southern Ocean. 10 species. (Kussakin, 2003: diagnosis, key to 6 species; Malyutina and Brandt, 2007: discussion of species; Mursch et al., 2008: rediagnosis, discussion of subfamily placement, comparison of 5 species).

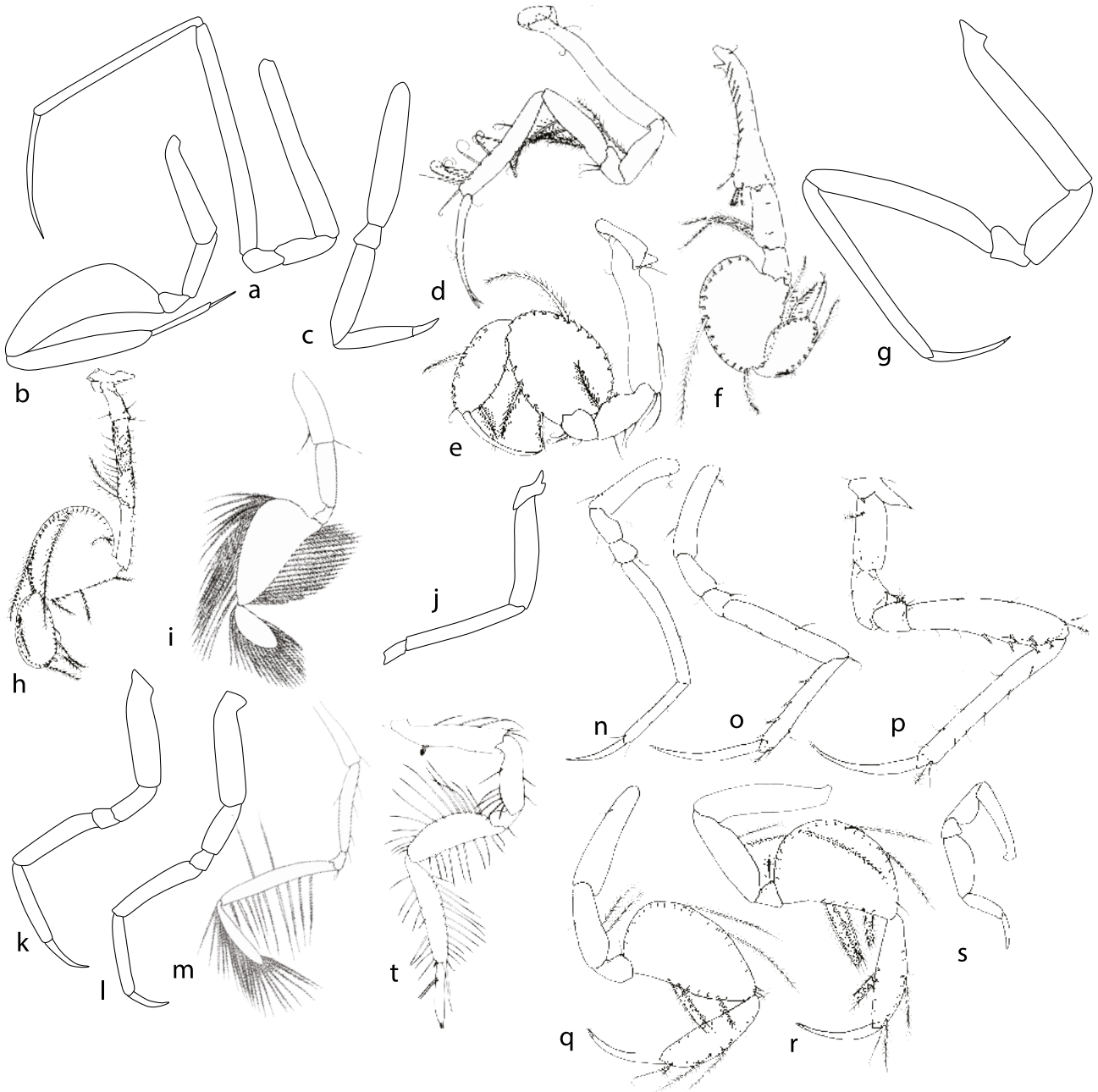


Figure 3.31. Munnopsidae. Pereopods. a, b, *Acanthocope* (p4, p5); c, *Bathyopsurus* (p1); d, e, *Lionectes* (p6, p7); f, *Liomera* (p5); g, *Microprotus* (p6); h, *Mimocopelates* (p5); i, *Paramunnopsis* (p5); j, *Pirinectes* (p2 coxa–merus); k, l, *Platyprotus* (p5, p6); m, *Pseudomunnopsis* (p5); n–s, *Storthyngura* (p1, p2, p4– p7); t, *Syneurycope* (p5).

Munnopsurus Richardson, 1912

Diagnosis. Body smooth or setose dorsally and laterally, without spines; rostrum absent. Pereonites 5–7 with complete dorsal articulation; pleotelson less than 1.5 times as long as wide. Antennulae dorsal; article 1 wide, much larger than article 2. Mandibular molar strong, rounded, with 1 or 2 bundles of small setae. Pereopods 2–4 bases similar; pereopod 1 slender, basis little longer than that of more posterior pereopods; pereopods 5–7 natatory, with broad carpi and propodi; dactyli small, less than half as long as propodi, without apical setae and claws. Uropod ventral, peduncle cylindrical, biramous, rami attached distally (fig. 3.29g).

Shelf–bathyal (40–3423 m). Arctic, Temperate Northern Atlantic, Temperate Northern W Pacific, Temperate Southern

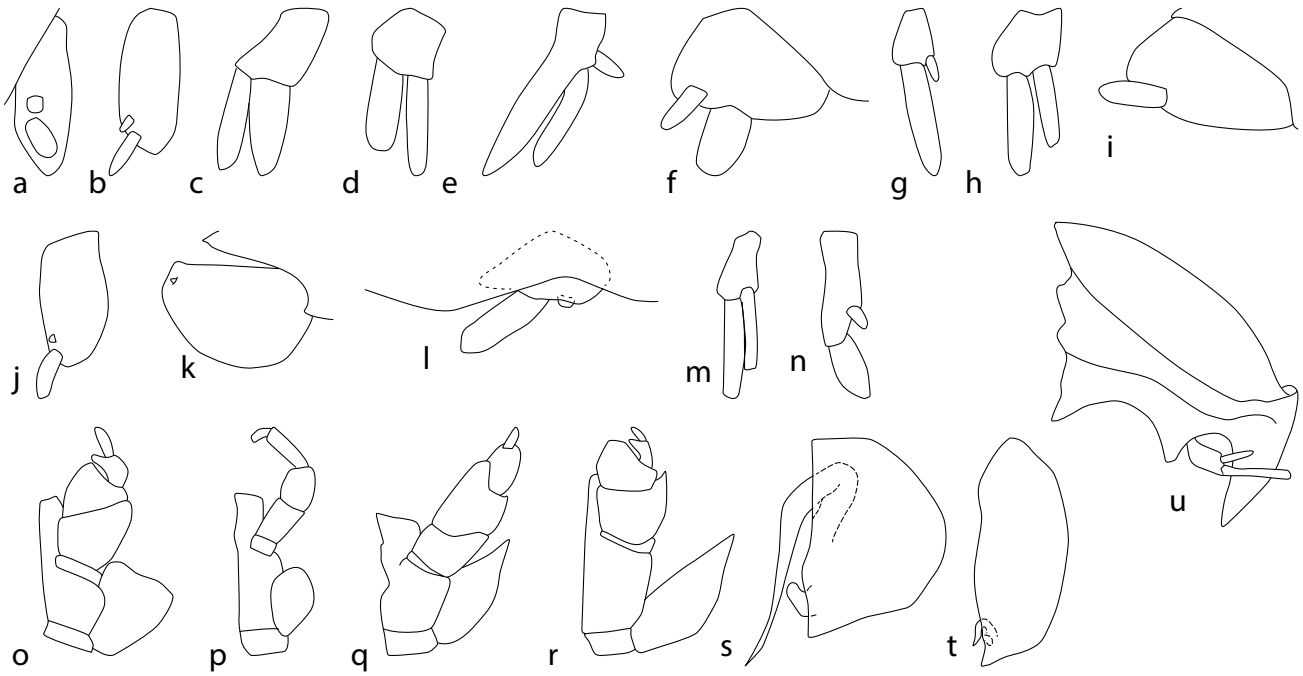


Figure 3.32. Munnopsidae. Uropod: a, *Amuletta*; b, *Aspidarachna*; c, *Bellibos*; d, *Belonectes*; e, *Betamorpha*; f, *Coperonus*; g, *Disconectes*; h, *Eurycope*; i, *Hapsidohedra*; j, *Ilyarachna*; k, *Lipomera*; l, *Mimocopelates*; m, *Munneurycope*; n, *Syneurycope*. Maxilliped: o, *Baeonectes*; p, *Bathyopsurus*; q, *Paropsurus*; r, *Tytthocope*. Male pleopod 2: s, *Eurycope*; t, *Munnicope*. Pleotelson (with left uropod, lateral view): u, *Dubinectes*.

Africa, Southern Ocean. 7 species (Sars, 1885: figure of type species; Richardson, 1912; Kussakin, 2003: key to 4 species).

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Nannoniscidae Hansen, 1916

Figures 3.33, 3.34

Nannoniscids are usually slender, blind asellotes but may be somewhat flattened. The pereonites are more or less similar. The pereopods are all ambulatory. Adults range in size from 1.3 mm to almost 6 mm in length; most are around 2–3 mm. The family occurs only in cold water, on the shelf in the Arctic but more commonly at greater depths throughout the world's oceans.

The family was diagnosed in a modern context by Siebenaller and Hessler (1977), but more recent literature has concentrated on differentiating its genera (Kaiser, 2009; Kaiser et al., 2018; Siebenaller and Hessler, 1981; Wilson, 2008). The following key to genera is based on that of Wilson (2008) with additions.

Diagnosis. Body elongate, flattened, with subparallel margins or narrow in middle; head frontal margin projecting forward

(usually); pereonites parallel-sided, pereonite 1 shorter than pereonite 2, pereonite 5 as long as pereonites 6 and 7, sometimes fused. Pleon of 1 segment. Anus not covered by pleopodal operculum. Eyes absent. Antennula shorter than head. Mandibular molar small, triangular, spinulose. Maxillipedal palp articles 1–3 wider than distal articles. Pereopods 1–7 or pereopods 2–7 ambulatory, articulating dorsolaterally or laterally; pereopod 4 coxa inserting on anterolateral margin; pereopodal 2–7 dactyli with 1 major claw. Uropod inserting posteroventrally.

Implicit generic attributes. Pereonites 4–5 wider than long; and pleon not broadly expanded laterally (distance from midline to posterior coxae greater than distance from coxae to lateral margin); pereonites 6, 7 and pleotelson free; without midventral peronal or opercular spines. Head anterolateral margin rounded, not projecting. Mandibles projecting anteroventrally, not prognathous, not visible in dorsal view; palp present. Pleopodal operculum more than half as wide as pleotelson. Female operculum without midventral spine. Uropod biramous.

Key to genera of Nannoniscidae

1. Antennula with 6 or more articles, terminal article tubular (fig. 3.34l, n, s) 2
– Antennula with 5 articles, terminal article usually bulbous (fig. 3.34m, o–r) 5
2. Pereonites and pleon broadly expanded laterally (distance from midline to posterior coxae subequal or less than distance from coxae to lateral margin) (fig. 3.33a). Pleopodal operculum less than half as wide as pleotelson (fig. 3.34a) ..... *Austroniscus*
– Pereonites and pleon not broadly expanded laterally (distance from midline to posterior coxae greater than distance from coxae to lateral margin). Pleopodal operculum more than half as wide as pleotelson (fig. 3.34b, c) 3
3. Head anterolateral margin projecting, angular. Mandibles projecting anteroventrally, not prognathous, not visible in dorsal view (fig. 3.33h) ..... *Nannoniscoides*
– Head anterolateral margin rounded, not projecting. Mandibles prognathous, projecting anteriorly in dorsal view (fig. 3.33l, m) 4
4. Pereonite 7 and female operculum each with midventral spine (fig. 3.34i). Female pleotelson with weak posterolateral angles (fig. 3.34d) ..... *Thaumastosoma*
– Pereonite 7 and female operculum each without midventral spine (fig. 3.34f). Female pleotelson with posterolateral spines (fig. 3.34e) ..... *Ketosoma*
5. Antennula article 4 margin with distomesial process (fig. 3.34p–r) 6
– Antennula article 4 distomesial margin unmodified, lacking projections (fig. 3.34m) or absent in male (fig. 3.34o) 12
6. Body narrow, pereonal margins rounded in cross-section, tergites curving ventrally. Pereonites 4, 5 about as long as wide (fig. 3.33b–e). Ventral surface without spines 7
– Body moderately broad, tergites projecting laterally, especially of pereonites 5–7. Pereonites 4–5 much wider than long (fig. 3.33i, j). Ventral surface often with spines or keels (fig. 3.34g–i) 9
7. Head with massive broad rostral crest. Antennula tiny, not projecting anteriorly. Antenna short, article 5 and flagellum together about as long as proximal articles, flagellum strongly tapering distally (fig. 3.33f, k). Mandibular palp absent ..... *Exiliniscus*
– Head with narrow rostrum or concave anteriorly (fig. 3.33d). Antennula projecting beyond margin of head. Antenna of normal length, article 5 and flagellum together distinctly longer than proximal articles, flagellum weakly tapering. Mandibular palp present 8
8. Pereonites 6, 7 pleotelson free ..... *Panetela*
– Pereonites 6, 7 pleotelson fused (fig. 3.33d, e) ..... *Nymphodora*
9. Pleon broad, elongate, wider than head or pereonites 5–7, distinctly longer than pereonites 5–7. Pereonites 6, 7 pleotelson free. Pleopods about as long as pleotelson (fig. 3.33i) ..... *Nannonisconus*
– Pleon small, less than or about as wide as head or pereonites 5–7, subequal or shorter than pereonites 5–7. Pereonites 6, 7 pleotelson fused dorsally. Pleopods distinctly shorter than pleotelson (fig. 3.33j) 10
10. Pereopod 1 robust, all articles wider than those of pereopod 2, carpus and propodus flexor margin with robust elongate setae (fig. 3.34x) ..... *Rapaniscus*

– Pereopod 1 not robust, articles about as wide as those of pereopod 2, carpus and propodus flexor margin with simple setae (fig. 3.34t, v) 11

11. Pereon or pleopodal surfaces with at most 1 ventromedial spine. Pereopod 1 carpus and propodus as wide as in pereopod 2, with similar setation (fig. 3.34t, u) ..... *Nannoniscus*

– Pereon or pleopodal surfaces with 2 or more ventromedial spines (fig. 3.34h). Pereopod 1 carpus and propodus narrower than in pereopod 2, with fewer robust setae (fig. 3.34v, w) ..... *Regabellator*

12. Uropod biramous (fig. 3.34j). Pleotelson as wide as long, shield-shaped, with distolateral spines (fig. 3.34b). Antennula article 5 slightly inflated, elongate (fig. 3.34m) ..... *Hebefustis*

– Uropod uniramous (fig. 3.34k). Pleotelson much longer than wide, ovoid, without distolateral spines (fig. 3.33g). Antennula of 2 articles in male; article 2 with mesiodistal projection, terminal article bulbous (fig. 3.34o) ..... *Micromesus*

Austroniscus Vanhöffen, 1914

Diagnosis. Body flattened; 2.5 times as long as width of pereonite 2; pereonites and pleon broadly expanded laterally (distance from midline to posterior coxae subequal or less than distance from coxae to lateral margin); pleotelson without posterolateral spines. Head with narrow rostrum; anterolateral margin projecting, angular. Antennula of 6 articles, distal article tubular; article 4 distal margin lacking projections. Pereopod 1 not robust, articles about as wide as those of pereopod 2, carpus and propodus with simple ventral setae. Pleopodal operculum less than half as wide as pleotelson. Maximum length 2.4 mm.

Shelf–abyssal (10–6135 m). Arctic, Atlantic, Temperate Northern Pacific, Tropical Eastern Pacific, Southern Ocean. 10 species (Siebenaller and Hessler, 1981: rediagnosis; Kaiser and Brandt, 2007: rediagnosis, list and distributions of species).

Exiliniscus Siebenaller and Hessler, 1981

Diagnosis. Body narrow, pereonal margins rounded in cross-section, tergites curving ventrally; at least 5 times as long as width of pereonite 2; pereonites 4–5 about as long as wide; pleotelson without posterolateral spines. Head with massive broad rostral crest. Antennula of 5 articles; terminal article bulbous, not projecting anteriorly; article 4 distal margin with distomesial process. Antenna short, article 5 and flagellum together about as long as proximal articles, flagellum strongly tapering distally. Palp absent. Pereopod 1 carpus and propodus narrower than in pereopod 1, with fewer robust setae. Maximum length 2.7 mm.

Shelf, abyssal (80–5023 m). Arctic, Temperate Northern Atlantic, Tropical Atlantic. 3 species (Siebenaller and Hessler, 1981: diagnosis, distributions of species).

Hebefustis Siebenaller and Hessler, 1977

Diagnosis. Body flattened; 3.8 times as long as width of pereonite 2; pereonites 6, 7 fused dorsally; pleotelson small, as wide as and shorter than pereonites 5–7, shield-shaped, with distolateral spines. Head with broad truncate rostrum. Antennula of 5 articles; article 5 slightly inflated, elongate; article 4 distal margin lacking projections. Pereopod 1 not robust, articles about as wide as those of pereopod 2, carpus and propodus with simple ventral setae. Maximum length 3.4 mm.

Slope–abyssal (587–5690 m). Temperate Northern Atlantic, Tropical Atlantic, Temperate Northern W Pacific, Temperate Atlantic South America. GOODS bathyal provinces: SE Pacific Ridges. 14 species (Siebenaller and Hessler, 1977: diagnosis, 7 species; 1981: rediagnosis; Kaiser, 2014: 1 new species, distribution of species, key to species).

Ketosoma Kaiser and Brix *in* Kaiser, Brix, Kihara, Janssen and Jennings, 2018

Diagnosis. Body moderately broad, tergites projecting laterally, especially of pereonites 5–7; 4.3 times as long as width of pereonite 2; pleotelson with posterolateral spines. Head with narrow rostrum. Antennula of 6–13 articles, distal article tubular; article 4 distal margin lacking projections. Mandibles prognathous, often projecting anteriorly in dorsal view. Pereopod 1 shorter, but more robust than pereopods 2–7. Maximum length 5.8 mm.

Abyssal (4133–5690 m). GOODS bathyal provinces: Northern N Pacific, N Atlantic, Cocos Plate, S Atlantic. 5 species (Kaiser et al., 2018: diagnosis, species descriptions).

Micromesus Birstein, 1963

Diagnosis. Body vermiform; pereonite 1 fused to head; 5.5 times as long as width of pereonite 2; pleotelson narrower and shorter than pereonites 5–7, tapering, without distolateral spines. Head with well-produced rostrum. Antennula of 2 articles in male; article 3 with mesiodistal projection; terminal article bulbous; article 4 distal margin lacking projections. Palp absent. Pereopod 1 not robust, articles about as wide as those of pereopod 2, carpus and propodus with simple ventral setae. Uropod uniramous. Maximum length 1.3 mm.

Abyssal (4000–4150 m). GOODS bathyal provinces: N Pacific. 1 species (Birstein, 1963; Svavarsson, 1984: species family placement).

Nannoniscoides Hansen, 1916

Diagnosis. Body flattened; about 3 times as long as width of pereonite 2; pereonites 6, 7 fused or free; pleotelson with posterolateral spines. Head with narrow rostrum; anterolateral margin lappet-like. Antennula of 6 (rarely 7) articles, distal article tubular; article 4 distal margin lacking projections.

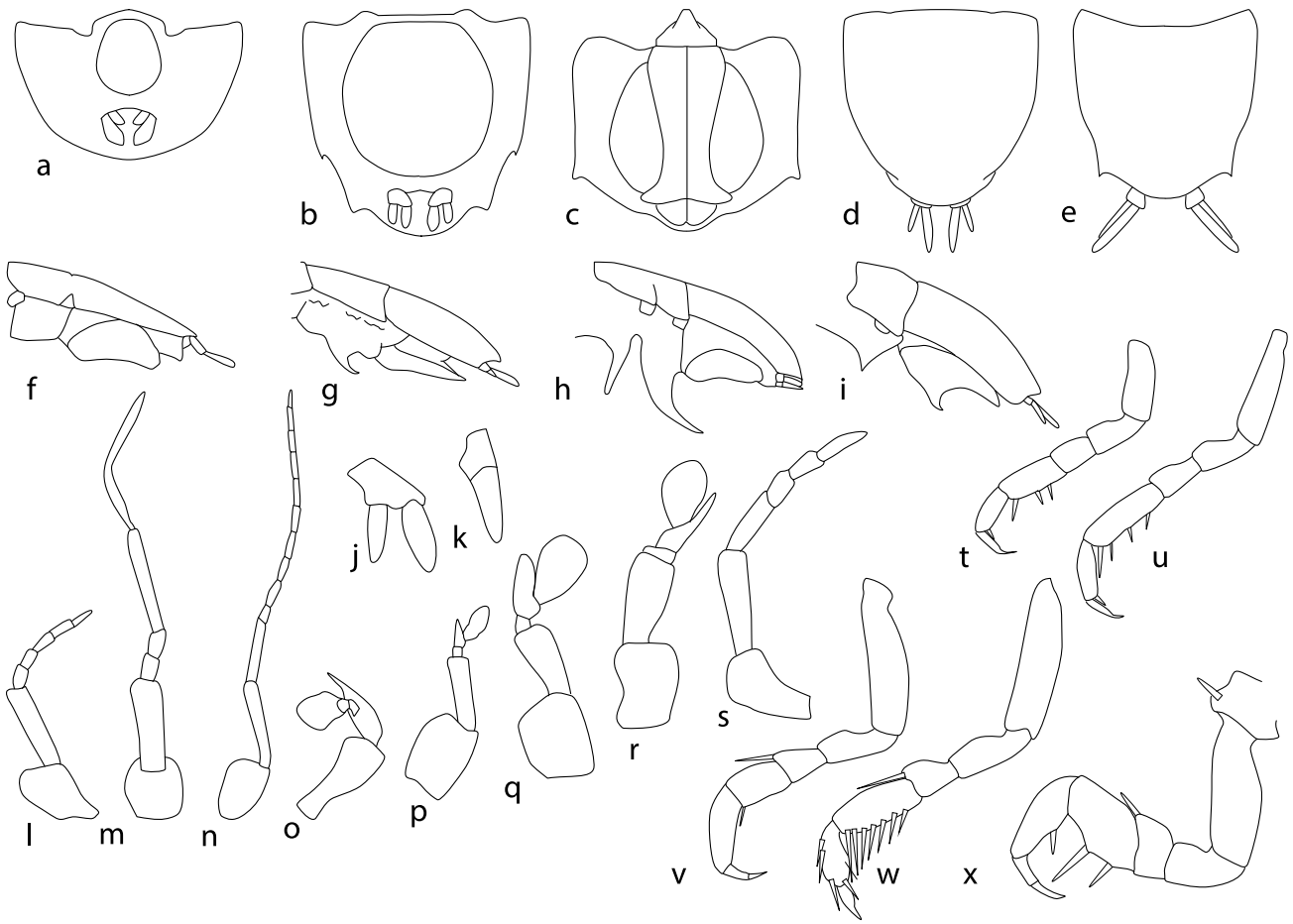


Figure 3.34. Nannoniscidae. Pleotelson, ventral view: a, *Austroniscus*; b, *Hebefustis*; c, *Nannoniscoides*. Pleotelson, dorsal view: d, *Thaumastosoma*; e, *Ketosoma*. Pereonite 6–pleotelson, lateral view: f, *Ketosoma*; g, *Rapaniscus*; h, *Regabellator* (with pereonite 6); i, *Thaumastosoma*. Uropod: j, *Hebefustis*; k, *Micromesus*. Left antennula: l, *Austroniscus*; m, *Hebefustis*; n, *Ketosoma*; o, *Micromesus*; p, *Nannonisconus*; q, *Nannoniscus*; r, *Regabellator*; s, *Thaumastosoma*. t, u, pereopods 1, 2, *Nannoniscus*. v, w, pereopods 1, 2, *Regabellator*. x, pereopod 1, *Rapaniscus*.

Maximum length 1.7 mm.

Shelf–abyssal (160–4833 m). Arctic, Temperate Northern Atlantic, Tropical Atlantic, Temperate Northern Pacific, Temperate Atlantic South America. 7 species (Siebenaller and Hessler, 1977: rediagnosis; 1981: rediagnosis, 4 species).

Nannonisconus Schultz, 1966

Diagnosis. Body moderately broad, tergites projecting laterally, especially of pereonites 5–7; 3.5 times as long as width of pereonite 2; pleotelson wider than head or pereonites 5–7, with posterolateral spines. Head with broad truncate rostrum; anterolateral margin projecting, angular. Antennula of 5 articles; terminal article bulbous; article 4 distal margin with distomesial process. Maximum length 2.8 mm.

Slope (456–1028 m). Tropical Atlantic, Temperate Northern Pacific, Eastern Indo-Pacific. 3 species (Siebenaller and Hessler, 1981: rediagnosis; Mezhov, 1986: third species; Brix and Svavarsson, 2010: undescribed species).

Nannoniscus G. O. Sars, 1870

Diagnosis. Body moderately broad, tergites projecting laterally, especially of pereonites 5–7; less than 4 times as long as width of pereonite 2; pereonites 6, 7 fused dorsally; pereonites 6 or 7 or female operculum with midventral spine; pleotelson broad, elongate, wider than head or pereonites 5–7, distinctly longer than pereonites 5–7. Antennula of 5 articles; terminal article bulbous; article 4 distal margin with distomesial process. Pereopod 1 carpus and propodus as wide as in pereopod 2, with similar setation. Uropod usually biramous. Maximum length 4.2 mm.

Shelf–abyssal (75–6328 m). Arctic, Temperate Northern

Atlantic, Tropical Atlantic, Temperate Northern W Pacific, Southern Ocean. GOODS bathyal provinces: Nazca Plate, Antarctic (possibly cosmopolitan). 35 species (Siebenaller and Hessler, 1981: rediagnosis; Kaiser et al., 2021: rediagnosis, list of species with distributions, key to 12 Pacific species).

Nymphodora Kaiser, 2009

Diagnosis. Body moderately broad, tergites projecting laterally, especially of pereonites 5–7; 4.3 times as long as width of pereonite 2; pereonites 6, 7 and pleotelson fused dorsally; pleotelson without posterolateral spines. Head with concave rostral margin. Antennula of 5 articles; article 4 with distolateral projection; terminal article bulbous; article 4 distal margin with distomesial process. Pereopod 1 shorter, but more robust than pereopods 2–7. Uropod biramous; endopod long, projecting beyond posterior margin of pleotelson; exopod minute. Maximum length 2.8 mm.

Slope (1740 m). Arctic (Canada Basin). 1 species (Kaiser, 2009).

Panetela Siebenaller and Hessler, 1981

Diagnosis. Body narrow, pereonal margins rounded in cross-section, tergites curving ventrally; at least 5 times as long as width of pereonite 2; pereonites 4–5 about as long as wide; pleotelson without posterolateral spines. Head with narrow rostrum. Antennula of 5 articles; terminal article bulbous; article 4 distal margin with distomesial process. Uropod biramous; endopod long, projecting beyond posterior margin of pleotelson; exopod minute. Maximum length 2 mm.

Slope–abyssal (1427–5495 m). Arctic, Temperate Northern and Temperate Northern W Pacific. 3 species (Siebenaller and Hessler, 1981; Malyutina and Kussakin, 1996: third species).

Rapaniscus Siebenaller and Hessler, 1981

Diagnosis. Body moderately broad, tergites projecting laterally, especially of pereonites 5–7; 3.5 times as long as width of pereonite 2; pereonites 6, 7 fused dorsally; pleotelson without posterolateral spines. Head with broad truncate rostrum. Antennula of 5 articles; terminal article bulbous; article 4 distal margin with distomesial process. Pereopod 1 robust, all articles wider than those of pereopod 2, carpus and propodus with robust elongate ventral setae. Maximum length 1.4 mm.

Slope–abyssal (220–5389 m). Temperate Northern and Tropical Atlantic. 3 species (Siebenaller and Hessler, 1981; Brandt, 2002: third species).

Regabellator Siebenaller and Hessler, 1981

Diagnosis. Body moderately broad, tergites projecting laterally, especially of pereonites 5–7; 3.4 times as long as width of pereonite 2; pereonites 6, 7 fused dorsally; pereonites 6 and 7 each with midventral spine; pleotelson small, as wide as and shorter than pereonites 5–7. Head with broad truncate rostrum. Antennula of 5 articles; terminal article bulbous; article 4 distal margin with distomesial and distolateral processes. Pereopod 1 carpus and propodus narrower than in pereopod 1, with fewer robust setae. Uropod biramous; endopod long, projecting beyond posterior margin of pleotelson; exopod minute. Maximum length 3.1 mm.

Slope–abyssal (472–5415 m). Temperate Northern Atlantic, Tropical Atlantic, Temperate Atlantic South America, Southern Ocean. 4 species (Siebenaller and Hessler, 1981; Kaiser, 2015: rediagnosis, species distributions, key to species).

Thaumastosoma Hessler, 1970

Diagnosis. Body moderately broad, tergites projecting laterally, especially of pereonites 5–7; 5 times as long as width of pereonite 2; pereonites 7 or 6 and 7 each with midventral spine; pleotelson with posterolateral spines. Head with narrow rostrum. Antennula of 6 articles, distal article tubular; article 4 distal margin lacking projections. Mandibles prognathous, often projecting anteriorly in dorsal view. Pereopod 1 shorter, but more robust than pereopods 2–7. Female operculum with midventral spine. Maximum length 4 mm.

Bathyal, abyssal (2886–4308 m). GOODS bathyal provinces: Northern N Atlantic, N Atlantic, S Atlantic. 3 species (Kaiser et al., 2018: rediagnosis, species redescriptions).

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Paramunnidae Vanhöffen, 1914

Figures 3.35–3.40

Paramunnidae[1] are one of the largest family in the suborder Asellota, comprising 185 species in 44 genera, all of which are tiny (maximum length 0.6–3 mm) benthic dwellers known worldwide from shallow tidal to abyssal depths (Just and Wilson, 2004, 2006, 2007). Most genera are endemic to the Southern Hemisphere. For example, in the Ross Sea, paramunnids were reported to be the most abundant and most frequently collected isopod family (Choudhury and Brandt, 2007).

Wolff (1962) included paramunnids in Munnidae, providing a key to 11 genera. Wilson (1980) treated paramunnids as a separated family that he called Pleurogoniidae Nordenstam, 1933, including 11 genera. Just (1990) synonymised Abyssianiridae Menzies, 1956 with Paramunnidae. Wilson (1980) recognised suprageneric relationships within three clusters: *Pleurogonium*, *Pleurosignum* and *Antennulosignum*, based on their mandibular molar with a pointed or rounded apex; *Notoxenus, Coulmannia* and *Notoxenoides* with dorsal spines; and the more loosely knit *Paramunna*, *Austrosignum* and other genera. The *Paramunna* complex within the last cluster was reinterpreted by Just and Wilson (2004), who provided a key to 12 genera of which nine were new, and documented their geographical and depth distribution. This complex has no dorsally visible pereopodal coxae, lacks pereonal spines, has bulging eyestalks and truncate mandibular molars. Similarly, two new genera were introduced to the smaller *Austronanus* complex (Just and Wilson, 2006). Just and Wilson (2007, 2021) dealt with the confused *Austrosignum-Munnogonium* complex, providing a key to ten genera, of which eight were new.

Males often differ from females, notably in having swollen shoulders on pereonite 1 (cf. fig. 3.37e, f).

Several papers have dealt with regional faunas, sometimes with keys to species: Magellan Strait, Chile (Winkler, 1994); Southern Ocean (Doti et al., 2009); North Pacific (Golovan and Malyutina, 2019, 2022); and Japan (Shimomura, 2009).

Just and Wilson (2004, 2007) treated *Metamunna* Tattersall, 1905 and its only species, *M. typica* Tattersall, 1905, as nomina dubia, arguing that the type species was poorly known. The genus name has been used (e.g. by Wolff and Brandt (2000)) for species of *Austrosignum* and *Munnogonium*. Bamber and Robbins' (2010) redescription of the type species fits easily within the diagnosis of *Boreosignum* Just and Wilson, 2007, one of the few genera with species in the Northern Hemisphere. *Boreosignum* is treated here as a junior synonym of *Metamunna*.

Diagnosis. Body broad, ovate, often with lateral plates. Pleon of 1 free pleonite plus pleotelson. Anus covered by pleopodal operculum. Eyes on lateral process (if present). Pereopod 1 prehensile; pereopods 2–7 ambulatory. Uropod inserting posterodorsally, minute, without peduncle.

Implicit generic attributes. Pereonites 1–7 and pleonite 1 without middorsal spines. Mandibular molar process strong, subcylindrical-dilating, truncate; palp present.

Key to genera of Paramunnidae

The first couplet relies on a difficult interpretation of the shape of the mandibular molar process, whether truncate or with an oblique, rounded or pointed apex. Habitus figures and the mandibles of the four genera with a narrow molar process are included in figure 3.40. All other genera are in alphabetical order in figures 3.35–3.39.

1. Mandibular molar process strong, subcylindrical-dilating, truncate (fig. 3.39c–e) 2

[1] Three genera have been added since this was compiled: Just, J. 2026. Review of *Pleurosignum* Vanhöffen, 1914, with re-descriptions, new genera and species in a new *Pleurosignum* group in Paramunnidae (Isopoda, Asellota), with remarks on *Pleurogonium* Sars, 1863. *Zootaxa* 5782:249–282. http://doi.org/10.11646/zootaxa.5782.2.2

– Mandibular molar process narrow, apex oblique, rounded or pointed (fig. 3.40f–h) 41

2. Some or all pereonites with prominent lateral and/or dorsal spines 3

– Pereonites without lateral or dorsal spines, lateral margins rounded or triangular; body oval (spines on coxae may be present; *Kussakinella* with short middorsal cones) 11

3. Mandibular palp absent (fig. 3.39c) 4

– Mandibular palp present (fig. 3.39d, e) 6

4. Head with medial crest bearing tuft of setae on posterior part. Pereonite 7 reduced; pereopod 7 absent (fig. 3.38f) ..... *Reductogonium*

– Head without medial crest bearing tuft of setae on posterior part. Pereonite 7 normal; pereopod 7 present 5

5. Pereonites 1–7 and pleonite 1 each with dorsal spine or crest, sometimes duplicated. Head frontal margin convex, without anterolateral angle (fig. 3.36d, e) ..... *Coulmannia*

– Pereonites 1–7 sometimes with sharp dorsal spine, never duplicated; pleonite 1 without dorsal spine. Head frontal margin with anterolateral angle at base of antenna (fig. 3.36i) ..... *Heterosignum*

6. Pereonites 1–7 with low median projection, without lateral spines (fig. 3.37j) ..... *Notoxenus*

– Pereonites 1–7 projecting laterally or with lateral spines 7

7. Head with prominent eyestalks 8

– Head without eyestalks 10

8. Head frontal margin simply convex between antennae (fig. 3.35c) ..... *Acutomunna*

– Head frontal margin with medial and/or anterolateral spines between antennae 9

9. Head with anterior medial spine or tooth, pair of anterolateral spines (fig. 3.38d) ..... *Pentaceration*

– Head without anterior medial spine, upright outgrowths at base of 2 lateral forward-pointing spines (fig. 3.36c) ..... *Compoceration*

10. Head with anterolateral projections (fig. 3.37i) ..... *Notoxenoides*

– Head without anterolateral projections (fig. 3.38h) ..... *Spinogonium*

11. Coxal plates 4, 5 or 6 to 7 visible in dorsal view (e.g. fig. 3.35h–j) 12

– No coxal plates visible in dorsal view (e.g. fig. 3.35d–g) 29

12. Coxal plates with lateral spines (figs 3.35h, 3.36a, 3.37a) 13

– Coxal plates without lateral spines 15

13. Pleotelson with narrow proximal half, bulb-like posteriorly. Eyestalks absent (fig. 3.35h) ..... *Austrogonium*

– Pleotelson flattened, with denticulate lateral margin. Eyestalks present (even if blind) 14

14. Pleotelson longer than wide. Coxal spines prominent. Eyestalks curving posterolaterally anterior to pereonite 1 (fig. 3.36a) ..... *Bathygonium*

– Pleotelson wider than long. Coxal spines barely protruding beyond pereonite lateral margins. Eyestalks extending laterally (fig. 3.37a) ..... *Holodentata*

15. Head with depressed frontal plate 16

– Head without depressed frontal plate 17

16. Head frontal margin dipping ventrally to thin horizontal convex plate with evenly serrate convex margin. Eyestalks present (fig. 3.35a, b) ..... *Abyssianira*

– Head frontal margin plate truncate with rounded anterolateral corners, barely serrate. Eyestalks absent (fig. 3.37d) ..... *Magellianira*

17. Head frontal margin produced as large subtriangular or rounded plate. Eyes not on eyestalks or eyestalks short 18

– Head frontal margin straight or rounded. Eyes on narrow eyestalks 20

18. Pleotelson tapering, lateral margins smooth (fig. 3.38k) ..... *Xigonus*

– Pleotelson rounded, lateral margins entirely or partially denticulate (fig. 3.35) 19

19. Head frontal margin evenly convex. Pleotelson anterolateral margin as long as posterolateral margin; denticles on lateral corner only (fig. 3.38j) ..... *Stephenseniellus*

– Head frontal margin with rounded or pointed angle. Pleotelson anterolateral margin shorter than lateral margin; lateral margin entirely denticulate (fig. 3.35i) ..... *Austronanus*

20. Pleotelson lateral margin smooth or with few denticles near uropod 21

– Pleotelson lateral margin denticulate along entire lateral curve 26

21. Pleotelson lateral margin with few denticles near uropod (fig. 3.38e) ..... *Quetzogonium*

– Pleotelson lateral margin smooth 22

22. Pereonites with short middorsal cones (fig. 3.37c) ..... *Kussakinella*

– Pereonites and pleotelson dorsally smooth or with low transverse ridges 23

23. Eyestalks vestigial, about as long as wide 24

– Eyestalks prominent, at least twice as long as wide 25

24. Eyestalks round, angled downward. Head frontal margin convex or straight (fig. 3.37g). Pereopod 1 carpus triangular, flexor margin with 3 straight robust setae (fig. 3.39n). Pereopod 2 carpus and propodus flexor margin with long, slender setae (fig. 3.39r) ..... *Munnogonium*

– Eyestalks conical, angled laterally. Head frontal margin concave in middle, laterally inflated (fig. 3.35d). Pereopod 1 carpus flexor margin with 2 straight robust setae (fig. 3.39h). Pereopod 2 carpus and propodus flexor margin with short robust setae (fig. 3.39q) ..... *Advenogonium*

25. Pereopod 1 carpus triangular, with 2 long and 1 short robust setae (fig. 3.39j). Mandibular palp absent. Uropod endopod acute, curved mediad (fig. 3.39g) ..... *Austrosignum*

– Pereopod 1 carpus oval, with 2 robust setae (fig. 3.39k). Mandibular palp present (fig. 3.39d). Uropod endopod rounded truncate (fig. 3.39f) ..... *Cryosignum*

26. Head frontal margin concave in middle, laterally prominently rounded (fig. 3.38l). Mandibular palp of 3 articles. Antennal article 3 lateral margin expanded (fig. 3.39b) ..... *Zizzygonium*

– Head frontal margin convex or nearly straight. Mandibular palp absent or of 2 articles. Antennal article 3 lateral margin straight 27

27. Antennular peduncle article 1 shorter than or as long as eyestalk. Pleotelson posterior projection with fringe of long setae around apex (fig. 3.37e, f). Pereopod 1 propodus with 1 or 2 robust setae on opposing margin ..... *Meridiosignum*

– Antennular peduncle article 1 at least twice as long as eyestalk. Pleotelson posterior projection without short setae near apex. Pereopod 1 propodus without robust setae on opposing margin 28

28. Pereopod 1 carpus oval, with 3–5 curved robust setae; dactylus with acute posterior spine proximal to accessory claw (fig. 3.39p) ..... *Tethygonium*

– Pereopod 1 carpus triangular, with 2–4 straight robust setae; dactylus without posterior spine proximal to accessory claw (fig. 3.39m) ..... *Metamunna*

29. Pereonite 4 margin not extending laterally as far as margins of 1–3, 5 and 6 (fig. 3.37h) ..... *Neasellus*

– Pereonite 4 lateral margin more or less aligned with other pereonites 30

30. Pleotelson with denticles along entire lateral margin (e.g. fig. 3.38c) 31

– Pleotelson smooth (or 1 or few denticles) along entire lateral margin (e.g. fig. 3.38i) 36

31. Head frontal margin with 2 dorsolateral forward-pointing, flat, rounded or acute projections (fig. 3.38c) ..... *Paramunna*

– Head frontal margin without dorsolateral projections 32

32. Head frontal margin with median projection (fig. 3.37l) ..... *Pagonana*

– Head frontal margin without median projection 33

33. Entire head frontal margin protruding 34

– Head frontal margin not projecting, straight or weakly convex 35

34. Head frontal margin forming broadly rounded curve without lateral corners, anterior and lateral edges upcurved (fig. 3.38a, b) ..... *Palanana*

– Head frontal margin weakly convex to straight; anterior edge only upcurved (fig. 3.38g) ..... *Spiculonana*

35. Head frontal margin projection inconspicuous, convex (fig. 3.36g). Pereonite lateral margins denticulate. Pleotelson posterior margin barely produced, denticulate (fig. 3.36f) ..... *Epipedonana*

– Head frontal margin not produced, straight to weakly convex. Pereonite lateral margins smooth. Pleotelson posterior margin produced, smooth (fig. 3.37k) ..... *Omonana*

36. Head frontal margin with median projection 37

– Head frontal margin straight or broadly rounded, without median projection 39

37. Body tapering posteriorly. Pleotelson lateral margin tapering (fig. 3.38i). Antenna article 3 as long as wide. Pereopod 1 carpus projecting (fig. 3.39o) ..... *Sporonana*

– Body oval in dorsal view. Pleotelson lateral margin rounded. Antenna article 3 longer than wide. Pereopod 1 carpus oval (fig. 3.39i) 38

38. Antennular article 1 cylindrical, inflated. Antenna article 3 subcylindrical, lateral margin convex. Uropods just dorsal to pleotelson margin (fig. 3.36h) ..... *Harrietonana*

– Antennular article 1 expanded, curved ventrally under base of antenna and eyestalk. Antenna article 3 rectangular, laterally expanded (fig. 3.39a). Uropods ventral to pleotelson margin (fig. 3.35e) ..... *Allorostrata*

39. Head frontal margin dorsoventrally flattened, convex, with prominent rounded lateral corners (most species with short median slit). Pleotelson tapering. Uropods fully dorsal on pleotelson, uniramous (fig. 3.35f) ..... *Ascionana*

– Head frontal margin straight or broadly rounded. Pleotelson broadly rounded. Uropods marginal on pleotelson, biramous 40

40. Head frontal margin nearly straight, with angular lateral corners. Pereonite 5 as wide as pereonites 4 and 6 (fig. 3.35g). Pereopod 1 carpus triangular (fig. 3.39i) ..... *Austrimunna*

– Head frontal margin broadly rounded, without angular lateral corners. Pereonite 5 narrower than pereonites 4 and 6 (fig. 3.37b). Pereopod 1 carpus projecting (fig. 3.39l) ..... *Kiklonana*

41. Head without eyes or eyestalks 42

– Head with long eyestalks 43

42. Pereonites 1–6 posterolateral margins and pleotelson margin denticulate (fig. 3.40b) ..... *Dentigonium*

Pereonites 1–6 posterolateral margins and pleotelson margin smooth (fig. 3.40c) ..... *Pleurogonium*

43. Antennular peduncle article 2 with distal spine-like projection exceeding flagellum (fig. 3.40e) ..... *Antennulosignum*

– Antennular peduncle article 2 not projecting (fig. 3.40d) ..... *Pleurosignum*

Abyssianira Menzies, 1956

Diagnosis. Head frontal margin dipping ventrally to thin horizontal plate with evenly serrate convex margin; with long eyestalks. Coxal plates 5–7 visible in dorsal view. Pleotelson lateral margin serrate.

Slope–abyssal (400–5293 m). Tropical Atlantic, Temperate Atlantic South America, Temperate Australasia. 6 species (Menzies, 1956: type species; Just, 1990: rediagnosis; Doti and Roccatagliata, 2006: Atlantic species).

Acutomunna Winkler, 1994

Diagnosis. Head frontal margin convex or subtruncate; with long eyestalks, without ommatidia. Pereonites 1–7 with evenly tapered lateral spines. Coxal plates not visible in dorsal view. Pleotelson more or less flattened; lateral margin denticulate.

Slope, bathyal (1677–2470 m). Tropical Atlantic, Temperate Northern W Pacific. 2 species (Chardy, 1975: type species; Shimomura, 2009; Winkler, 1994: second species).

Advenogonium Just and Wilson, 2007

Diagnosis. Head frontal margin concave in middle, laterally inflated; with eyestalks conical, angled laterally. Coxal plates 5–7 visible in dorsal view. Pleotelson lateral margin smooth. Antennular peduncle article 1 shorter than eyestalk. Pereopod 1 carpus triangular, flexor margin with 2 straight robust setae. Pereopod 1 propodus with 2 robust setae on opposing margin. Pereopod 2 carpus and propodus flexor margin with short robust setae. Uropod endopod apex truncate.

Shelf (15–35 m). Temperate South America (Beagle Channel). 1 species (Doti and Roccatagliata, 2005: description of type species, *Austrosignum fuegiae*; Just and Wilson, 2007).

Allorostrata Winkler, 1994

Diagnosis. Head frontal margin with rounded flat median projection. Coxal plates not visible in dorsal view. Pleotelson with produced posterior margin beyond uropods; lateral margin smooth. Antennular peduncle article 1 longer and wider than article 2, expanded, curved ventrally under base of antenna and eyestalk. Antenna article 3 rectangular, laterally expanded. Pereopod 1 carpus triangular. Uropod ventral to lateral margin.

Shelf (9–60 m). Temperate South America (Magellan Strait). 2 species (Just and Wilson, 2004: rediagnosis).

Antennulosignum Nordenstam, 1933

Diagnosis. Head frontal margin evenly convex; with long eyestalks. Pereonites 2–7 margins with lateral spine. Coxal plates not visible in dorsal view. Pleotelson lateral margin smooth. Antennular peduncle article 2 with distal spine-like projection exceeding flagellum. Mandibular molar process narrow, apex oblique, rounded or pointed.

Shelf (22 m). Temperate South America (Falkland Is). 1 species (Brandt, 1999; Nordenstam, 1933: only species refigured as *Pleurosignum chilense* Menzies, 1962).

Ascionana Just and Wilson, 2004

Diagnosis. Head frontal margin dorsoventrally flattened, convex, with prominent rounded lateral corners (most species with short median slit). Coxal plates not visible in dorsal view. Pleotelson tapering; lateral margin smooth, sometimes with few denticles near uropod. Mandibular palp present, or absent. Pereopod 1 carpus rectangular. Uropod dorsal and well removed from lateral margin.

Subtidal, shelf (1–204 m). Temperate Northern Pacific, Central Indo-Pacific, Temperate Southern Africa, Temperate Australia. 14 species (Just and Wilson, 2004: key to 13 species).

Austrimunna Richardson, 1906

Diagnosis. Head frontal margin almost straight. Coxal plates not visible in dorsal view. Pleotelson subcircular, with produced posterior margin; lateral margin smooth. Mandibular palp absent. Pereopod 1 carpus triangular. Uropod just dorsal to lateral margin.

Shelf (12–60 m). Temperate South America. 1 species (Just and Wilson, 2004: rediagnosis).

Austrogonium Hodgson, 1910

Diagnosis. Head frontal margin evenly convex; without eyes or eyestalks. Coxal plates 2–7 with prominent lateral spines visible in dorsal view. Pleotelson anteriorly narrow, posteriorly bulbous; lateral margin serrate.

Slope (1651–3318 m). Temperate Northern W Pacific, Temperate Pacific South America. 2 species (Shimomura, 2009).

Austronanus Hodgson, 1910

Diagnosis. Head frontal margin angular with pointed or blunt midpoint; with short eyestalks. Coxal plates 5–7 visible in dorsal view. Pleotelson rounded; anterolateral margin shorter than lateral margin; lateral margin entirely denticulate.

Shelf (12–55 m). Temperate South America, Southern Ocean. 6 species (Just and Wilson, 2006: key to 6 species).

Austrosignum Hodgson, 1910

Diagnosis. Head frontal margin evenly convex; with prominent eyestalks, at least twice as long as wide. Coxal plates 5–7 visible in dorsal view. Pleotelson lateral margin smooth. Mandibular palp absent. Pereopod 1 carpus triangular, with 2 long and 1 short robust setae. Pereopod 2 carpus and propodus flexor margin with short robust setae. Uropod endopod acute, curved mediad.

Shelf (13–45 m). Temperate Northern Pacific, Southern Ocean. 4 species (Just and Wilson, 2007; 2021: key to 4 species, distributions).

Bathygonium Kussakin and Vasina, 1984

Diagnosis. Head frontal margin convex, with anterolateral projections; with eyestalks curving posterolaterally anterior to pereonite 1, blind. Coxal plates 2–7 with prominent lateral spines visible in dorsal view. Pleotelson longer than wide; lateral margin serrate.

Slope (807–912 m). Southern Ocean (Scotia Sea). 1 species (Kussakin and Vasina, 1984).

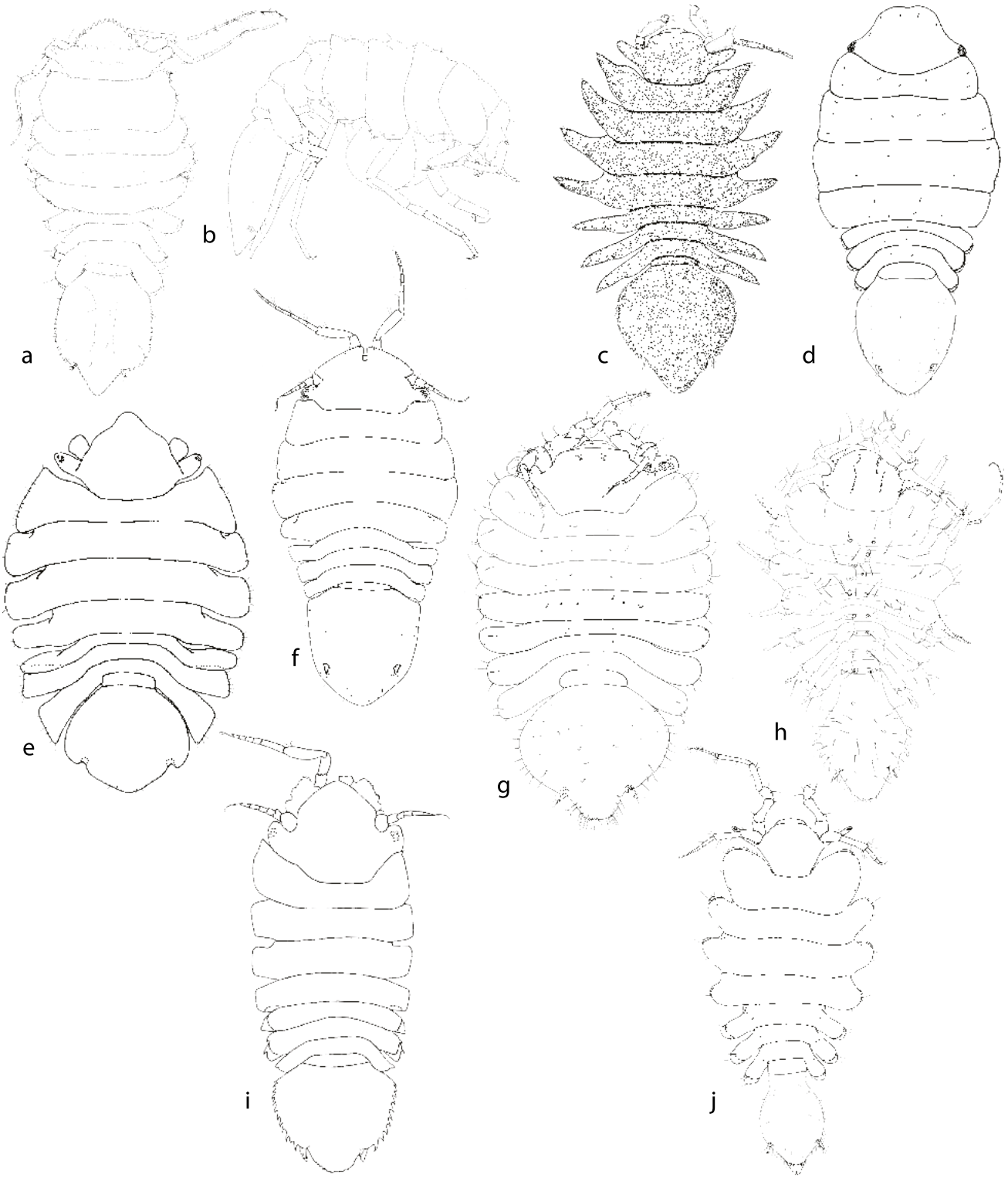


Figure 3.35. Paramunnidae. a, b, *Abyssianira bathyalis* Just, 1990 (dorsal, lateral); c, *Acutomunna foliacea* (Chardy, 1975); d, *Advenogonium fuegiae* (Doti and Roccatagliata, 2005); e, *Allorostrata ovalis* (Winkler, 1994); f, *Ascionana darwinia* Just and Wilson, 2004; g, *Austrimunna antarctica* (Richardson, 1906); h, *Austrogonium japonicum* Shimomura, 2009; i, *Austronanus glacialis* Hodgson, 1910; j, *Austrosignum glaciale* Hodgson, 1910.

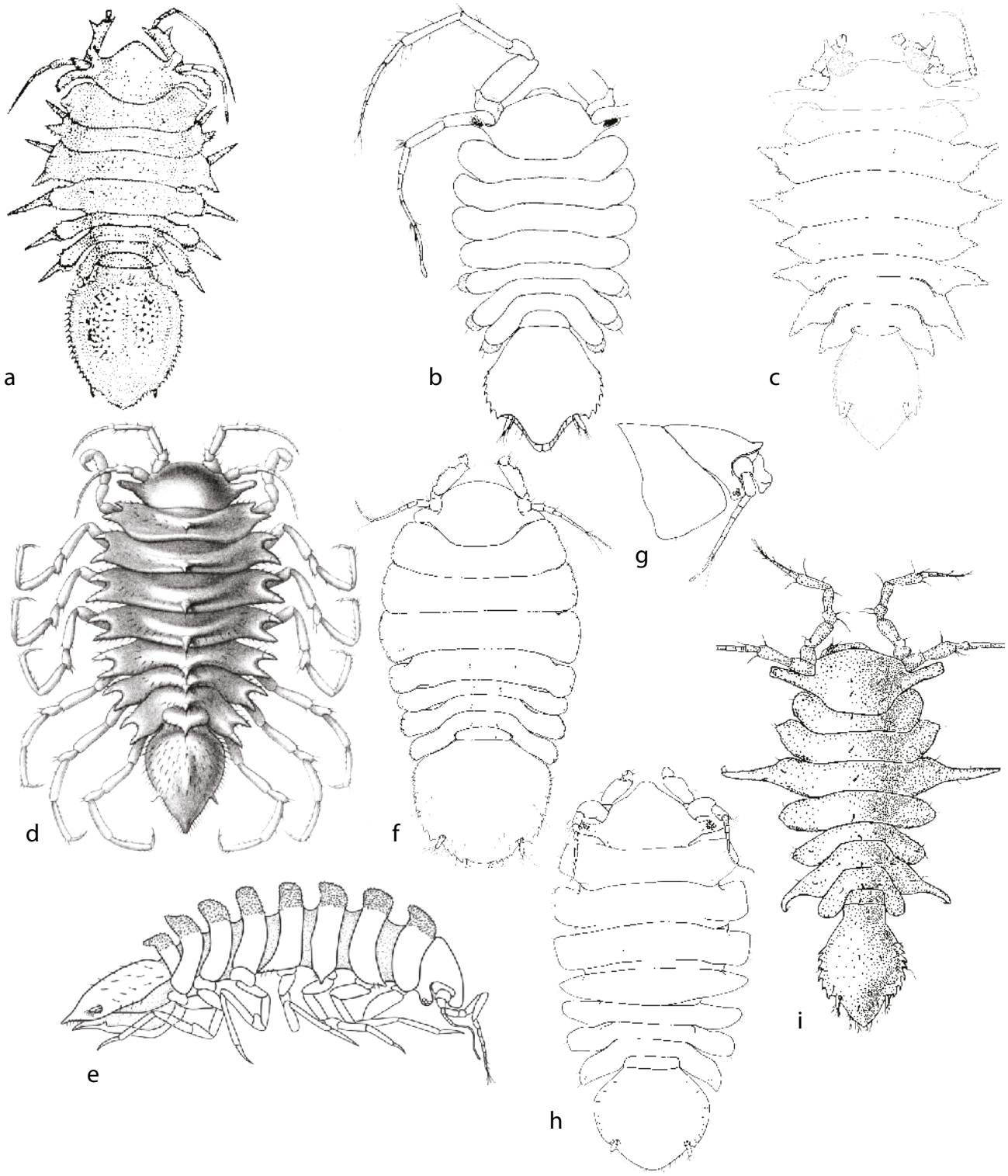


Figure 3.36. Paramunnidae. a, *Bathygonium moskalevi* Kussakin and Vasina, 1984; b, *Metamunna maltini* (Schiecke and Fresi, 1972); c, *Compoceration garyi* Just, 2009; d, *Coulmannia australis* Hodgson, 1910; e, *Coulmannia rossensis* Choudhury, Doti and Brandt, 2011; f, g, *Epipedonana profunda* Just and Wilson, 2004 (dorsal, pereonite 1 and head lateral); h, *Harrietonana subtriangulata* (Richardson, 1908); i, *Heterosignum mutsuensis* Shimomura and Mawatari, 2002.

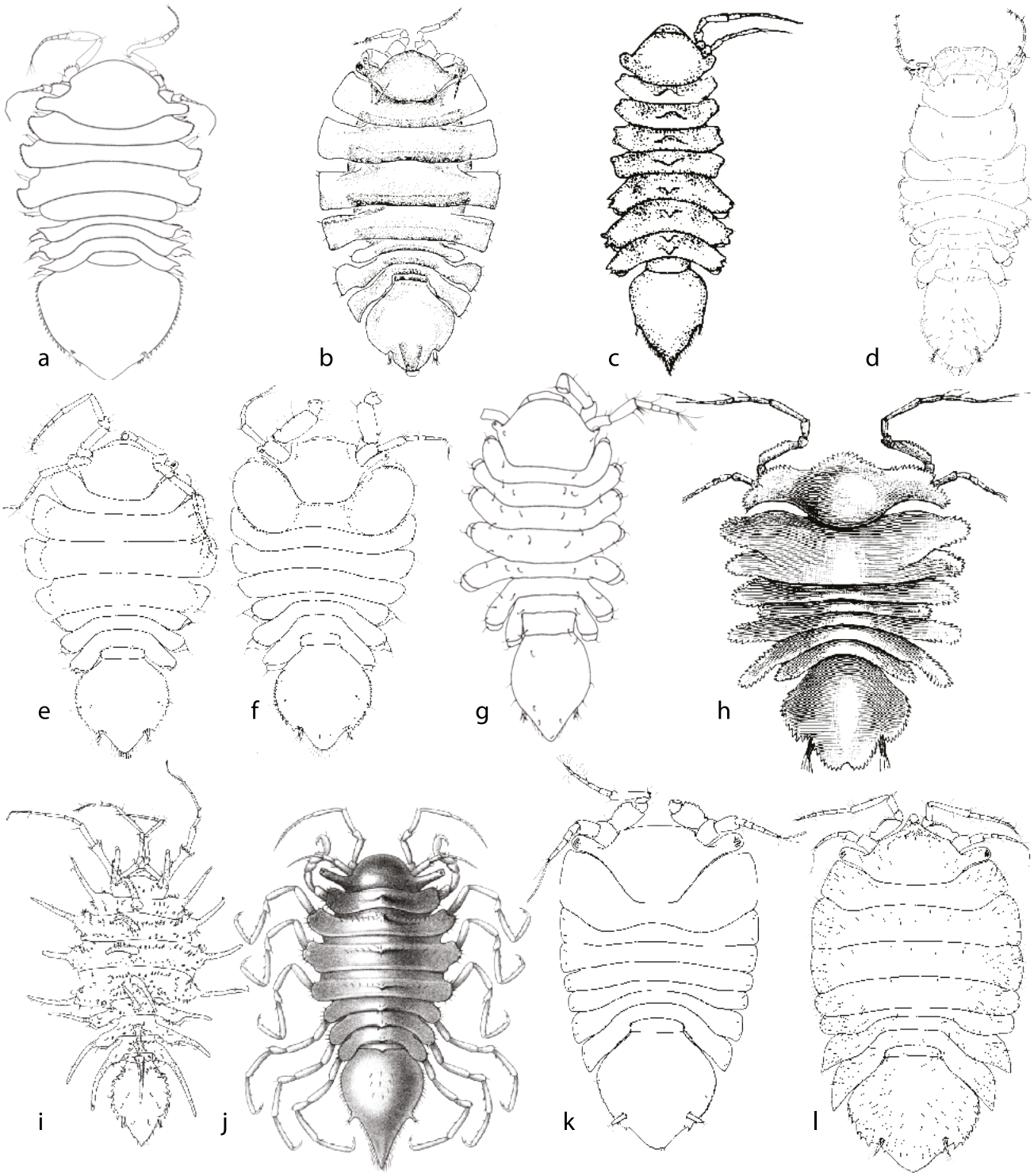


Figure 3.37. Paramunnidae. a, *Holodentata caeca* Doti, Choudhury and Brandt, 2009; b, *Kiklonana arnaudi* (Amar, 1974); c, *Kussakinella spinosum* (Kussakin, 1982); d, *Magellianira serrata* (Winkler, 1994); e, f, *Meridiosignum minidenticulatum* Just and Wilson 2007 (female, male); g, *Munnogonium globifrons* (Menzies, 1962); h, *Neasellus kerguelensis* Beddard, 1885; i, *Notoxenoides setosa* Shimomura, 2009; j, *Notoxenus spinifer* Hodgson, 1910; k, *Omonana brachycephala* Just and Wilson, 2004 (male); l, *Pagonana rostrata* (Hodgson, 1910).

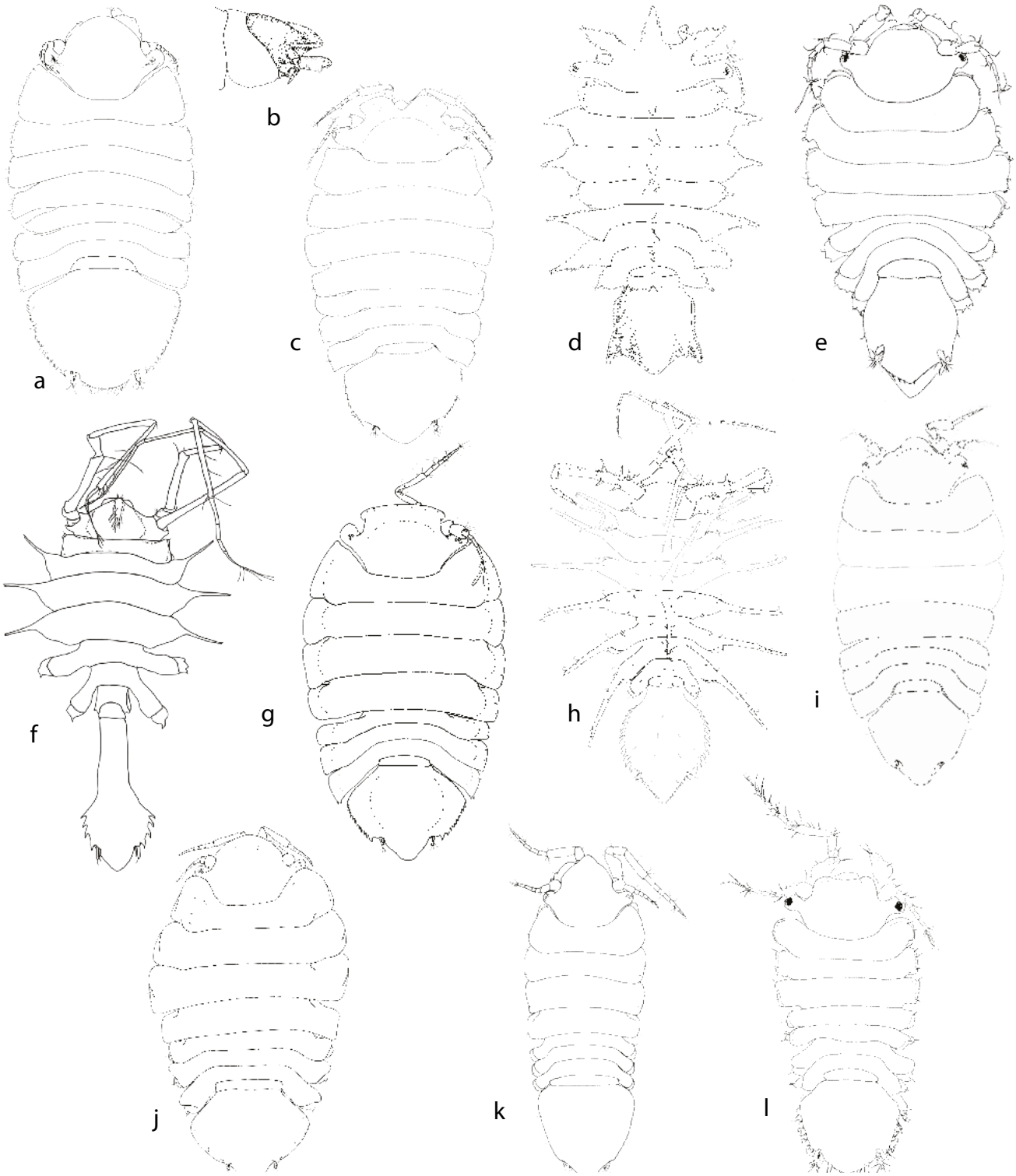


Figure 3.38. Paramunnidae. a, b, *Palanana serrata* (Richardson, 1913) (dorsal, pereonite 1 and head lateral); c, *Paramunna bilobata* G.O. Sars, 1866; d, *Pentaceration bassiana* Just, 2009; e, *Quetzogonium dentatum* (Winkler, 1994); f, *Reductogonium iroquois* Golovan and Malyutina, 2019; g, *Spiculonana platysoma* Just and Wilson, 2004; h, *Spinogonium spinosum* Shimomura, 2009; i, *Sporonana robusta* Just and Wilson, 2004; j, *Stephenseniellus palliolatipes* Just and Wilson, 2006; k, *Xigonus patagoniensis* (Winkler, 1994); l, *Zizzygonium magellanensis* (Winkler 1994).

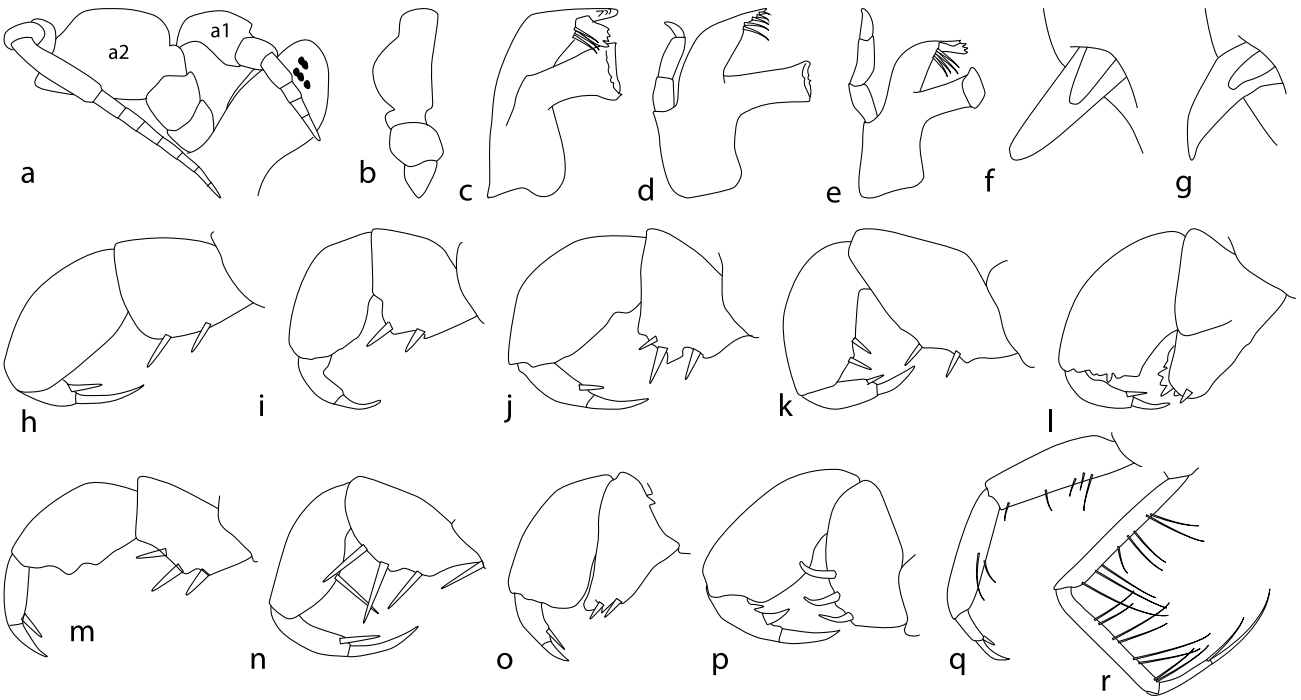


Figure 3.39. Paramunnidae. a, *Allorostrata*, a1 = antennula, a2 = antenna (ventral view, left); b, *Zizzygonium* antennula. Mandibles: c, *Coulmannia*; d, *Cryosignum*; e, *Pentaceration*. Left uropod (dorsal view): f, *Cryosignum*; g, *Austrosignum*. Pereopod 1, carpus–dactylus: h, *Advenogonium*; i, *Austrimunna*; j, *Austrosignum*; k, *Cryosignum*; l, *Kiklonana*; m, *Metamunna*; n, *Munnogonium*; o, *Sporonana*; p, *Tethygonium*. Pereopod 2, carpus–dactylus: q, *Advenogonium*; r, *Munnogonium*.

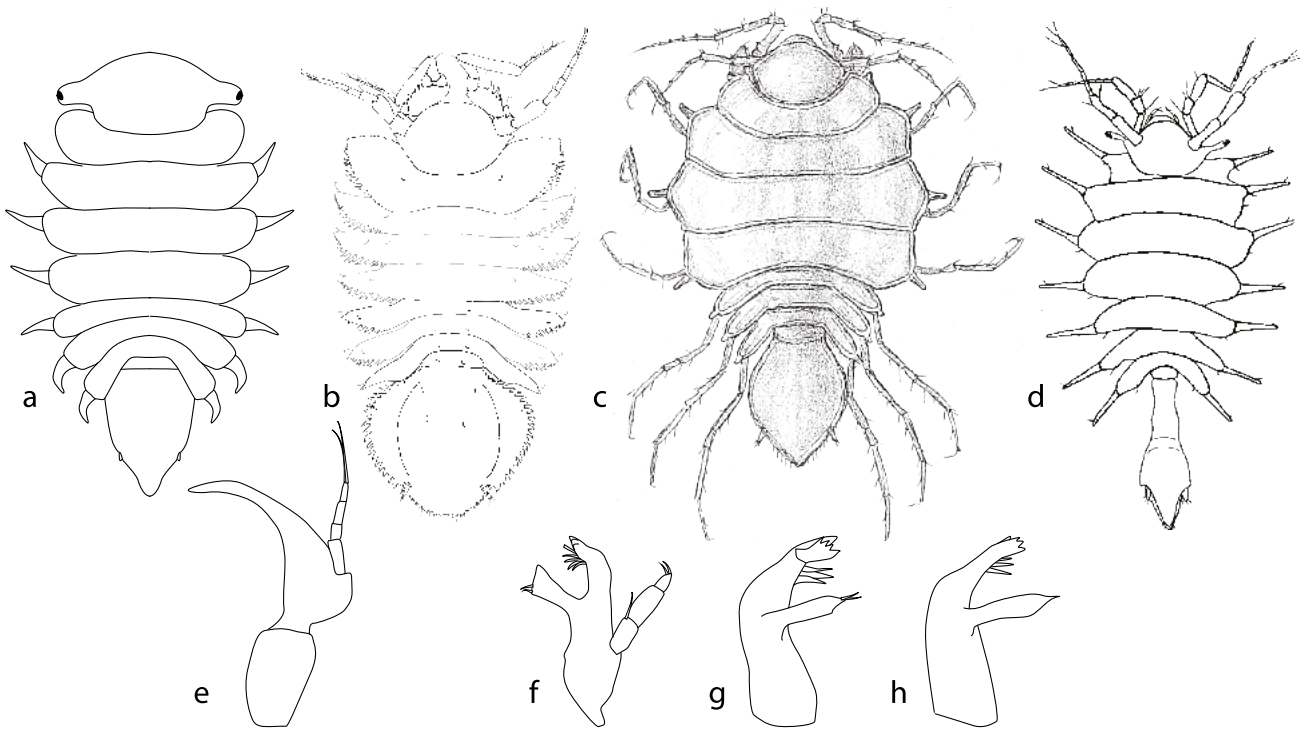


Figure 3.40. Paramunnidae. a, *Antennulosignum elegans* Nordenstam, 1933; b, *Dentigonium tantulum* Shimomura, 2009; c, *Pleurogonium rubicundum* G.O. Sars, 1897; d, *Pleurosignum elongatum* Vanhöffen, 1914; e, *Antennulosignum*, antennula. Mandible: f, *Dentigonium*; g, *Pleurogonium*; h, *Pleurosignum*.

***Compoceration* Just, 2009**

Diagnosis. Head frontal margin without anterior medial spine, upright outgrowths at base of 2 lateral forward-pointing spines; with long eyestalks. Pereonites 1–7 with lateral spines. Coxal plates not visible in dorsal view. Pleotelson more or less flattened; lateral margin serrate.

Slope (220 m). Temperate SE Australia. 1 species (Just, 2009b).

***Coulmannia* Hodgson, 1910**

Diagnosis. Head frontal margin convex, without anterolateral angle; with short eyestalks. Pereonites 1–7 and pleonite 1 each with dorsal spine or crest, sometimes duplicated. Coxal plates visible posteriorly or not. Pleotelson more or less flattened; lateral margin smooth. Mandibular palp absent.

Type species: *Coulmannia australis* Hodgson, 1910, herein designated.

Shelf, slope (89–474 m). Southern Ocean. 4 species (Hodgson, 1910; Choudhury et al., 2011: key to 4 species).

***Cryosignum* Just and Wilson, 2007**

Diagnosis. Head frontal margin evenly convex; with prominent eyestalks, at least twice as long as wide. Coxal plates 2–7 visible in dorsal view. Pleotelson lateral margin smooth. Pereopod 1 carpus oval, with 2 robust setae. Pereopod 1 propodus with 2 robust setae on opposing margin. Pereopod 2 carpus and propodus flexor margin with short robust setae. Uropod endopod apex truncate.

Subtidal, shelf (3–100 m). Temperate South America, Southern Ocean. 4 species (Just and Wilson, 2007; 2021: key to 4 species).

***Dentigonium* Shimomura, 2009**

Diagnosis. Head frontal margin evenly convex; without eyes or eyestalks. Pereonites 1–6 posterolateral margins and pleotelson margin denticulate. Coxal plates not visible in dorsal view. Antennular peduncle article 2 not projecting. Mandibular molar process narrow, apex oblique.

Slope (565–723 m). Temperate Northern W Pacific (Japan). 1 species (Shimomura, 2009).

***Epipedonana* Just and Wilson, 2004**

Diagnosis. Head frontal margin weakly produced, convex, with angular corners. Coxal plates not visible in dorsal view. Pleotelson rounded; lateral margin denticulate. Antenna article 3, 3 times as long as wide, with mesial spine. Pereopod 1 carpus oval. Uropod just dorsal to lateral margin.

Slope (930–1000 m). Temperate Australia. 1 species (Just and Wilson, 2004).

***Harrietonana* Just and Wilson, 2004**

Diagnosis. Head frontal margin with blunt median projection. Coxal plates not visible in dorsal view. Pleotelson subcircular, with weakly produced posterior margin; lateral margin denticulate near uropods. Antennular peduncle article 1 inflated, wider than article 2. Antenna article 3 subcylindrical, lateral margin convex. Pereopod 1 carpus oval. Uropod just dorsal to lateral margin.

Shelf (25 m). Southern Ocean. 1 species (Just and Wilson, 2004).

***Heterosignum* Gamô, 1976**

Diagnosis. Head frontal margin convex, with anterolateral angle at base of antenna; with long eyestalks. Pereonites 1–7 sometimes with sharp dorsal spine, never duplicated; pleonite 1 without dorsal spine. Coxal plates not visible in dorsal view. Pleotelson anteriorly narrow, posteriorly bulbous; lateral margin serrate. Mandibular palp absent.

Shelf (30–135 m). Temperate Northern W Pacific (Japan), Southern Ocean (Amsterdam I.). 7 species (Gamô, 1976; Shimomura and Mawatari, 2002: revised diagnosis, 3 new species; Khalaji-Pirbalouty & Al-Kandari, 2024; key to males).

***Holodentata* Doti, Choudhury and Brandt, 2009**

Diagnosis. Head frontal margin evenly convex; with short eyestalks, with or without ommatidia. Coxal plates 1–7 with short lateral spines visible in dorsal view. Pleotelson wider than long; lateral margin serrate. Mandibular palp absent.

Shelf, slope (84–1584 m). Southern Ocean. 3 species (Doti et al., 2009).

***Kiklonana* Just and Wilson, 2004**

Diagnosis. Head frontal margin broadly rounded, without lateral corners. Coxal plates not visible in dorsal view. Pleotelson subcircular, with produced posterior margin; lateral margin smooth. Antennular peduncle article 1 inflated, wider than article 2. Pereopod 1 carpus distally projecting. Uropod on lateral margin.

Shelf (13–20 m). Southern Ocean (Terre Adélie). 1 species (Amar and Roman, 1974: figures; Just and Wilson, 2004: redescription).

***Kussakinella* Just and Wilson, 2007**

Diagnosis. Head frontal margin evenly convex; with short eyestalks. Pereonites 1–7 with short middorsal conies. Coxal plates 5–7 visible in dorsal view. Pleotelson apex with acute apical spine-like projection; lateral margin smooth. Mandibular palp absent. Pereopod 1 carpus triangular, with 2 straight robust setae; dactylus without posterior spine proximal to accessory claw. Pereopod 2 carpus and propodus flexor margin with short robust setae. Uropod endopod apex truncate.

Shelf (17 m). Temperate South America. 1 species (Kussakin, 1982: type species; Just and Wilson, 2007).

***Magellianira* Winkler, 1994**

Diagnosis. Head frontal margin plate truncate with rounded anterolateral corners, barely serrate; without eyestalks. Coxal plates 1–7 visible in dorsal view. Pleotelson lateral margin denticulate.

Subtidal (10 m). Temperate South America (Magellan Strait). 1 species (Winkler, 1994).

Meridiosignum Just and Wilson, 2007

Diagnosis. Head frontal margin almost straight; with prominent eyestalks, at least twice as long as wide. Coxal plates 5–7 visible in dorsal view. Pleotelson posterior projection with fringe of long setae around apex; lateral margin serrate. Antennular peduncle article 1 shorter than or as long as eyestalk. Mandibular palp absent. Pereopod 1 carpus triangular, with 2 straight robust setae; dactylus without posterior spine proximal to accessory claw. Pereopod 1 propodus with 1 or 2 robust setae on opposing margin. Pereopod 2 carpus and propodus flexor margin with short robust setae. Uropod endopod apex truncate.

Subtidal, shelf (0–129 m). Temperate Atlantic South America, Temperate Australasia, Southern Ocean. 7 species (Just and Wilson, 2007; 2021: key to 7 species).

Metamunna Tattersall, 1905

Diagnosis. Head frontal margin almost straight; with prominent eyestalks, at least twice as long as wide. Coxal plates 2–7 or 5–7 visible in dorsal view. Pleotelson posterior projection with short lateral setae, without setae on apex; lateral margin serrate. Antennular peduncle article 1 longer and wider than article 2, longer than eyestalk. Mandibular palp absent. Pereopod 1 carpus subtriangular, with 2–4 straight robust setae. Pereopod 1 propodus with simple setae on opposing margin. Uropod endopod apex truncate.

Subtidal–slope (0–300 m). Temperate Northern Atlantic, Tropical Atlantic, Temperate Northern W Pacific, Eastern Indo-Pacific, Tropical Eastern Pacific, Temperate Australasia. 8 species. The type species *Metamunna typica* Tattersall, 1905 was redescribed by Bamber and Robbins (2010). *Boreosignum* Just and Wilson, 2007 is treated as a junior synonym and its included species transferred to *Metamunna*. Its type species, *Austrosignum maltinii*, was figured by Schiecke and Fresi (1972).

Munnogonium George and Stromberg, 1968

Diagnosis. Head frontal margin evenly convex, or straight; with eyestalks round, angled downward. Coxal plates 5–7 visible in dorsal view. Pleotelson lateral margin smooth. Antennular peduncle article 1 at least twice as long as eyestalk. Mandibular palp absent. Pereopod 1 carpus triangular, flexor margin with 3 straight robust setae. Pereopod 2 carpus and propodus flexor margin with long, slender setae. Uropod endopod apex truncate.

Subtidal–slope (0–660 m). Temperate Northern Pacific, Temperate South America, Temperate Australasia, Southern Ocean. 11 species (Just and Wilson, 2007: rediagnosis; 2021: key to 8 species; Golovan and Malyutina, 2022: list and distributions of 10 species).

Neasellus Beddard, 1885

Diagnosis. Head frontal margin sinuous; eyestalk club-shaped, curved backwards in distal half, with or without ommatidia. Pereonites 1–3, 5, 6 projecting as rounded spatulate processes; pereonite 4 lateral margin not extending as far as lateral margins of pereonites 3 and 5. Coxal plates not visible in dorsal view. Pleotelson wider than long; lateral margin serrate.

Shelf, slope (110–1373 m). Temperate Atlantic South America, Southern Ocean. 4 species (Beddard, 1885: figure of type species; Doti, 2017: rediagnosis, all species described).

Notoxenoides Menzies, 1962

Diagnosis. Head frontal margin convex, with anterolateral projections; without eyestalks. Pereonites 1–7 with middorsal and lateral spines. Coxal plates 5–7 visible in dorsal view. Pleotelson laterally convex; lateral margin serrate.

Slope, bathyal (565–4047 m). Temperate Northern W Pacific, Tropical Eastern Pacific, Temperate Southern Africa. 5 species (Kensley, 1984; Menzies, 1962; Shimomura, 2009).

Notoxenus Hodgson, 1910

Diagnosis. Head frontal margin evenly convex; with long eyestalks. Pereonites 1–7 with low median projection, without lateral spines. Coxal plates not visible in dorsal view. Pleotelson more or less flattened; lateral margin smooth.

Shelf. Southern Ocean. 1 species (Hodgson, 1910).

Omonana Just and Wilson, 2004

Diagnosis. Head frontal margin almost straight. Coxal plates not visible in dorsal view. Pleotelson laterally rounded, posterior margin produced; lateral margin denticulate. Antennular peduncle article 1 as long as article 2. Pereopod 1 carpus oval. Uropod dorsal and well removed from lateral margin.

Subtidal, shelf (9–100 m). Temperate South America (Magellan Strait), Temperate Australasia (New Zealand). 4 species (Just and Wilson, 2004).

Pagonana Just and Wilson, 2004

Diagnosis. Head frontal margin with median projection. Coxal plates not visible in dorsal view. Pleotelson laterally rounded, posterior margin produced; lateral margin denticulate. Antennular peduncle article 1 longer and wider than article 2. Antenna article 3 with crenulate lateral flange. Pereopod 1 carpus oval. Uropod on lateral margin, or just dorsal to lateral margin.

Shelf. Temperate South America (Magellan Strait), Southern Ocean (Kerguelen I.). 4 species (Just and Wilson, 2004: key to 4 species).

Palanana Just and Wilson, 2004

Diagnosis. Head frontal margin forming broadly rounded curve without lateral corners, anterior and lateral edges upcurved. Coxal plates not visible in dorsal view. Pleotelson laterally rounded, posterior margin produced; lateral margin denticulate. Antennular peduncle article 1 longer and wider than article 2. Pereopod 1 carpus triangular. Uropod on lateral margin.

Subtidal (0.5–23 m). Southern Ocean (Antarctica). 2 species (Just and Wilson, 2004).

Paramunna G. O. Sars, 1866

Diagnosis. Head frontal margin with 2 dorsolaterally projecting lobes. Coxal plates not visible in dorsal view. Pleotelson with produced posterior margin beyond uropods; lateral margin denticulate. Antennular peduncle article 1 as long as article 2, inflated. Pereopod 1 carpus triangular. Uropod on lateral margin.

Subtidal–slope (1–481 m). Temperate Northern Atlantic, Temperate Northern Pacific, Temperate South America, Temperate Southern Africa, Temperate Australasia. 11 species (Just, 1990: type species; Just and Wilson, 2004: rediagnosis,

key to 8 species).

Pentaceration Just, 2009

Diagnosis. Head frontal margin with anterior medial spine or tooth, pair of anterolateral spines; with long eyestalks. Pereonites 1–7 with lateral spines. Coxal plates not visible in dorsal view. Pleotelson more or less flattened; lateral margin serrate.

Subtidal–abyssal (7–5340 m). Central Indo-Pacific, Temperate South America, Temperate Australasia. Atlantic. 23 species (Just, 2009a, 2011: key to 16 Australian species; Doti, 2017: Atlantic species; Peart and Schnabel, 2024: diagnosis; key to 8 New Zealand species).

Pleurogonium G.O. Sars, 1864

Diagnosis. Head frontal margin evenly convex; without eyes or eyestalks. Coxal plates 5–7 or more visible in dorsal view. Pleotelson lateral margin smooth. Antennular peduncle article 2 not projecting. Mandibular molar process narrow, apex oblique, rounded or pointed.

Intertidal–slope (0–1769 m). Arctic, Temperate Northern Atlantic, Temperate Northern Pacific, Southern Ocean. 20 species (figures: Sars, 1896–1899; Shimomura and Mawatari, 2001; Shimomura, 2009).

Pleurosignum Vanhöffen, 1914

Diagnosis. Head frontal margin evenly convex; with long eyestalks. Pereonites 1–7 margins with lateral spine. Coxal plates not visible in dorsal view. Pleotelson lateral margin smooth. Antennular peduncle article 2 not projecting. Mandibular molar process narrow, apex oblique, rounded or pointed.

Intertidal–shelf (22–183 m). Temperate South America, Temperate Southern Africa. 4 species (figures: Kensley, 1977; Vanhöffen, 1914).

Quetzogonium Just and Wilson, 2007

Diagnosis. Head frontal margin concave in middle; with short eyestalks. Coxal plates 5–7 visible in dorsal view. Pleotelson with few denticles near uropod. Antennular peduncle article 1 shorter than eyestalk. Pereopod 1 carpus triangular, with 2 straight robust setae. Pereopod 1 propodus with 2 robust setae on opposing margin. Pereopod 2 carpus and propodus flexor margin with short robust setae. Uropod endopod apex truncate.

Shelf (12–40 m). Temperate South America. Magellan Strait. 1 species (Winkler, 1994: type species; Just and Wilson, 2007).

Reductogonium Golovan and Malyutina, 2019

Diagnosis. Head frontal margin with medial crest bearing tuft of setae on posterior part; without eyestalks. Pereonites 2–4 with long lateral spines. Coxal plates 5, 6 visible in dorsal view; pereonite 7 reduced, without pereopod. Pleotelson anteriorly narrow, posteriorly bulbous; lateral margin serrate. Mandibular palp absent.

Abyssal (5215–5266 m). Temperate Northern W Pacific. 1 species (Golovan and Malyutina, 2019).

Spiculonana Just and Wilson, 2004

Diagnosis. Head frontal margin weakly convex to straight; anterior edge only upcurved. Coxal plates not visible in dorsal view. Pleotelson wider than long; lateral margin denticulate. Antennular peduncle article 1 as long as article 2, tubular. Antenna article 3 tubular. Pereopod 1 carpus triangular. Uropod on lateral margin.

Subtidal–slope (3–400 m). Temperate Australasia. 3 species (Just and Wilson, 2004: key to 3 species).

Spinogonium Shimomura, 2009

Diagnosis. Head frontal margin without anterolateral projections; without eyestalks. Pereonites 1–6 with lateral spines; pleonites 1–3 with middorsal spine. Coxal plates 1–7 visible in males; 1 and 5–7 visible in females in dorsal view. Pleotelson laterally convex; lateral margin serrate.

Slope (565–1769 m). Temperate Northern W Pacific. 2 species (Shimomura, 2009).

Sporonana Just and Wilson, 2004

Diagnosis. Head frontal margin with broad truncate median projection, dorsoventrally thick, rounded. Coxal plates not visible in dorsal view. Pleotelson tapering; lateral margin smooth. Antennular peduncle article 1 as long as article 2, inflated. Antenna article 3 as long as wide. Mandibular palp absent. Pereopod 1 carpus distally projecting. Uropod just dorsal to lateral margin.

Subtidal, shelf (0–20 m). Temperate South America, Temperate Australasia (subantarctic), Southern Ocean. 3 species (Just and Wilson, 2004: key to 3 species).

Stephenseniellus Just and Wilson, 2006

Diagnosis. Head frontal margin produced as large rounded plate; with short eyestalks. Coxal plates 5–7 visible in dorsal view. Pleotelson rounded; anterolateral margin as long as posterolateral margin; denticles on lateral corner only.

Intertidal. Southern Ocean (subantarctic New Zealand, Australia). 2 species (Just and Wilson, 2006: key to 2 species).

Tethygonium Just and Wilson, 2007

Diagnosis. Head frontal margin evenly convex; eyestalk vestigial to twice as long as wide. Coxal plates 1–7 or 5–7 visible in dorsal view. Pleotelson posterior projection with short lateral setae, without setae on apex; lateral margin serrate. Antennular peduncle article 1 at least twice as long as eyestalk. Mandibular palp absent. Pereopod 1 carpus oval, with 3–5 curved robust setae; dactylus with acute posterior spine proximal to accessory claw. Pereopod 2 carpus and propodus flexor margin with short robust setae. Uropod endopod apex truncate.

Shelf, slope (35–1000 m). Temperate Northern Atlantic, Temperate Northern W Pacific, Western Indo-Pacific, Temperate Australasia. 4 species (Just and Wilson, 2007; 2021: key to 4 species).

Xigonus Just and Wilson, 2006

Diagnosis. Head frontal margin angular with pointed or blunt midpoint; with short eyestalks. Coxal plates 5–7 visible in dorsal view. Pleotelson tapering; lateral margin smooth.

Subtidal (12 m). Temperate South America (Magellan Strait). 1 species (Just and Wilson, 2006).

Zizzygonium Just and Wilson, 2007

Diagnosis. Head frontal margin concave in middle, laterally prominently rounded; with prominent eyestalks, at least twice as long as wide. Coxal plates 5–7 visible in dorsal view. Pleotelson lateral margin denticulate. Antennular peduncle article 3 lateral margin expanded. Antenna article 3 lateral margin expanded. Pereopod 1 carpus oval, with 2 robust setae. Pereopod 1 propodus with 1 robust seta on opposing margin. Pereopod 2 carpus and propodus flexor margin with short robust setae. Uropod endopod apex truncate.

Subtidal (9–12 m). Temperate South America (Magellan Strait). 1 species (Winkler, 1994: type species; Just and Wilson, 2007).

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Pleurocopidae Fresi and Schiecke, 1972

Figure 3.41

Pleurocopids are small (<1 mm long) isopods of shallow coral rubble. They are instantly recognised by the large biramous uropods attached near the front of the pleotelson.

Diagnosis. Body flat; pereonites 2–4 and coxa 5–7 with tubular extensions. Pleon of 1 segment, tapering posteriorly. Eyes absent. Antennula flagellum of 6 or 7 articles. Mandible without palp. Maxillipedal palp articles 1–5 narrow, less than half as wide as endite. Pereopod 4 coxa inserting on midlateral margin; pereopodal 2–7 dactyli with 1 unguis. Uropod inserting on anterolateral surface of pleotelson, biramous.

Pleurocope Walker, 1901

Subtidal, shelf (4–17 m). Temperate Northern and Tropical Atlantic, Western and Central Indo-Pacific. 4 species (Shimomura and Naruse, 2015: rediagnosis, key to species).

Reference

Shimomura, M., and Naruse, T. 2015. Two new species of Asellota (Crustacea, Isopoda) from coral reefs on Iriomote Island, Okinawa, Japan. *ZooKeys* 520: 27–40. https://doi.org/10.3897/zookeys.520.5943

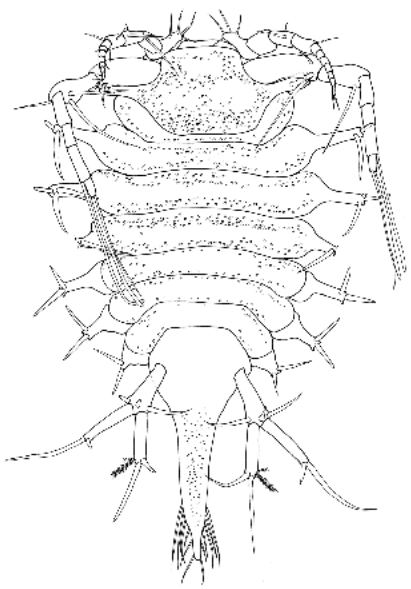


Figure 3.41. Pleurocopidae, *Pleurocope iriomotensis* Shimomura and Naruse, 2015.

Santiidae Kussakin, 1988

Figure 3.42

Santiids are small (usually <2 mm long) isopods of shallow coral or rubble sediments; some are associated with sponges. All are more or less oval, about twice as long as wide, have eyes on short stalks and an exposed anus. *Halacarsantia*, *Santia* and *Spinosantia* are recognisable by the numerous robust setae around the margins of the body and/or coxae. The family and four of its five genera were diagnosed by Wolff (1989). The fifth genus was included in Wolff's key but not named until later (Wolff and Brandt, 2000).

Diagnosis. Body oval, usually flat; head frontal margin usually convex; pereonites similar, wider than long. Pleon of 1 free pleonite plus pleotelson, or of 1 segment. Anus not covered by pleopodal operculum. Eyes on lateral process. Antennula much shorter than head width; flagellum with at most 3 articles. Antennal scale small, or absent. Maxillipedal palp articles 1–5 narrow, less than half as wide as endite. Pereopod 1 prehensile; pereopods 2–7 ambulatory; pereopod 4 coxa inserting on midlateral margin; pereopodal 2–7 dactyli with 2 claws. Uropod inserting posterolaterally, usually biramous.

Implicit generic characters. Epistome not or scarcely projecting. Antennula article 1 rounded distally. Male pleopod 2 not extending laterally beyond pleotelson margins.

Key to genera of Santiidae

1 . Pleotelson much longer than wide, tapering over posterior third. Male pleopod 2 strongly inflated, extending laterally well beyond pleotelson margins, visible dorsally (fig. 3.42c, h) ..... *Prethura*

– Pleotelson oval or pyriform or with truncate distal margin. Male pleopod 2 not extending laterally beyond pleotelson margins 2

2. Epistome strongly projecting, longer than head (fig. 3.42b) ..... *Kuphomunna*

– Epistome not projecting 3

3. Head frontal margin with large, broadly rounded lobe with fringe of spines. Pleon comprising pleotelson only (fig. 3.42a). Uropod uniramous (fig. 3.42g) ..... *Halacarsantia*

– Head frontal margin usually straight, occasionally with 2 rounded lobes. Pleon comprising free pleonite 1 plus pleotelson. Uropod biramous (fig. 3.42e, i) 4

4. Pleotelson posterior apex rounded (fig. 3.42d). Antennula article 1 rounded distally ..... *Santia*

– Pleotelson hexagonal, posterior apex almost straight (fig. 3.42e). Antennula article 1 with distolateral extension with strong spine (fig. 3.42f) ..... *Spinosantia*

Halacarsantia Wolff, 1989

Diagnosis. Body flat. Head frontal margin with large, broadly rounded lobe with fringe of robust setae. Pleon comprising pleotelson only; pleotelson pentagonal, posterior apex rounded. Uropod uniramous.

Subtidal (often with sponges). Tropical Atlantic, Temperate Northern Pacific, Central and Eastern Indo-Pacific, Temperate Australasia. 8 species (Wolff, 1989; Shimomura and Ariyama, 2004: association with sponges; Shimomura and Bruce, 2012: rediagnosis, key to 7 species; Ortiz and Winfield, 2015: key to 8 species).

Kuphomunna Barnard, 1914

Diagnosis. Body flat. Head frontal margin concave-straight; epistome strongly projecting in male, less so in female, longer than head. Pleon comprising free pleonite 1 plus pleotelson; pleotelson tapering. Uropod biramous.

Subtidal. Temperate Southern Africa. 1 species (Barnard, 1914; Wolff, 1989: rediagnosis).

Prethura Kensley, 1982

Diagnosis. Body vaulted. Head frontal margin concave–straight. Pleon comprising free pleonite 1 plus pleotelson; pleotelson much longer than wide, tapering over posterior third. Male pleopod 2 strongly inflated, extending laterally well beyond pleotelson margins, visible dorsally. Uropod uniramous, peduncle extended beyond endopod.

Shelf (coral reef). Central Indo-Pacific (Qld, Australia; Ryukus, Japan). 2 species (Kensley, 1982; Shimomura and Naruse, 2015: seceond species).

Santia Sivertsen and Holthuis, 1980

Diagnosis. Body flat. Head frontal margin convex. Pleon comprising free pleonite 1 plus pleotelson; pleotelson posterior apex rounded. Uropod biramous.

Intertidal, subtidal. Tropical Atlantic, Temperate Northern Pacific, Western Indo-Pacific, Temperate South America, Southern Ocean. Chile. 19 species (Wolff, 1989: rediagnosis, key to 13 species; Kensley and Schotte, 2002: key to 4 Indian Ocean species).

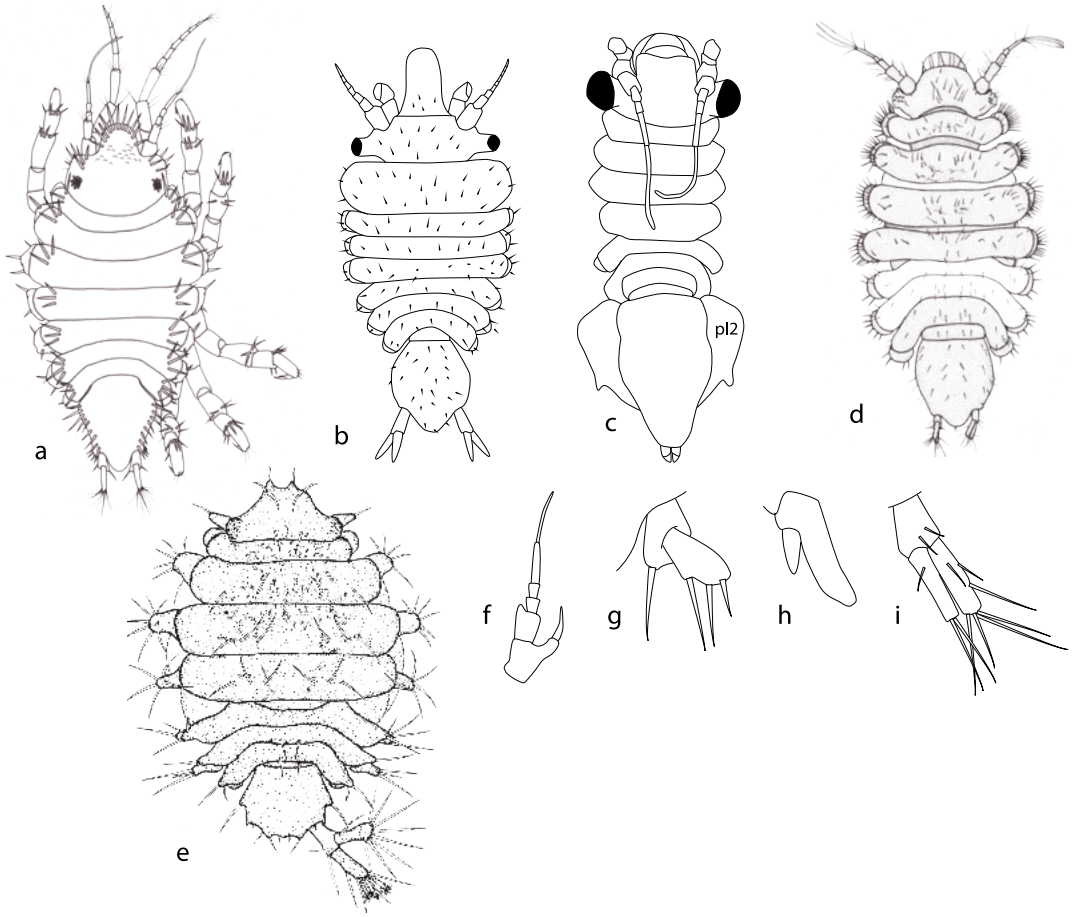


Figure 3.42. Santiidae. a, *Halacarsantia justi* Wolff, 1989; b, *Kuphomunna rostrata* Barnard 1914; c, *Prethura tuberculata* Shimomura and Naruse, 2015 (pl2 = male pleopod 2); d, *Santia lisbethae* Wolff and Brandt, 2000; e, *Spinosantia muelleri* Wolff and Brandt, 2000; f, antennula, *Spinosantia*. Left uropod: g, *Halacarsantia*; h, *Prethura*; i, *Santia*.

Spinosantia Wolff and Brandt, 2000

Diagnosis. Body vaulted. Head frontal margin concave. Pleon comprising free pleonite 1 plus pleotelson; pleotelson hexagonal, posterior apex transverse. Antennula article 1 with distolateral extension with strong spine. Uropod biramous.

Subtidal (0–30 m). Tropical Atlantic (Barbados, Columbia). 1 species (Wolff and Brandt, 2000).

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Thambematidae Stebbing, 1912

Figure 3.43

Thambematids are slender subcylindrical blind isopods, adults being 2.4–8.5 mm long (Harrison, 1987). They are notable in that pleopods 1 and 2 cover the remaining pleopods incompletely. Although Harrison (1987) rediagnosed the family, Zemko and Kaiser (2012) discussed problems distinguishing the family from 'Microjanirinae' (a nomen nudum) and Microparasellidae. While thambematids are relatively rare among families of deep-sea asellotes, Zemko and Kaiser (2012) noted reports of unidentified specimens in several deep-sea surveys. Harrison (1987) discussed potential differences between the antennae of the two genera, but these are difficult to interpret.

Diagnosis. Body elongate, subcylindrical; head frontal margin projecting forward; pereonites 2–7 longer than wide. Pleon of one free pleonite plus pleotelson. Anus not covered by pleopodal operculum. Eyes absent. Antennal scale absent. Maxillipedal palp articles 1–3 wider than distal articles. Pereopod 1 subchelate; pereopods 2–7 ambulatory, dactyli with one unguis plus small accessory unguis or long seta; pereopod 4 coxa inserting on anterolateral margin. Pleopods 1, 2 covering pleopods 3–5 incompletely. Uropod inserting posteriorly, biramous.

Microthambema Birstein, 1961

Diagnosis. Maxilla lobes of similar length (fig. 3.43e). Pleopod 3 uniramous (fig. 3.43h). Maximum length, 2.7 mm.

Abyssal (4820–5690 m). GOODS bathyal province: Northern N Pacific. 1 species (Birstein, 1961; Harrison, 1987: difference between genera).

Thambema Stebbing, 1912

Diagnosis. Maxilla middle lobe shorter than inner and outer lobes (fig. 3.43f). Pleopod 3 biramous (Fig. 3.43i). Maximum length 2.8–8.5 mm.

Shelf–hadal (45–8192 m). Temperate Northern Atlantic, Central Indo-Pacific, Temperate Australasia. GOODS bathyal provinces: Antarctic, S Atlantic. 5 species (Harrison, 1987: descriptions of 4 species; Zemko and Kaiser, 2012: rediagnosis, key to species).

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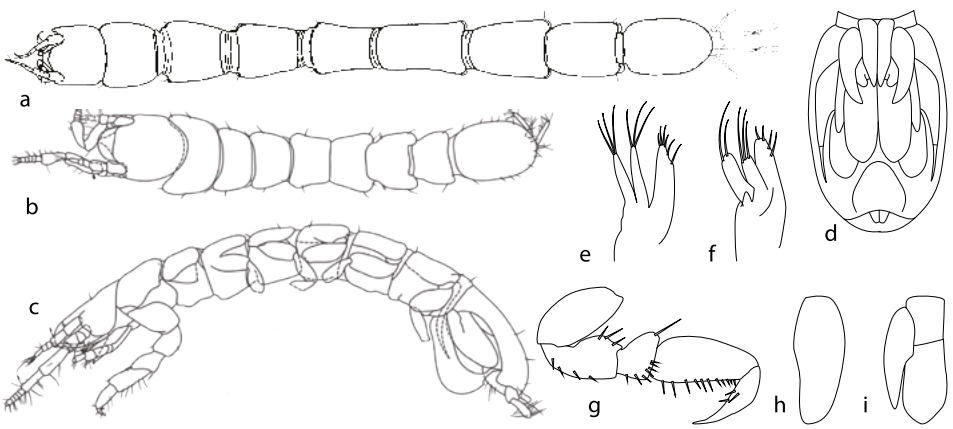


Figure 3.43. Thambematidae. a, *Thambema amicorum* Stebbing 1912; b, c, *Thambema thunderstruckae* Zemko and Kaiser, 2012; d, male pleon, ventral view (showing pleopods), *Thambema*. Maxilla: e, *Microthambema*; f, *Thambema*. g, Pereopod 1, *Thambema*. Pleopod 3: h, *Microthambema*; i, *Thambema*.

Urstylidae Riehl, Wilson and Malyutina, 2014

Figure 3.44

Urstylids occur in abyssal soft sediments near manganese nodules and hydrothermal vents. They are similar to macrostylids but have spade-like heads and lack the pereonal fusion seen in the larger family (Riehl et al., 2014). Adults reach 2 mm in length.

Diagnosis. Body elongate, subcylindrical; head frontal margin projecting forward; pereonites 2–4 similar, rectangular, 5–7 trapezoid, without lateral projections. Pleon of 1 free pleonite plus pleotelson. Anus not covered by pleopodal operculum. Eyes absent. Antennal scale small. Maxillipedal palp articles 1–3 wider than distal articles. Pereopod 1 simple, carpus trapezoidal; pereopods 2–7 ambulatory; 4 coxa inserting on anterolateral margin. Uropod inserting on posterolateral margin, peduncle long, exopod rudimentary.

Urstylis Riehl, Wilson and Malyutina, 2014

Bathyal, abyssal (2730–5223 m). GOODS bathyal provinces: S Atlantic, N Pacific. 3 species (Riehl et al., 2014).

Reference

Riehl, T., Wilson, G.D.F., and Malyutina, M. 2014. Urstylidae – a new family of abyssal isopods (Crustacea: Asellota) and its phylogenetic implications. *Zoological Journal of the Linnean Society* 170: 245–296. https://doi.org/10.1111/zoj.12104

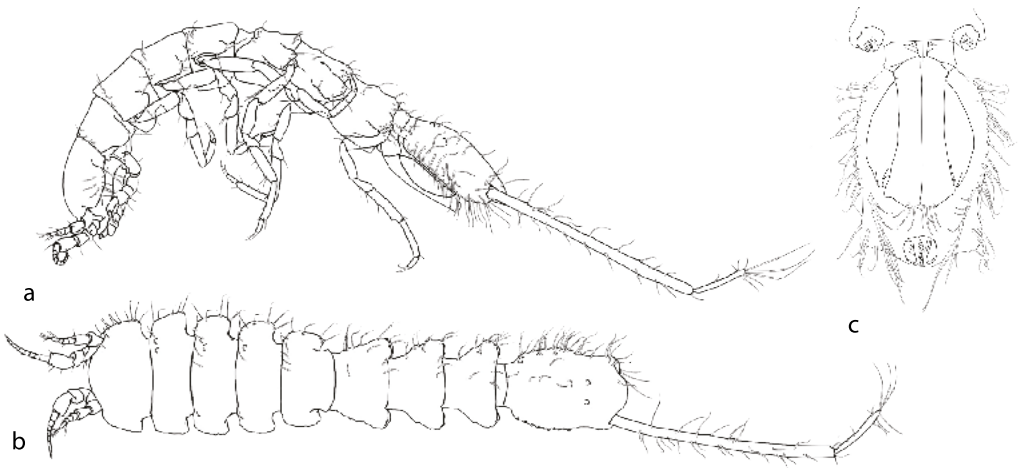


Figure 3.44. Urstylidae, *Urstylis zapiola* Riehl, Wilson and Malyutina, 2014. a, b, lateral, dorsal; c, pleotelson, male (ventral).

Xenosellidae Just, 2005

Figure 3.45

The only species *Xenosella coxospinosa* Just, 2005 is small, 1.4 mm long, and resembles some paramunnids, but has the uropods inserting more dorsally and has long external penes (Just, 2005). The largest individual is 1.4 mm long.

Diagnosis. Body flat; pereonites 5–7 (and 1–4 in male) lateral parts tubular, with large intersegmental gaps. Pleon with 1 free pleonite; pleotelson with elongate anterior neck. Eyes absent. Antennula longer than antenna. Maxillipedal palp articles 1–5 narrow, less than half as wide as endite. Pereopod 1 subchelate; pereopods 2–7 ambulatory; pereopodal 2–7 dactyli with 1 unguis. Uropod inserting posterodorsally, minute, without peduncle.

Xenosella Just, 2005

Slope (800–1600 m). Temperate SE Australia. 1 species (Just, 2005).

Reference

Just, J. 2005. Xenosellidae, a new family of Janiroidea (Asellota: Isopoda: Crustacea), for *Xenosella coxospinosa* gen. nov., sp. nov., from the marine bathyal of eastern Australia. *Zootaxa* 1085: 21–32. https://doi.org/10.11646/zootaxa.1085.1.2

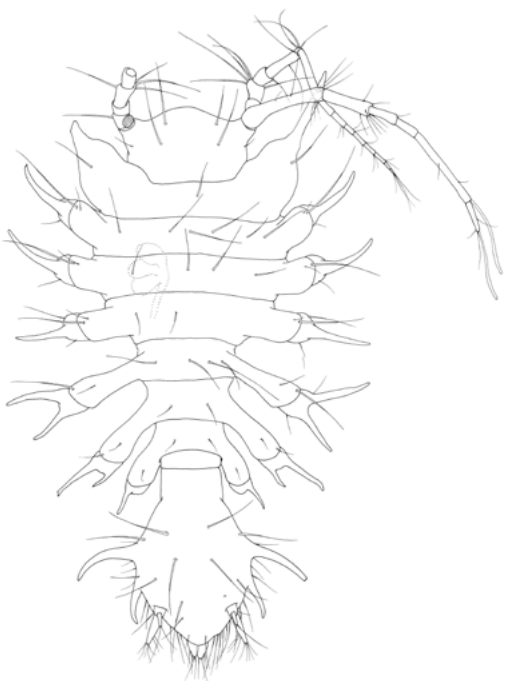


Figure 3.45. Xenosellidae, *Xenosella coxospinosa* Just, 2005 (female).

Janiroidea incertae sedis

Figure 3.46

Four genera can not be placed in any of the janiroid families as currently diagnosed.

Angeliera Chappuis and Delamare-Deboutteville, 1952

Diagnosis. Body elongate, subcylindrical. Anus not covered by pleopodal operculum. Eyes absent. Antennula with 7 articles. Antennal scale absent. Maxillipedal palp of 4 articles, last article sickle-shaped. Pereopods 1–7 ambulatory; pereopod 5 sexually dimorphic, in male subchelate, stout; pereopodal 2–7 dactyli with 3 claws. Uropod inserting posteriorly, biramous.

Intertidal marine beaches, sometimes with depressed salinity, freshwater. Temperate Northern and Tropical Atlantic, Western Indo-Pacific. NE Australia. 9 species (fig. 3.46a, e). The genus has been referred to the Microparasellidae (Wilson and Wägele, 1994) but with reassessment of this and other families its position became less certain (Galassi et al., 2016; Just and Poore, 1992). The antennula with 7 articles and the last article of the maxillipedal palp are unique within Janiroidea. Species of *Angeliera* are small, about 1 mm long, extremely elongate. Four species live in interstitial sands. Stock (1977) reviewed species groups but others have been described since (Kensley, 1984), including one from a stream in Australia (Stock, 1985).

Sugoniscus Menzies and George, 1972

Diagnosis. Body oblong, depressed; head with frontal margin projecting well forward, head including rostrum twice as long as wide; pereonites much wider than long, with acute spinulose lateral extensions. Pleon of 1 segment. Eyes absent. Antennula longer than head. Mouthparts projecting strongly anteriorly. Mandible lanceolate, exposed in dorsal view. Maxillipedal palp of 3 articles, much wider than endite. Pereopods 1–7 ambulatory; pereopod 4 coxa inserting on anterolateral margin; pereopodal 2–7 dactyli with 1 unguis. Uropod inserting posteriorly, biramous.

Abyssal (3909–4925 m). GOODS bathyal provinces: Nazca Plate. 1 species (fig. 3.46b). Menzies and George (1972) placed their new genus in Nannoniscidae but Siebenaller and Hessler (1981) excluded it in their review of this family. The only species has a prominent rostrum and mouthparts.

Trichopleon Beddard, 1886

Diagnosis. Body elongate–oval, splayed laterally; head frontal margin projecting forward; pereonites similar, rectangular, without lateral projections. Pleon of 1 segment. Eyes absent. Antennula half as long as body. Antenna peduncle more than half body length, flagellum multiarticulate; antennal scale present. Maxillipedal palp articles 1–3 wider than distal articles, as wide or wider than endite. Pereopods 1–7 ambulatory; pereopod 4 coxa inserting on anterolateral margin; pereopodal 2–7 dactyli with 2 claws. Uropod inserting posteriorly, biramous.

Slope (900 m). Central Indo-Pacific. 1 species (Beddard, 1886a, b) (fig. 3.46c). Wilson and Wägele (1994) rediagnosed *Trichopleon* but were unable to place the only species in any family. They believed it may be related to *Xostylus*.

Xostylus Menzies, 1962

Diagnosis. Body flat, slender, almost parallel-sided; head frontal margin projecting forward; pereonites similar, rectangular, without lateral projections. Pleon of 1 free pleonite plus pleotelson. Eyes absent. Antennula as long as head width. Maxillipedal palp articles 1–3 wider than distal articles, as wide or wider than endite. Pereopods 2–7 ambulatory; pereopod 4 coxa inserting on anterolateral margin.

Abyssal (5005–5056 m). GOODS bathyal provinces: Northern N Pacific, N Atlantic. 2 species (Birstein, 1970; Menzies, 1962) (fig. 3.46d). *Xostylus* was originally placed in Abyssianiridae, now Paramunnidae. Wilson and Wägele (1994) could not place the genus among other deep-sea families that shared some similarities. Species of *Xostylus* are rather undistinguished, with a parallel-side pereon.

Other genera

Five other genera remain even more poorly known.

Ianthe Bovallius, 1881. This name has a complicated taxonomic history, replacing *Tole* Ortmann, 1901 (Boyko, 2024). Richardson (1905) figured the type species as *Ianella spinosa* (Harger, 1879).

Jaerella Richardson, 1911. Vanhöffen (1914) figured the pleotelson of the only species.

Leptaspidia Bate and Westwood, 1868 was described and figured in the original description and may be a member of Paramunnidae.

Rhacura Richardson, 1908. Vanhöffen (1914) figured the pleotelson of the only species.

Urias Richardson, 1911. The only species has not been figured but may be similar to *Dendrotion* G.O. Sars, 1872.

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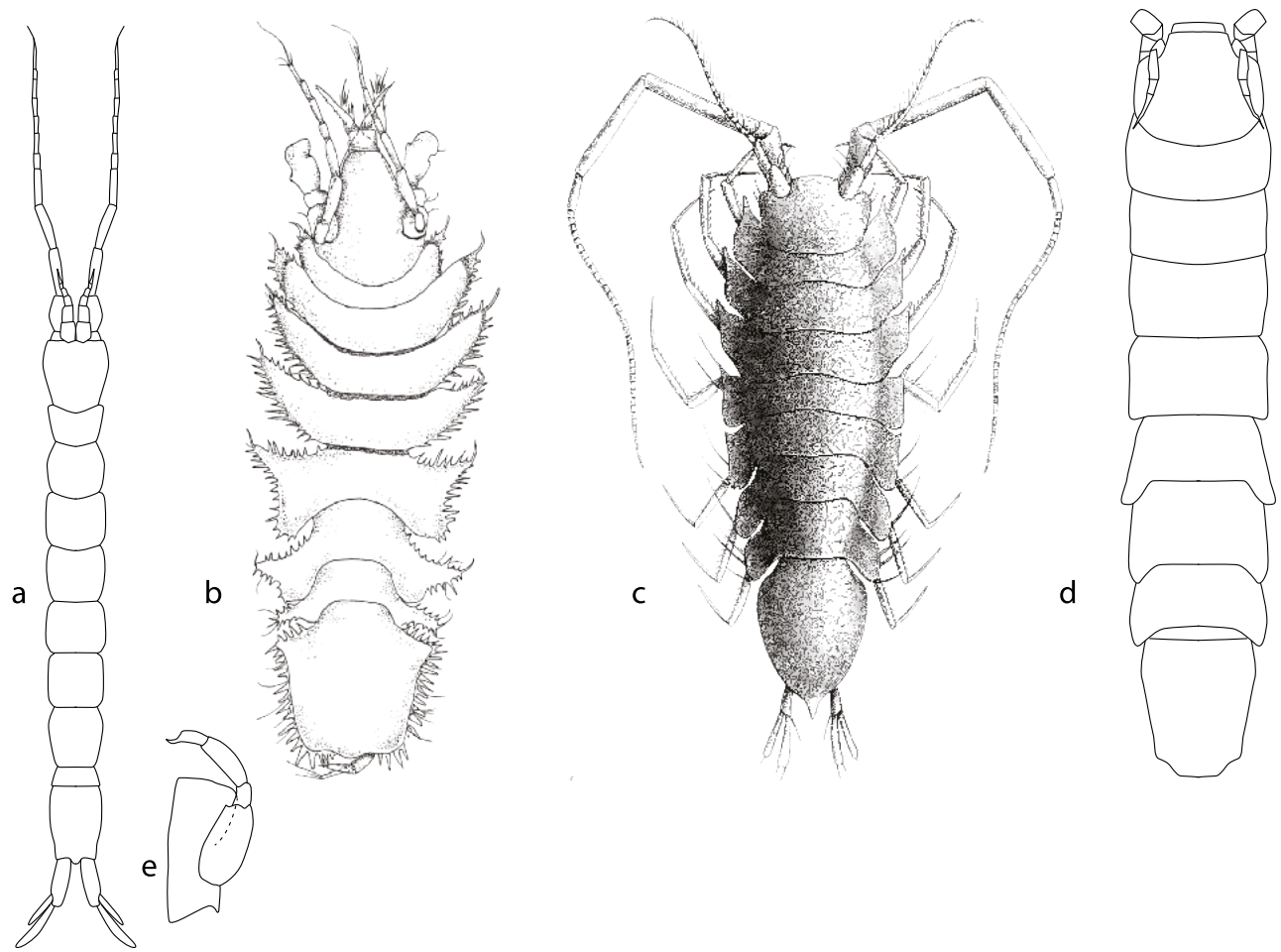


Figure 3.46. Janiroidea incertae sedis. a, *Angeliera*; b, *Sugoniscus parasitus* Menzies, 1972; c, *Trichopleon ramosum* Beddard, 1886; d, *Xostylus parallilus* Menzies, 1962; e, *Angeliera*, maxilliped.

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Superfamily Stenetrioidea Hansen, 1905

The superfamily was diagnosed in detail by Serov and Wilson (1999), who settled on its composition by including two families.

Diagnosis. Male pleopods 1 and 2 much smaller than pleopod 3; peduncles of male pleopods 1 fused. Female pleopods 2 forming small, pear-shaped operculum. Pleopods 3 forming an operculum over pleopods 4 and 5 (figs 3.47e, 3.48r, s).

Key to families of Stenetrioidea

1. Male pleopod 2 peduncle with large distal extension; appendix masculina elongate, narrow, with ventrolateral groove originating proximally; exopod inserting medially (fig. 3.47f–h). Penes adjacent to sternal spine, directed posteriorly, distally pointed (fig. 3.47e) ..... Pseudojaniridae

– Male pleopod 2 peduncle without distal extension; appendix masculina with short ventrolateral pocket or groove originating at midlength; exopod inserting distomedially (fig. 3.48o–q). Penes emerging midway between coxae and sternal spine, directed medially, distally rounded (fig. 3.48r) ..... Stenetriidae

Reference

Serov, P.A., and Wilson, G.D.F. 1999. A revision of the Pseudojaniridae Wilson, with a description of a new genus of Stenetriidae Hansen (Crustacea: Isopoda: Asellota). *Invertebrate Taxonomy* 13: 67–116. https://doi.org/10.1071/IT96038

Pseudojaniridae Wilson, 1996

Figure 3.47

Pseudojanirids are small flat asellote isopods with subchelate first pereopods. Pseudojanirids differ from stenetriids in the absence of posterior extensions on the male pleopod 2 peduncle and a more elongate appendix masculina. Body lengths are up to 5.3 mm. They inhabit marine subtidal and shelf waters in the Southern Hemisphere (Serov and Wilson, 1999).

Diagnosis. Male pleopod 2 peduncle with large distal extension; appendix masculina elongate, narrow, with ventrolateral groove originating proximally; exopod inserting medially (fig. 3.47f–h). Penes adjacent to sternal spine, directed posteriorly, distally pointed (fig. 3.47e).

Key to genera of Pseudojaniridae

1. Pereonal tergites broad, laterally extended, without dorsally visible coxal lobes. Antennal spine on frontal margin of head blunt, markedly reduced or absent (fig. 3.47b). Appendix masculina curved laterally (fig. 3.47g) ..... *Pseudojanira*

– Pereonal tergites with coxal lobes visible on pereonite 4 at least. Antennal spine on frontal margin of head prominent, acutely angular. Appendix masculina straight (fig. 3.47f, h) 3

2. Pereonal tergites sharply angled with single, visible coxal lobe on pereonite 4. Antennal spine on frontal margin of head shorter than lateral spine (fig. 3.47c). Male pleopod 2 peduncle distal extension distally widened, with stylet guide on distal margin (fig. 3.47h) ..... *Schottea*

– Pereonal tergites rounded, with double coxal lobes on pereonite 4, and single lobe on pereonite 5. Antennal spine on frontal margin of head subequal to lateral spine (fig. 3.47a). Male pleopod 2 peduncle distal extension rounded, without stylet guide on distal margin (fig. 3.47f) ..... *Adajinoperus*

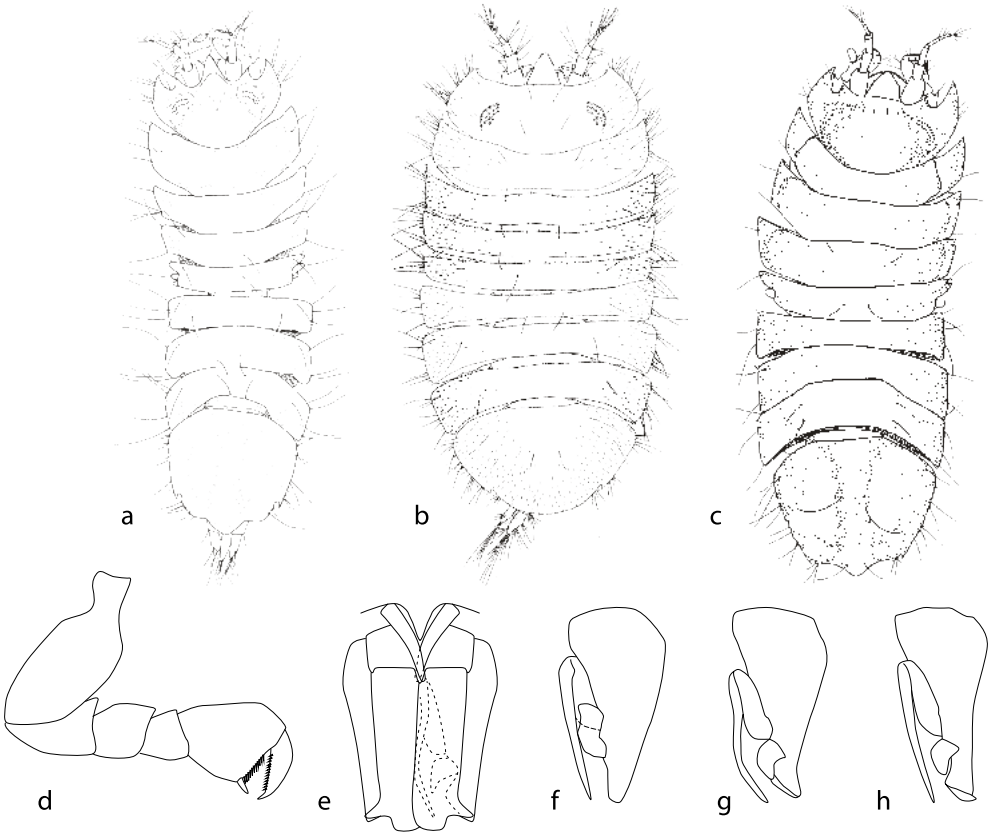


Figure 3.47. Pseudojaniridae. a, *Adajinoperus tetanomorphus* Serov and Wilson, 1990; b, *Pseudojanira fremantlensis* Serov and Wilson, 1990; c, *Schottea taupoensis* Serov and Wilson 1999. d, pereopod 1, *Pseudojanira*. e, penes, male pleopods 1, 2, *Pseudojanira*. Male pleopod 2: f, *Adajinoperus*; g, *Pseudojanira*; h, *Schottea*.

Pseudojanira Barnard, 1925

Diagnosis. Pereonal tergites broad, laterally extended, without dorsally visible coxal lobes. Antennal spine on frontal margin of head blunt, markedly reduced or absent. Male pleopod 2 peduncle distal extension produced into rounded tip, with stylet guide on distal margin; appendix masculina curved laterally.

Subtidal, shelf. Western Indo-Pacific, Temperate Southern Africa, Temperate Australasia. 5 species (Poore and Just, 1990; Serov and Wilson, 1999: rediagnosis, key to 4 species; Kensley and Schotte, 2002: key to 3 Indian Ocean species).

Schottea Serov and Wilson, 1999

Diagnosis. Pereonal tergites sharply angled with single, visible coxal lobe on pereonite 4. Antennal spine on frontal margin of head prominent, acutely angular, shorter than lateral spine. Male pleopod 2 peduncle distal extension distally widened, with stylet guide on distal margin; appendix masculina straight.

Shelf (134–154 m). Temperate Australasia (Taupo Seamount, New Zealand). 1 species (Serov and Wilson, 1999).

Adajinoperus Serov and Wilson, 1999

Diagnosis. Pereonal tergites rounded, with double coxal lobes on pereonite 4, and single lobe on pereonite 5. Antennal spine on frontal margin of head prominent, acutely angular, subequal to lateral spine. Male pleopod 2 peduncle distal extension rounded, without stylet guide on distal margin; appendix masculina straight.

Shelf (51–133 m). Temperate SE Australia. 1 species (Serov and Wilson, 1999).

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Stenetriidae Hansen, 1905

Figure 3.48

Stenetriids are flat elongate isopods up to 6.5 mm long, occurring worldwide in shallow temperate to tropical environments and occasionally in the deep sea. The first pereopod is subchelate, and variously ornamented and enlarged relative to other pereopods. The family was diagnosed in detail by Serov and Wilson (1995) and later revised by Serov and Wilson (1999), Bruce and Buxton (2013) and Bruce and Cumming (2015). An earlier work (Wolff, 1962) provided a key to species of *Stenetrium*, some now in other genera.

Diagnosis. Male pleopod 2 peduncle without distal extensions; appendix masculina with short ventrolateral pocket or groove originating at midlength; exopod inserting distomedially. Penes emerging midway between coxae and sternal spine, directed medially, distally rounded.

Implicit generic attributes. Pereonite 4 without coxae visible in dorsal view. Antenna article 1 lateral spine absent. Male pereopod 1 merus without blade; dactylus subequal to palm. Male pleopod 1 without angular lateral extensions, distolateral margin straight or medially curved. Appendix masculina without large ungrooved distal spine.

Key to genera of Stenetriidae

1. Male pleopod 1 with angular lateral extensions on distal margin (fig. 3.48m). Male pleopod 2 appendix masculina with pocket-like groove from midlength to base of elongate tubular spine (fig. 3.48o) ..... *Lexcenium*
– Male pleopod 1 without angular lateral extensions, distolateral margin straight or medially curved (fig. 3.48n). Male pleopod 2 appendix masculina without large ungrooved distal spines or, if spines present, with 2 or more thin elongate distal spines 2
2. Male pereopod 1 carpus lower margin with large distal process (fig. 3.48g, h, k) 3
– Male pereopod 1 carpus lower margin without distal process 6
3. Male pereopod 1 dactylus subequal to palm (fig. 3.48h). Head without lateral spines (fig. 3.48c) ..... *Liocoryphe*
– Male pereopod 1 dactylus longer than palm. Head with lateral spines 4
4. Pereopod 1 merus with anteriorly projecting blade; palm lower proximal margin with long, acute distal process (fig. 3.48k) ..... *Onychatrium*
– Pereopod 1 merus without blade; palm lower proximal margin without distal process 5
5. Pereopod 1 propodus robust; palm oblique, with 2 teeth (fig. 3.48a, g) ..... *Hansenium*
– Pereopod 1 propodus lower margin bladelike; palm transversely truncate or distally inflected (fig. 3.48i) ..... *Machatrium*
6. Male pleopod 2 appendix masculina distally pointed, with several elongate accessory spines or setae (fig. 3.48q) ..... *Tristenium*
– Male pleopod 2 appendix masculina without both elongate pointed form and several elongate accessory spines or setae 7
7. Male pleopod 2 appendix masculina distally complex with cuticular fan and medially curved narrow process (fig. 3.48p). Male pereopod 1 propodus elongate, much longer than wide, palm narrow (fig. 3.48l) ..... *Stenobermuda*
– Male pleopod 2 appendix masculina without distal cuticular fan and medially curved narrow process. Male pereopod 1 various, with well-developed propodal palm and robust propodus 8
8. Head without lateral extension or spines, antennal spines and rostrum reduced. Pereopod 1 not sexually dimorphic, propodus robust, much wider than head (fig. 3.48d, j) ..... *Mizothenar*
– Head with well-developed lateral spines and lateral fields. Pereopod 1 sexually dimorphic; female propodus less robust than male propodus, narrower than head 9
9. Rostrum robust, more than half as long as head (fig. 3.48e). Pereonite 4 without coxae visible in dorsal view ..... *Protallocoxa*

– Rostrum variable, always less than half as long as head. Pereonite 4 with coxae visible in dorsal view 10

10. Head lateral spines longer than antennal spines. Antenna article 1 spine absent (fig. 3.48f) ..... *Tenupedunculus*

– Head lateral spines as long as antennal spines. Antenna article 1 spine prominent (fig. 3.48b) ..... *Stenetrium*

Hansenium Serov and Wilson, 1995

Diagnosis. Head with lateral spines; rostrum trapezoid, wider than long. Male pereopod 1 carpus lower margin with bladelike serrate process; propodus palm oblique, with 2 teeth; dactylus as long or longer than palm.

Subtidal (coral reefs). Western and Eastern Indo-Pacific. 2 species (Serov and Wilson, 1995; Bruce and Buxton, 2013: rediagnosis, comparison of genera).

Lexcenium Serov and Wilson, 1999

Diagnosis. Head with lateral and antennal spines subequal to rostrum; rostrum denticulate, acute. Propodus with 1 simple robust seta. Male pleopod 1 with angular lateral extensions on distal margin. Appendix masculina with pocket-like groove from midlength to base of elongate tubular spine.

Subtidal, shelf. Temperate Australia. 2 species (Serov and Wilson, 1999).

Liocoryphe Serov and Wilson, 1995

Diagnosis. Head without lateral spines; rostrum short, wide, rounded. Male pereopod 1 carpus lower margin with large distal process; propodus palm serrate.

Subtidal. Tropical W Atlantic, Indo West-Pacific. 4 species (Serov and Wilson, 1995).

Machatrium Bruce and Buxton, 2013

Diagnosis. Head with lateral spines; rostrum trapezoid, wider than long. Male pereopod 1 carpus lower margin with large distal process; propodus lower margin bladelike; palm transversely truncate or distally inflected, lower proximal margin without distal process; dactylus longer than palm.

Subtidal (coral reefs). Tropical Atlantic, Western and Central Indo-Pacific. 8 species (Bruce and Buxton, 2013).

Mizothenar Serov and Wilson, 1995

Diagnosis. Head without lateral extension or spines, antennal spines reduced; rostrum weak, bilobed. Male pereopod 1 carpus lower margin without large distal process; not sexually dimorphic, propodus robust, much wider than head.

Subtidal. Tropical W Atlantic, Eastern Indo-Pacific. 3 species (Serov and Wilson, 1995).

Onychatrium Bruce and Cumming, 2015

Diagnosis. Head with lateral spines; rostrum trapezoid, wider than long. Male pereopod 1 merus with anteriorly projecting blade; carpus lower margin with large distal process; propodus lower margin thick, palm lower proximal margin with long, acute distal process; dactylus longer than palm.

Subtidal (coral reefs). Central and Eastern Indo-Pacific. 4 species (Bruce and Cumming, 2015).

Protallocoxa Schultz, 1978

Diagnosis. Head with lateral spines; rostrum robust, more than half as long as head. Pereonite 4 without coxae visible in dorsal view without coxae visible in dorsal view. Male pereopod 1 carpus lower margin without large distal process; sexually dimorphic; female propodus less robust than male propodus, narrower than head.

Bathyal, abyssal (2818–4540 m). GOODS bathyal provinces: New Zealand/Kermadec, Antarctic. 2 species (Serov and Wilson, 1995: rediagnosis).

Stenetrium Haswell, 1881

Diagnosis. Head with lateral spines as long as antennal spines; rostrum triangular, less than half as long as head. Antenna article 1 lateral spine prominent. Male pereopod 1 carpus lower margin without large distal process; sexually dimorphic; female propodus less robust than male propodus, narrower than head. Appendix masculina without large ungrooved distal spine, distally complex with cuticular fan and medially curved narrow process.

Subtidal–slope (0–460 m). Temperate Northern and Tropical Atlantic, Western Indo-Pacific, Temperate Southern Africa, Temperate Australasia. 26 species (Serov and Wilson, 1995: rediagnosis).

Stenobermuda Schultz, 1979

Diagnosis. Head with sharp triangular lateral spines, reduced antennal spines; rostrum long, robust, acute. Male pereopod 1 carpus lower margin without large distal process; propodus elongate, much longer than wide, palm narrow. Appendix masculina without large ungrooved distal spine, distally complex with cuticular fan and medially curved narrow process.

Subtidal, anchialine cave. Tropical W Atlantic, Temperate Southern Africa. 6 species (Serov and Wilson, 1995: rediagnosis).

Tenupedunculus Schultz, 1979

Diagnosis. Head with lateral fields, lateral spines longer than antennal spines; rostrum triangular, less than half as long as head. Male pereopod 1 carpus lower margin without large distal process; sexually dimorphic; female propodus less robust than male propodus, narrower than head. Appendix masculina with subdistal lateral setal ridge.

Slope–abyssal (500–4696 m). GOODS bathyal provinces: Antarctic, Subantarctic, S Atlantic. 4 species (Serov and Wilson, 1995: rediagnosis).

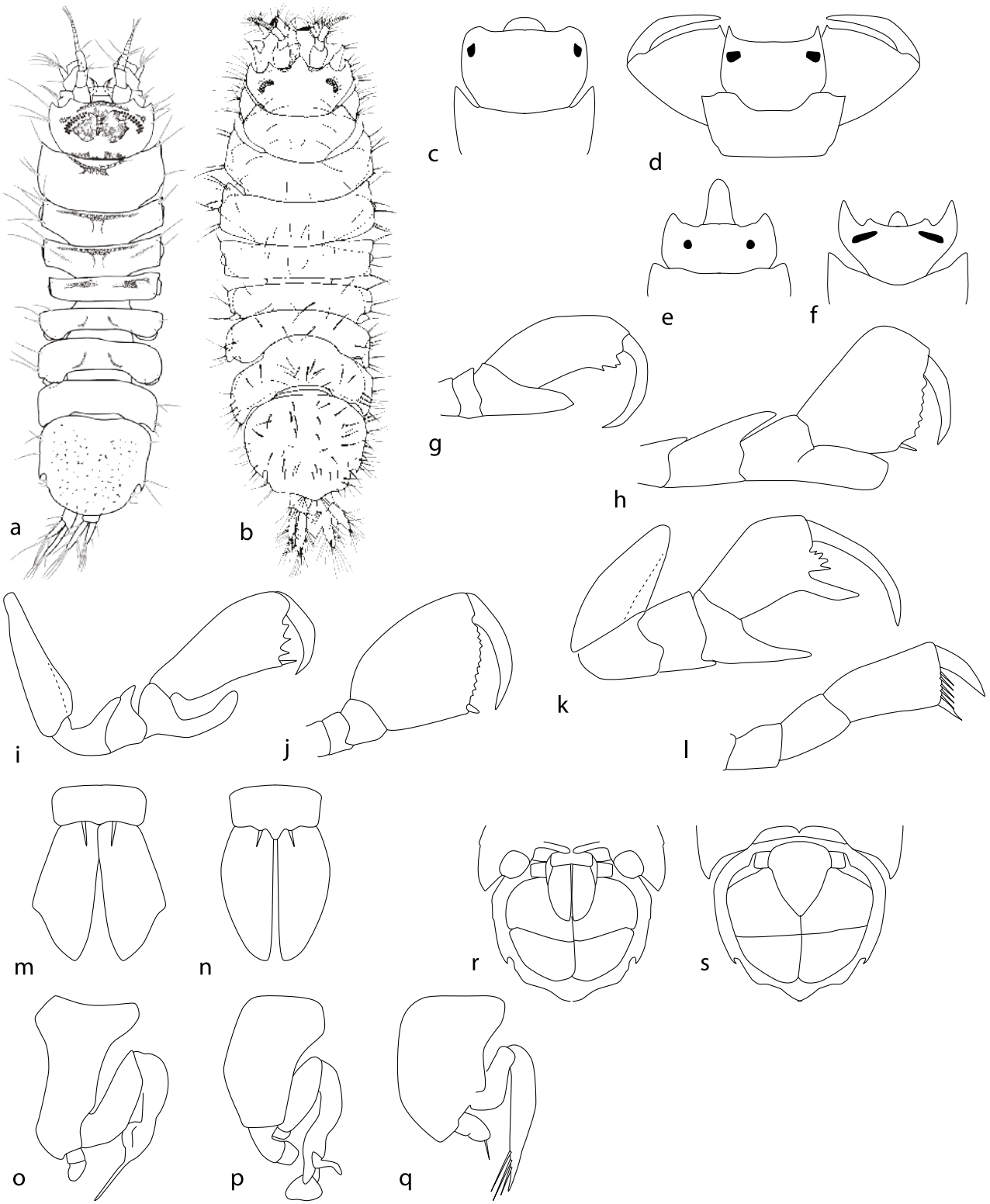


Figure 3.48. Stenetriidae. a, *Hansenium hanseni* (Nobili, 1906); b, *Stenetrium adrianae* Serov and Wilson, 1995. Head, pereonite 1: c, *Liocoryphe*; d, *Mizothenar* (with pereopod 1); e, *Protallocoxa*; f, *Tenupedunculus*. Male pereopod 1: g, *Hansenium*; h, *Liocoryphe*; i, *Machatrium*; j, *Mizothenar*; k, *Onychatrium*; l, *Stenobermuda*. Male pleopods 1: m, *Lexcenium*; n, *Stenetrium*. Male pleopod 2: o, *Lexcenium*; p, *Stenobermuda*; q, *Tristenium*. Pereonite 7, pleotelson (ventral view), *Stenetrium*: r, male (penes, pleopods 1, 3); s, female (fused pleopods 2, pleopods 3).

Tristenium Serov and Wilson, 1995

Diagnosis. Head with weak lateral and antennal spines. Male pereopod 1 carpus lower margin without large distal process; propodus broad, robust, with setae and broad blunt teeth on palm. Appendix masculina without large ungrooved distal spine, distally pointed, with several elongate accessory spines or setae.

Subtidal, slope (0–235 m). Indo-West Pacific. 3 species (Serov and Wilson, 1995).

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Chapter 4. Suborder Microcerberidea

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Diagnoses and illustrated keys are provided for two families and two genera of marine families of isopods of the suborder Microcerberidea. The ecology and distribution of each taxon are discussed with citation of literature critical for further investigation and identification to species.

Keywords Atlantasellidae, Microcerberidae, dichotomous keys

Introduction

The Microcerberidea Lang, 1961[1] are minute interstitial Isopoda found in freshwater environments (Coineau, 1986) and in the groundwater of sandy marine or estuarine beaches or anchialine systems. Some are euryhaline (Albuquerque et al., 2009; Kim et al., 2018). The suborder comprises two families, Atlantasellidae and Microcerberidae.

Atlantasellids are flat oval isopods but members of Microcerberidae are especially slender isopods, a shape typical of many interstitial crustaceans. They were considered members of the superfamily Anthuroidea until Lang (1961) established the suborder Microcerberidea based on the shape of the mouthparts and pereopods. Two phylogenetic analyses found slightly different results for the affinities of Microcerberidea. Wägele (1982) showed that microcerberids, with a highly specialised copulatory male pleopod 2, are not related to anthuroids – he included them in the Asellota superfamily Aselloidea. Brusca and Wilson (1991) found that Microcerberidea, including both Atlantasellidae and Microcerberidae, are a sister taxon to all Asellota. Thomas Thorpe (2024) concluded from molecular evidence that Microcerberidea is a sister taxon to Aselloidea alone.

Diagnosis. Head free from pereonite 1. Pereopodal coxal dorsal plates absent. Pleonites 1, 2 free; pleonites 3–6 fused into pleotelson. Pleotelson underside flat, without ventrolateral ridges (pleopods not enclosed laterally). Telsonic region of pleotelson short, anus situated posteriorly on pleotelson. Mandibular lacinia mobilis present on both sides; molar tapering; palp present. Maxilla trilobed, or bilobed. Maxillipedal endite reaching at least distal margin of palp article 2, usually distally truncate and setose. Pereopods 1–7 similar, directed more or less laterally. Penial processes medial, closer to midpoint than to pereopods. Pleopodal exopods biarticulate. Pleopod 1 absent in both sexes (rarely present in male). Pleopod 2 biramous in male, variously digitate; absent in female. Pleopod 3 peduncle and ramus fused, operculate; endopod more or less oval or rectangular, rounded distally. Uropod terminal; peduncle not operculate; rami terminal.

Key to families of Microcerberidea

1. Body broad, 3 times as long as wide, able to roll. Uropod vestigial, ovoid, not articulating (fig. 4.1a) ..... Atlantasellidae
– Body narrow, about 10 times as long as wide. Uropod biramous, articulating (fig. 4.1b) ..... Microcerberidae

[1] 1 Since this chapter was written Douady et al. (2026) concluded that Microcereberidae belong within Asellota and are sister family to Stenasellidae. Douady, C.J., Malard, F., Coineau, N., Francois, C., Issartel, C., Kim, J., Konecny-Dupré, L., Lefebure, T., Merrin, K.L., and Thomas Thorpe, J.A. 2026. Molecular evidence for the placement of Microcerberidae (Crustacea: Isopoda) within the suborder Asellota and invalidity of the suborder Microcerberidea. *Zoologica Scripta*. https://doi.org/10.1111/zsc.70063

Family Atlantasellidae Sket, 1979

Figure 4.1a

Atlantasellidae, with only one genus, was described as a member of the Asellota similar to the freshwater Asellidae (Sket, 1979). The two species, 1–2 mm long, are confined to a hypersaline coastal cenote in the Dominican Republic and an anchialine cave in Bermuda (Jaume, 2001).

Diagnosis. Body broad, 3 times as long as wide, able to roll. Uropod vestigial, ovoid, not articulating.

Atlantasellus Sket, 1979

Hypersaline coastal cenotes and anchialine caves. 2 species.

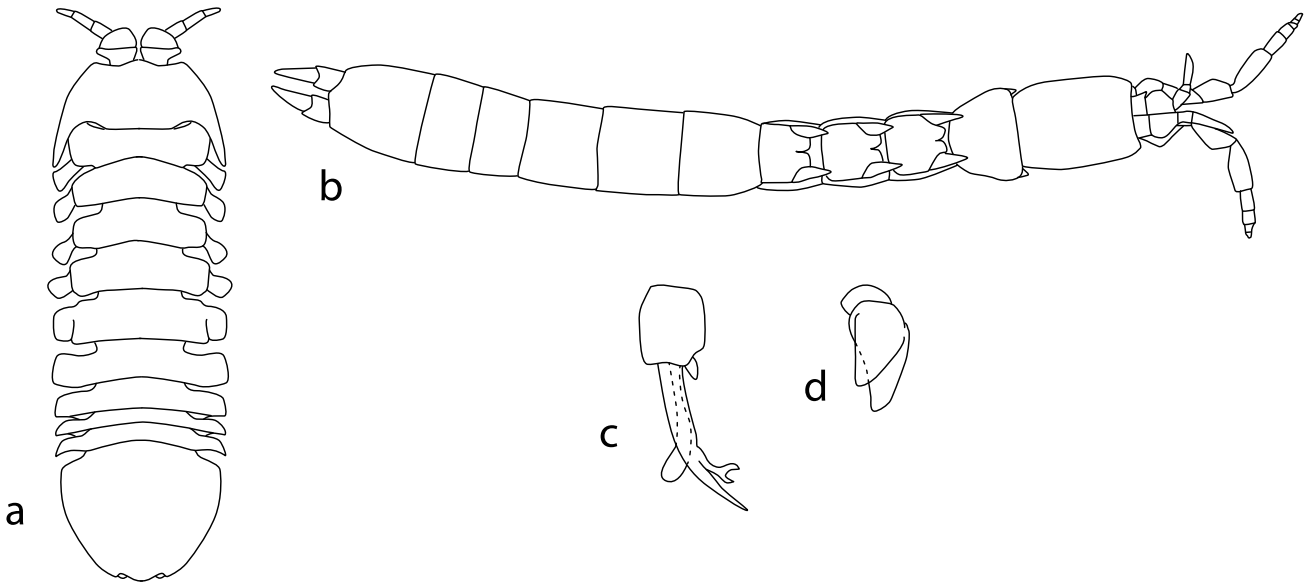


Figure 4.1. Microcerberidea. a, Atlantasellidae, *Atlantasellus*. Microcerberidae, *Robustura*: b, habitus; c, male pleopod 2; d, male pleopod 3.

Family Microcerberidae Karaman, 1940

Figure 4.1b–c

Microcerberids are tiny, no more than 2 mm long, vermiform interstitial isopods (Chappuis and Delamare-Deboutteville, 1954; Karaman, 1940). Wägele (1983a) diagnosed the family. *Microcerberus* Karaman, 1933, with 7 species, inhabits fresh inland ground waters in or near the Mediterranean (Wägele et al., 1995). Six of the eight genera, five of which have only one species, are exclusively from fresh water (Coineau, 1986). *Afrocerberus* Wägele, 1983 and *Protocerberus* Wägele, 1983 are both from rivers in Southern Africa (Wägele, 1983b). *Mexicerberus* Schultz, 1974 is from a pool cave at 1500 m above sea level in Mexico (Schultz, 1974). *Bulgarocerberus* Baldari and Argano, 1984 is from a river in Bulgaria. *Isoyvesia* Özdikmen, 2009 (replacement name for *Yvesia* Coineau and Botosaneanu, 1973) is from a well in Cuba. *Texicerberus* Hutchins, Schwartz and Coleman, 2022, with three species is from subterranean fresh water in Texas, USA. None of these exclusively freshwater genera is included in this key to marine genera. The only key to identification of species does not include all species or recent generic names (Chappuis and Delamare-Deboutteville, 1958). The marine origin of the family has been the subject of considerable discussion (Coineau, 1986; Wägele, 1983a, b; Wägele et al., 1995). One genus has marine representatives. Because individuals are so small and morphological distinctions between species are difficult to discern, molecular differentiation of populations have suggested the existence of cryptic species (Kim et al., 2021).

Diagnosis. Body narrow, about 10 times as long as wide. Uropod biramous, articulating.

Robustura Gnanamuthu, 1954

Diagnosis. Coxae 2–4 transformed into dorsal plates, anterior margin protruding as point. Male pleopod 1 absent. Male pleopod 2 endopod apically bifid or trifid. Pleopod 4 short, rami well covered by pleopod 3, biramous (fig. 4.1c, d).

Brackish, marine ground waters of marine beaches and intertidal zones. Temperate Northern and Tropical Atlantic, Temperate Northern Pacific, Western and Central Indo-Pacific. 33 species (Albuquerque, 1978: Brazilian species as *Microcerberus*; Wägele et al., 1995: diagnosis, species list; Kim et al., 2018: Asian species). *Coxicerberus* Wägele, Voelz and McArthur, 1995 includes *Robustura predatoris* Gnanamuthu, 1954, type species of *Robustura* Gnanamuthu, 1954. *Robustura* is therefore the subjective senior synonym of the commonly used *Coxicerberus*.

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Chapter 5. Suborder Cymothoida

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Abstract Poore, G.C.B., and Bruce, N.L. 2026. Chapter 5. Suborder Cymothoida. *In*: Poore, G.C.B. (ed.) Marine Crustacea Isopoda: guide to families and genera of the world. *Memoirs of Museum Victoria* 86: 135–228.

Diagnoses and illustrated keys are provided for one superfamily of six families, and the remaining nine families, comprising in total 180 marine genera of the Isopoda suborder Cymothoida. The ecology and distribution of each taxon are discussed with citation of literature critical for further investigation and identification to species.

Keywords Aegidae, Antheluridae, Anthuridae, Anthuroidea, Anuropidae, Barybrotidae, Cirolanidae, Corallanidae, Cymothoidae, Cymothooidea, Expanathuridae, Gnathiidae, Hyssuridae, Leptanthuridae, Paranthuridae, Protognathiidae, Tridentellidae, dichotomous keys

Introduction

The Cymothoida Wägele, 1989 include those families of the former Flabellifera that are scavengers, ectoparasites, blood-suckers or predators (Dreyer and Wägele, 2001). According to these authors, the group has evolved from the scavenging and predatory feeding strategy towards parasitism on fish and other Crustacea. In the most basal families (e.g. Cirolanidae), the mandibular molar is an articulating toothed blade. This structure and the whole mandible is variously modified and reduced to a more piercing structure in the more parasitic families.

Brandt and Poore (2003) summarised the nomenclatural history of Flabellifera to which this suborder formerly belonged. Their morphological cladistic analysis, building on those of Wägele (1989) and Brusca and Wilson (1991), has given rise, more or less, to the accepted classification. Brandt and Poore (2003) assumed the monophyly of the easily recognisable superfamily Anthuroidea. They found the remaining cymothoidan families, including the Epicaridea, to be polyphyletic. They treated Epicaridea collectively as two monophyletic superfamilies Bopyroidea and Cryptoniscoidea within Cymothoida, following Dreyer and Wägele (2001). More recently, molecular data has provided support for a monophyletic Epicaridea that does not form a sister group relationship with any cymothoidan (An et al., 2022; Thomas Thorpe, 2024; Yu et al., 2018), meaning that parasitism of Crustacea was separately derived from parasitism of fishes.

Diagnosis. Head-pereonite 1 free. Dorsal pereopodal coxal plates present (secondarily reduced in some species); coxal plate of pereopod 1 fused to tergite; coxal plate 7 present; ventral coxal plates 1–7 (medial extension of coxa replacing sternite) obsolete (not distinguished from sternite). Pleotelson incorporating pleonite 6 only, pleonites 1–5 free. Pleotelson underside flat, without ventrolateral ridges (pleopods not enclosed laterally). Penial processes medial, closer to midpoint than to pereopods. Mandibular lacinia mobilis absent; molar flat triangular blade-like or conical process, or sometimes reduced or absent, or absent (rarely); palp present. Maxilla trilobed (reduced in Anthuroidea, absent Gnathiidae). Maxillipedal endite rarely longer than palp article 1 (or absent), distally tapering and with few setae. Pereopods 1–3 more or less prehensile or ambulatory, directed anteriorly; pereopods 4–7 directed posteriorly. Pleopodal exopods uniarticulate. Pleopod 1 biramous. Pleopod 2 biramous. Pleopod 3 biramous; endopod more or less oval or rectangular, rounded distally. Telsonic region of pleotelson elongate, anus situated anteriorly on pleotelson. Uropod inserted ventrally or anterolaterally on pleotelson; peduncle not operculate; rami ventral to pleotelson, articulating from side to side in vertical axis inside branchial chamber.

This is contribution number 1043 from the Water Research Group, North-West University, South Africa.

Key to superfamilies and families of Cymothoida

1. Body elongate, cylindrical. Pereopodal coxal plates without free ventrolateral margin. Uropodal endopod terminal, exopod more or less dorsally and proximally displaced, sometimes mesially directed or erect (except *Leipanthura*) (figs 5.1–5.10) ..... Anthuroidea ... 2

– Body flattened or weakly vaulted, somewhat cylindrical in Gnathiidae. Pereopodal coxal plates with free ventrolateral margin. Uropodal endopod distal; exopod set distally or proximolaterally on peduncle, laterally or posteriorly directed (figs 5.11–5.35) 7

2. Pleonites 1–5 free and as long as wide. Slender body form (pereonite 7 longer than wide, little or not shorter than pereonites 6) (fig. 5.7a). Pleopods 1–5 equal (fig. 5.7k, l). Pereopods 2 and 3 with carpus produced posterodistally (fig. 5.7n) ..... Hyssuridae ... p. 154

– Pleonites 1–5 free or fused, some at least shorter than wide. Body form not exceptionally slender (at least pereonite 7 wider than long) (figs 5.1–5.6, 5.8–5.10). Pleopod 1 exopod at least slightly wider than rami of other pleopods (fig. 5.6h–j). Pereopods 2 and 3 with carpus rarely produced posterodistally (fig. 5.4i–k) 3

3. Mouthparts not strongly and acutely produced (fig. 5.2m); mandible compact, incisor usually transverse and weakly toothed (fig.5.2n–x) 4

– Mouthparts strongly and acutely produced (fig. 5.8b); mandible tapering, incisor a simple spike (fig. 5.8f–h) 6

4. Pair of statocysts at base of telson. Pleonites 1–5 fused (or weakly indicated even though immobile) (fig. 5.2b, c, e, f, j). Pereopods 4–7 propodi with no or one posterodistal robust seta, rarely one posterior. Pereopod 7 propodus without anterodistal lateral serrate seta (fig. 5.4l–p) ..... Anthuridae ... p. 140

– Single medial (fig. 5.1c–e) or no statocyst (fig. 5.5a, b) at base of telson. Pleonites 1–5 free (rarely fused) (fig. 5.5a, b, f). Pereopods 4–7 propodi with at least one posterior seta in addition to posterodistal robust seta (fig. 5.90–q). Pereopod 7 propodus usually with anterodistal lateral serrate seta or setae (if not, one of other characters apply) (fig. 5.1g, h) 5

5. Telson without statocyst (fig. 5.5a, b). Maxilliped usually with narrow acute endite and narrow tapering palp of 4–5 articles (fig. 5.5q) or single broad article or vestigial (fig. 5.5p, q). Uropodal exopod typically leaf-life (fig. 5.5a, f) or with strong dorsal spike (fig. 5.5b, h–j) ..... Expanathuridae ... p. 150

– Telson with single medial statocyst (fig. 5.1a–e). Maxilliped usually with broad short endite and broad palp of 5 articles (fig. 5.1f). Uropodal exopod typically leaf-like, never with strong dorsal spike (fig. 5.5a–d) ..... Antheluridae ... p. 138

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– Pereopod 7 present in adults 10

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Contributions of the authors

GCBP was the leading author for Anthuroidea, Anuropidae, Barybrotidae Corallanidae, Gnathiidae, Protognathiidae and Tridentellidae, while NLB was the leading author for Aegidae, Cirolanidae and Cymothoidae.

Credits

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Fig. 5.2a, Poore and Lew Ton (1986); b, Poore and Kensley (1981). Fig. 5.5a, Poore and Kensley (1981); b, c, Poore and Lew Ton (2002). Fig. 5.7a, Poore and Lew Ton (1988). Fig. 5.8a, b, Poore and Lew Ton (1990). Fig. 5.10a, Poore (1984b). Fig. 5.11a, b, d–g, Bruce (2009); c, Ho and Tonguthai (1992); h, Bruce (1993). Fig. 5.13a, Lincoln and Jones (1973). Fig. 5.14a, Pillai (1967). Fig. 5.15a, Jones and Icely (1981); b, Bruce and Bussawarit (2004); c, Bruce (1995a); d, Bruce (2004); e, Moore and Brusca (2003); f, i, Bruce (1986); g, Bruce and Jones (1981); h, Barnard (1920); j, Bruce (1980); k, Bruce (2003); l, Brusca et al. (1995); m, Bruce (1995c); n, Bruce (1996); o, Bruce and Javed (1987); p, Jansen (1978). Fig. 5.16o, Moore and Brusca (2003); r, Bruce (1986). Fig. 5.17d–h, Bruce (1985). Fig. 5.18b, Bowman (1977); l, Bruce (2004); m, Bruce and Rodcharoen (2021); n, Bruce (1986); o, Bruce (1981); p, q, Bruce (2004); r, Bruce (1994). Fig. 5.19a, h, l, Bruce (2004); b, m, Bowman et al. (1981); c, d, f, g, Bruce (1986); e, Sidabalok and Bruce (2018c); i, Bruce and Rodcharoen (2021); j, Bruce (2003); k, p, Bruce (1993); n, Sidabalok and Bruce (2018c); q, Moore and Brusca (2003). Fig. 5.20a, Bruce (1993); b, Bruce and Svavarsson (2004); c, m, Bruce (1986); d, n, Bruce (2004); e, Brusca et al. (1995); f, Bruce and Olesen (2002); g, Bruce (2003); h, Sidabalok and Bruce (2015); i, k, Kensley (1978); j, Bruce (1993); o, Bruce and Soares (1996). Fig. 5.21a, Bruce and Javed (1987); b, Bruce and Soares (1996); c, Brusca et al. (1995); d, Bruce and Rodcharoen (2021); e, Bruce (2003); f, Bruce (1986); g, Riseman and Brusca (2002); h, Jansen (1978); i, Bruce (2004). Fig. 5.22a, Muller (1991); b, c, Santos Silva and Souza–Filho (2017). Fig. 5.23a, b, Bruce (1987a); c, Bruce et al. (2019); d, Bruce (1990); e–g, Bruce (1987b); h, Aneesh et al. (2020); i, Aneesh et al. (2025); j, Bunkley–Willams and Williams (1986). Fig. 5.24a, b, e, Bruce (1990); c, Aneesh et al. (2025); d, Helna et al. (2023); f, Williams and Williams (1985); g, h, Bruce (1986); i, j, Williams and Williams (1994); k, Aneesh et al. (2024). Fig. 5.25a, Martin et al. (2015); b, Martin et al. (2016); c, Trilles (2007); d, Martin et al. (2014); e, Avdeev (1975); f, Hale (1926). Fig. 5.26a, Martin et al. (2015); b, Hadfield et al. (2010); c, d, j, Martin et al. (2016); e, Schioedte and Meinert (1883, redrawn); f, Bruce and Bowman (1989); g, Aneesh et al. (2021); h, Martin et al. (2014); i, Bruce (1990); k, Trilles (2007). Fig. 5.27a, b, f, Bruce (1987a); c, d, h, i, Bruce (1987c); e, Hadfield et al. (2017); g, Bruce (1987b). Fig. 5.28a, c, f–i, Bruce (1990); b, Bowman and Tareen (1983); d, j, Bruce (1986); e, Aneesh et al. (2024). Fig. 5.30a–d, k, Bruce (1987a); e, g, j, o, p, Bruce (1990); f, Martin et al. (2015); h, Pillai (1964); i, Bruce (1987c); l, Bruce et al. (2019); m, Hadfield et al. (2010); n, Bruce et al. (2016). Fig. 5.31a–c, Erasmus et al. (2023). Fig. 5.32a, c–e, Cohen and Poore (1994); b, Beddard (1886). Fig. 5.34a, Wägele and Brandt (1988). Fig. 5.35a, Brandt and Poore (2001).

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Superfamily Anthuroidea Leach, 1814

Anthuroids, for many years treated as the suborder Anthuridea of Isopoda, are recognisable initially from their elongate cylindrical bodies. This general form is combined with the attitude of the uropodal exopod variously elevated and sitting over or alongside the pleotelson. Only one exception, *Leipanthura casuarina* Poore, 2009, has more typical flat posteriorly directed uropodal rami. Some anthuroid families have compact mouthparts but others have the mandible, maxillula and maxilliped produced as interacting stylets. These particularly are micropredators feeding by sucking fluids and tissue from their prey (Wägele, 1982, 1985). Anthuroids are protogynous hermaphrodites in which the terminal phase is a male with large eyes, extended swimming limbs and more numerous aesthetascs on the antennulae. The basis for systematics of the groups was established 100 years ago (Barnard, 1925). Wägele (1981) undertook a thorough review of the phylogeny and systematics of the group, generating many insights into its biology. The most recent synthetic review of the taxonomy of all families was by Poore (2001); few genera and species have been added since.

Diagnosis. Freeliving, predators or ectoparasitic on fishes or invertebrates. Body elongate, cylindrical. Antennula, antenna well developed. Mandibular molar absent or reduced; lacinia mobilis and spine row more or less fused into a lamina dentata; incisor process blunt or acute. Maxilla absent, fused into hypopharynx. Pereopods 1 or 1–3 more or less prehensile; pereopodal coxal plates without free ventrolateral margin. Pleopod 1 exopod operculiform, pleopods 2–4 rami lamellate, or pleopods 1–5 biramous, rami lamellate (Hyssuridae only). Uropodal endopod terminal; exopod more or less dorsally and proximally displaced, sometimes mesially directed or erect (except *Leipanthura*).

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Antheluridae Poore and Lew Ton, 1988

Figure 5.1

Antheluridae are a small family with mouthparts not produced anteriorly in a cone and a single median telsonic statocyst. All have a row of serrate setae along the extensor margin of pereopod 7 (Poore, 2001; Poore and Lew Ton, 1988).

Diagnosis. Body 10–15 times as long as wide, non-males rarely more elongate (pereonite 7 wider than long, much shorter than pereonite 6); pleonites with plumose setae on margins of epimera or posterior margins of pleonite 5 and sometimes pleonite 4; pleonites 1–5 together not more than twice as long as wide; pleonites 1–5 free and articulating (fig. 5.1b); telson statocyst single. Antennal flagellum of numerous articles. Mouthparts not produced anteriorly. Mandible compact and with weakly-toothed transverse incisor. Maxillipedal palp broad (c. twice as long as wide; fig. 5.1f). Pereopods 2–3 carpus not or weakly produced posterodistally. Pereopod 7 propodus anterodistal serrate setae present (fig. 5.1g, h). Pleopod 1 exopod operculiform alone.

Key to genera of Antheluridae

1. Pereopods 4–7 carpus much longer than wide (fig. 5.1h). Telson with longitudinal ridge and no statocyst pore (fig. 5.1d) ..... *Anthelura*

– Pereopods 4–7 carpus about as long as wide (fig. 5.1g). Telson domed or flat and with statocyst pore (fig. 5.1c, e) 2

2. Telson domed, with slit-like pore (fig. 5.1c). Antennal flagellum of male of 5 or more articles ..... *Ananthura*

– Telson flat, with small pore (fig. 5.1e). Antenna flagellum of male of 2 or 3 articles ..... *Anthomuda*

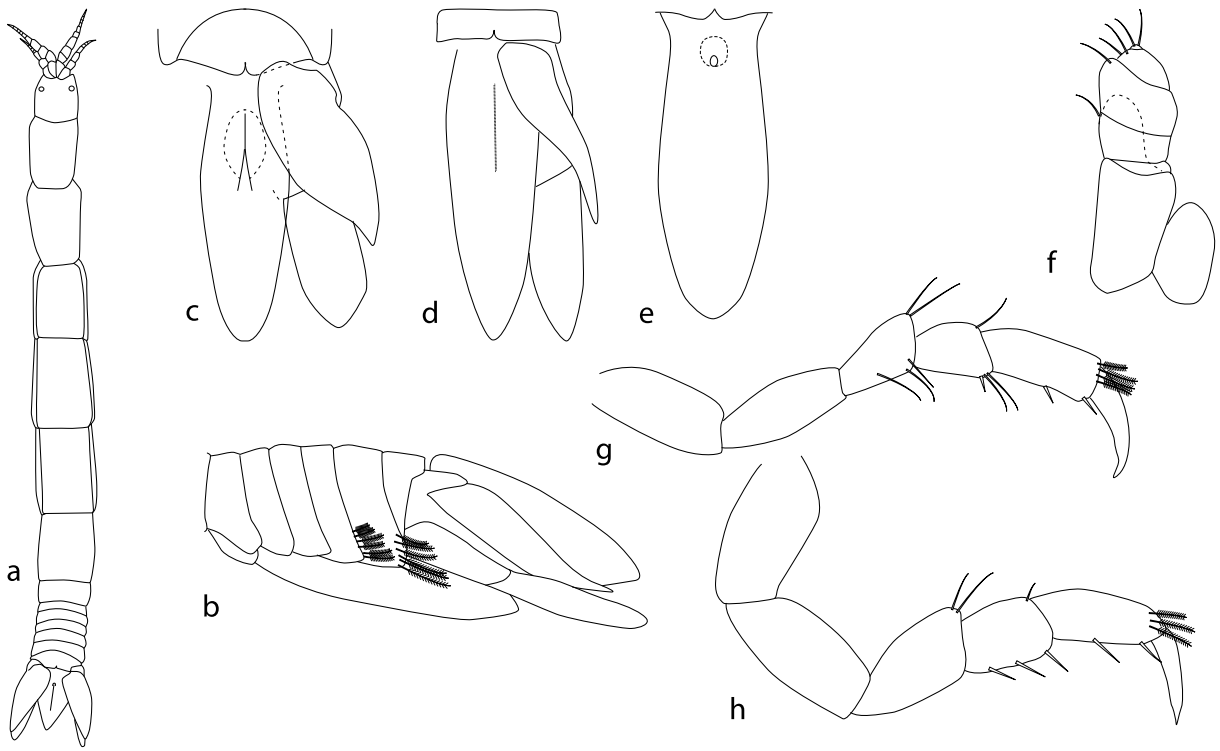


Figure 5.1. Antheluridae. a, dorsal habitus, *Ananthura*. b, lateral pleon, left uropod endopod, telson, right uropod exopod, *Ananthura*. Telson, right uropod: c, *Ananthura*; d, *Anthelura*. e, telson, *Anthomuda*. f, maxilliped, *Anthelura*. Pereopod 7: g, *Ananthura*; h, *Anthelura*.

Ananthura Barnard, 1925

Diagnosis. Body not pigmented. Eyes present in both sexes. Pereopod 1 merus as wide as narrow propodus. Pereopods 4–7 carpus longer than wide, with 2 robust setae along cutting edge. Telson twice as long as wide, with slit-like pore. Uropodal rami tapering to narrow apices.

Shelf–abyssal. Temperate Northern Atlantic, Temperate Northern W Pacific, Temperate Australasia, Southern Ocean. 9 species (Barnard, 1925; Negoescu, 2005; Poore and Lew Ton, 1988).

Anthelura Norman and Stebbing, 1886

Diagnosis. Body not pigmented. Eyes absent. Antennal flagellum of male of 1 basal article + c. 20 aesthetasc articles. Pereopod 1 merus broader than tapering propodus. Pereopods 4–7 carpus longer than wide, with 4 robust setae along cutting edge. Telson 2.5 times as long as wide, with slit-like pore. Uropodal rami tapering to narrow apices.

Shelf–abyssal. Temperate Northern NE Atlantic. 1 species (Kensley, 1994; Wägele, 1980).

Anthomuda Schultz, 1979

Diagnosis. Body not pigmented, or pigmented. Eyes present in both sexes. Antennal flagellum of male of 1 basal article + c. 10 aesthetasc articles. Pereopod 1 merus as wide as narrow propodus. Pereopods 4–7 carpus about as long as wide, with short anterior margin, with 2 robust setae along cutting edge. Telson 2.5 times as long as wide, with small pore. Uropodal rami apically rounded.

Subtidal, shelf. Tropical Atlantic, Indo West-Pacific, Temperate Southern Africa. 8 species (Kensley, 1994; Müller, 1990).

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Anthuridae Leach, 1814

Figures 5.2–5.4

Anthurids are more or less cylindrical isopods with a tail fan comprising telson and uropods with the exopod held dorsally (with one exception). The mouthparts do not produce forwards. The telson has two basal statocysts (Poore, 2001). Adults are benthic, sometimes building tubes in all forms of sediment from estuarine mud to coral rubble. They appear to be predators on micro-invertebrates or scavengers. As far as is known, anthurids are protogynous hermaphrodites, that is, juvenile develop into females after the manca stage and later become males (Burbanck and Burbanck, 1974). Males are rarer than females and are differentiated from other stages, as in all anthuroids, by the possession of long antennulae with numerous aesthetascs, large eyes, and a more elongate body form. Males are presumed swimmers (Burbanck et al., 1979; Wägele, 1979, 1980a).

Diagnosis. Body 10–15 times as long as wide, non-males rarely more elongate (pereonite 7 wider than long, much shorter than pereonite 6); pleonites without marginal plumose setae on pleonal epimera or posterior borders of pleonites 4 and 5; pleonites 1–5 together not more than twice as long as wide; pleonites 1–5 fused; telson statocysts paired. Antennal flagellum of fewer than 10 articles, shorter than peduncle. Mouthparts not produced anteriorly. Mandible compact and with weakly toothed transverse incisor. Maxillipedal palp broad (c. twice as long as wide). Pereopods 2–3 carpus not or weakly produced posterodistally. Pereopod 7 propodus anterodistal serrate setae absent. Pleopod 1 exopod operculiform alone.

Implicit generic attributes. Body of usual proportions; total length of adult more than 4 mm; smooth. Head more or less parallel-sided in both sexes (not wider anteriorly), without produced chin. Pleonites 1–5 together as long as or longer than greatest width, fused, sutures visible only laterally. Pleotelson with posterior margin of pleonite 6 indicated dorsally, delineated from telson. Antennular flagellum in juvenile and female of 3–4 articles (second longest). Eyes present. Mandibular incisor directed transversely (exceeded by palp); molars blunt; palp of 3 articles; palp article 3 with 1–4 setae on distal margin. Maxillipedal endite obsolete or absent. Pereopod 1 subchelate, dactylus and terminal unguis closing on axial palm, carpus and propodus separated by suture; propodus swollen, subchelate, overlapping merus; propodus palm straight or sinuous, without prominent tooth; palm without strong proximal seta; dactylus smooth, closing on palm. Pereopods 2–7 merus-propodus setose on posterior margin, group of setae on anterodistal margin of merus. Pereopods 2, 3 carpus without robust seta posterodistally. Pereopods 4–7 carpus with 1 robust seta on posterodistal angle. Pereopods 4–7 propodus with 1 posterodistal robust seta only. Pereopod 7 present on adults. Pleopod 1 endopod apically rounded. Uropodal exopod leaf-shaped, articulating along peduncle.

Key to genera of Anthuridae

1. Uropodal exopod terminal, cylindrical (fig. 5.2f, g) ..... *Leipanthura*
– Uropodal exopod subterminal, dorsal, leaf-like (fig. 5.2a–e, h–j) 2
2. Pereopods 4–7 with carpus twice as wide as propodus, rectangular, with obvious free distal margin (usually with row of pectinate setae) defined by stout seta on posterodistal angle (fig. 5.4o). Maxillipedal endite half as long as palp, distally rounded; palp articles 1 and 2 separated by suture (4 or 5 articles visible) (fig. 5.3k) ..... *Quantanthura*

– Pereopods 4–7 with carpus of similar width to propodus, or if wider triangular, with short free distal margin between base of dactylus and stout seta (fig. 5.4l–o, p). Maxillipedal endite weak or absent, acute if present; palp articles 1–2 and 4–5 fused (maximum of 3 articles visible) (fig. 5.3a–j) 3

3. Pereopods 2–7 ischium-propodus bearing long setae on flexor and extensor margins (fig. 5.4k). Blind or eyes weakly pigmented 4

– Pereopods 2–7 ischium-propodus bearing few short setae, most on flexor margin (merus-carpus posteriorly lobed and setose in some *Apanthura*). Eyes usually pigmented 5

4. Pereopods 4–7 carpus longer and wider than propodus (fig. 5.4k). Mandibular palp of 3 articles ..... *Notanthura*

– Pereopods 4–7 carpus shorter than propodus. Mandibular palp of 2 articles (fig. 5.2s) ..... *Cortezura*

5. Pereopods 4–7 with carpus more or less triangular, extensor margin much shorter than flexor margin, distal margin oblique and with posterodistal lobe (fig. 5.4l, m, p) 6

– Pereopods 4–7 with carpus more or less rectangular, extensor margin nearly as long as flexor margin, distal margin tansverse and without posterodistal lobe (fig. 5.4n) 16

6. Pereopod 4–7 carpus with one distal robust seta on extensor margin (fig. 5.4l) 7

- Pereopod 4–7 carpus without distal or marginal robust seta on extensor margin (fig. 5.4m, p) 13

7. Pereopod 1 palm straight, without step or prominent tooth (fig. 5.4h) ..... *Tinggianthura*

– Pereopod 1 palm with step or prominent tooth (fig. 5.4a, f) 8

8. Maxillipedal palp articles 1–2 fused, 3 free, fused articles 4–5 at least one third as long as article 3 (fig. 5.3i) 9

– Maxillipedal palp articles 1–2 fused, 3 free, fused articles 4–5 minute, without a free mesial margin between its suture and distal group of setae (fig. 5.3b) 10

9. Pereopod 1 chelate, propodus palm produced distally, dactylus with complexly ridged distal margin, unguis subterminal, carpus and propodus fused (fig. 5.4d) ..... *Chelanthura*

– Pereopod 1 subchelate, dactylus and terminal unguis closing on axial palm, carpus and propodus separated by suture (fig. 5.4f) ..... *Mesanthura*

10. Maxillipedal palp with fused articles 1–2 longer than broad. Mandibles asymmetrical, left molar with tooth fitting socket of right molar (fig. 5.2o, p). Pereopods 2 and 3 with propodus discoid (fig. 5.4i) ..... *Apanthuropsis*

– Maxillipedal palp with fused articles 1–2 broader than long (fig. 5.3b). Mandibles symmetrical (fig. 5.2n). Pereopods 2 and 3 with propodus linear 11

11. Pleonites 1–5 separated by sutures dorsally and laterally except dorsally between pleonites 4 and 5 (fig. 5.2c) ..... *Amakusanthura*

– Pleonites 1–5 indicated by shallow notches only ventrally (fig. 5.2e) 12

12. Antennal flagellum with 3 or 4 articles. Antennular flagellum of male with one basal + 10 aesthetasc-bearing articles, as long as head (fig. 5.2k). Head without produced chin except in some males ..... *Apanthura*

– Antennal flagellum with 1 or 2 articles. Antennular flagellum of male with one basal + 1–2 short aesthetasc-bearing articles, never as long as head (fig. 5.2l). Head with produced chin in both sexes (fig. 5.2m) ..... *Skuphonura*

13. Maxillipedal endite absent; palp articles 1–2 fused, 3 free, fused articles 4–5 at least as long as article 3 (fig. 5.3f) 14

– Maxillipedal endite present as triangular lobe; palp articles 1–5 fused (fig. 5.3j) 15

14. Uropodal exopod leaf-shaped, articulating along peduncle (fig. 5.2e). Marine and estuarine ..... *Cyathura*

– Uropodal exopod linear, articulating transversely (fig. 5.2j). Stygobiont in Caribbean ..... *Stygocyathura*

15. Pleon shorter than wide. Mandibular palp of one article with long seta (fig. 5.2v) ..... *Pendanthura*

– Pleon longer than wide (fig. 5.2b). Mandibular palp of 3 articles ..... *Sauranthura*

16. Maxilliped with endite; palp of 3 articles of similar length (fig. 5.3c). Mandible with spike-like molar on right side, absent on left (fig. 5.2q). Pleonite 6 not separated from telson by transverse ridge (fig. 5.2d) ..... *Apanthuroides*

– These characters not in combination. Mandible with triangular or blunt molar, symmetrical 17

17. Maxillipedal palp with articles 1–2 fused, 3 free, 4–5 fused or articles 3–5 fused; endite triangular or absent (fig. 5.3d, e, h) 18

– Maxillipedal palp with articles 1–3 fused and 4–5 fused, or all articles fused; endite absent (fig. 5.3a, d, g) 21

18. Maxillipedal palp with fused articles 4–5 contributing to mesial margin of palp, with setae on mesial margin (fig. 5.3h). Telson with longitudinal middorsal ridge. Uropodal endopod short, oblique (fig. 5.2h) ..... *Indanthura*

– Maxillipedal palp with fused articles 4–5 minute, triangular or semicircular, not contributing to mesial margin of palp, with setae on distal or distomesial margin (fig. 5.3d, e). Telson broadly rounded, rarely with longitudinal middorsal ridge. Uropodal endopod at least as long as wide, its suture with peduncle more or less transverse 19

19. Pereopod 1 merus barely touching cylindrical propodus on extensor margin (fig. 5.4c). Maxillipedal endite absent (fig. 5.3e). Antennular flagellum of male of 10 articles ..... *Cetanthura*

– Pereopod 1 merus cupping swollen subchelate propodus (fig. 5.4a). Maxillipedal endite present (fig. 5.3b). Antennular flagellum of male of 20 articles 20

20. Body covered at least in part with setules; pleonites 1–5 with sutures indicated dorsally (fig. 5.2i). Antennal flagellum of 7 articles. Eyes absent ..... *Pilosanthura*

– Body smooth, without setules; pleonites 1–5 without sutures indicated dorsally. Antennal flagellum of 5 articles. Eyes present ..... *Malacanthura*

21. Pereopod 1 palm with strong proximal seta about as long as unguis (fig. 5.4b). Maxillipedal palp with fused articles 4–5 small, transverse, lateral to distomesial lobe of fused articles 1–3 (fig. 5.3d). Mandibular palp of 1 or 2 articles (fig. 5.2r) ..... *Caenanthura*

– Pereopod 1 palm without strong proximal seta. Maxillipedal palp with fused articles 4–5 oblique (fig. 5.3g) or fused. Mandibular palp of 3 articles (fig. 5.2u, v) 22

22. Maxillipedal palp with articles 1–3 fused and 4–5 fused (fig. 5.3g) 23

– Maxillipedal palp with articles 1–5 fused (fig. 5.3a) 24

23. Pereopod 1 propodus swollen, subchelate; dactylus simple and closing on palm (fig. 5.4e). Body of usual proportions, rarely slender ..... *Haliophasma*

– Pereopod 1 propodus cylindrical; dactylus with teeth along flexor margin, not closing on palm (fig. 5.4g). Body slender, c. 20 times as long as wide ..... *Nemanthura*

24. Mandibular palp of 3 articles ..... *Anthura*

– Mandibular palp of 1 article (fig. 5.2x) 25

25. Pereopod 7 present ..... *Ptilanthura*

– Pereopod 7 absent ..... *Exallanthura*

Amakusanthura Nunomura, 1977

Diagnosis. Body not darkly pigmented. Head with produced chin in males. Pleonites 1–5 fused (but separated by folds dorsally and laterally except dorsally between 4 and 5) or fused, sutures visible only laterally. Antennular flagellum of male of 1 basal + c. 20 aesthetasc-bearing articles. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Maxillipedal endite present as a triangular lobe, or reaching palp article 3; palp articles 1–2 fused, 3 free and 4–5 fused; palp article 3 barely produced medially beyond articles 4–5 (if at all); palp terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male). Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin.

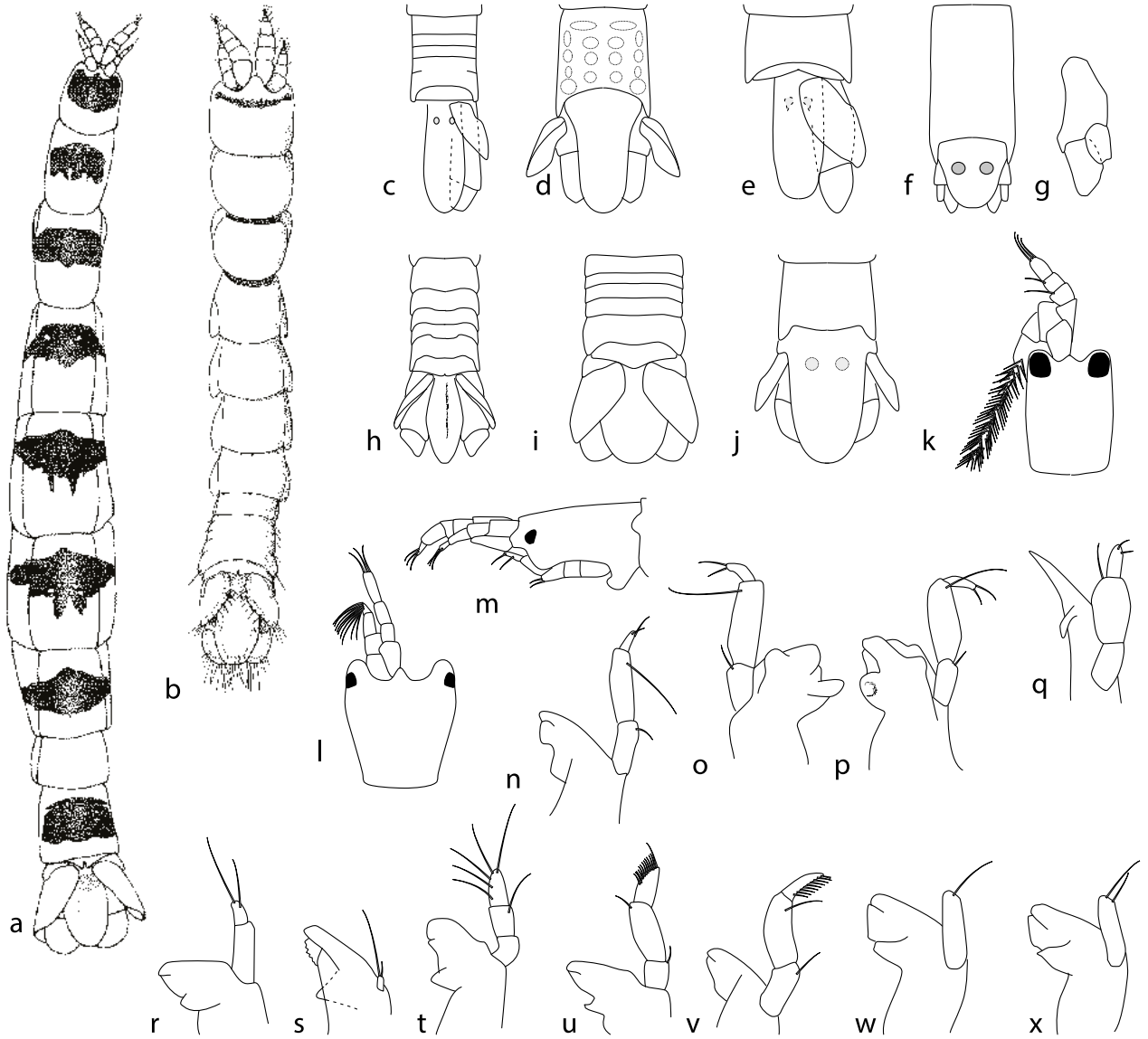


Figure 5.2. Anthuridae. a, *Chelanthura calaena* (Poore and Lew Ton, 1986); b, *Sauranthura goldmanorum* Poore and Kensley, 1981. Pleon, pleotelson, uropod: c, *Amakusanthura*; d, *Apanthuroides*; e, *Cyathura*; f, g, *Leipanthura* (with uropod); h, *Indanthura*; i, *Pilosanthura*; j, *Stygocyathura*. Male head, antennula, antenna: k, *Apanthura*; l, *Skuphonura*. m, male head, antennula, antenna, *Skuphonura*. Mandible: n, *Apanthura*; o, p, *Apanthuropsis* (pair); q, *Apanthuroides*; r, *Caenanthura*; s, *Cortezura*; t, *Haliophasma*; u, *Mesanthura*; v, *Pendanthura*; w, *Pilosanthura*; x, *Ptilanthura*.

Intertidal–bathyal. Temperate Northern and Atlantic, Temperate Northern Pacific, Western and Central Indo-Pacific, Temperate Southern Africa, Temperate Australasia. 48 species (Poore and Lew Ton, 1988a: rediagnosis, key to Australian species; Müller, 1992; Negoescu, 2004: comments on status of genus; Kim and Yoon, 2021: key to species in Far East).

Anthura Leach, 1814

Diagnosis. Body irregularly darkly pigmented. Antennular flagellum of male of 1 basal + c. 20 aesthetasc-bearing articles. Antennal flagellum of 7–9 articles, longer than article 5 of peduncle. Maxillipedal palp articles 1–5 fused. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe.

Intertidal, subtidal. Temperate Northern Atlantic. 1 species (Wägele, 1980b: redescription, figures).

Apanthura Stebbing, 1900

Diagnosis. Body not darkly pigmented or irregularly darkly pigmented. Head with produced chin in males. Antennular flagellum of male of 1 basal + c. 10 aesthetasc-bearing articles.

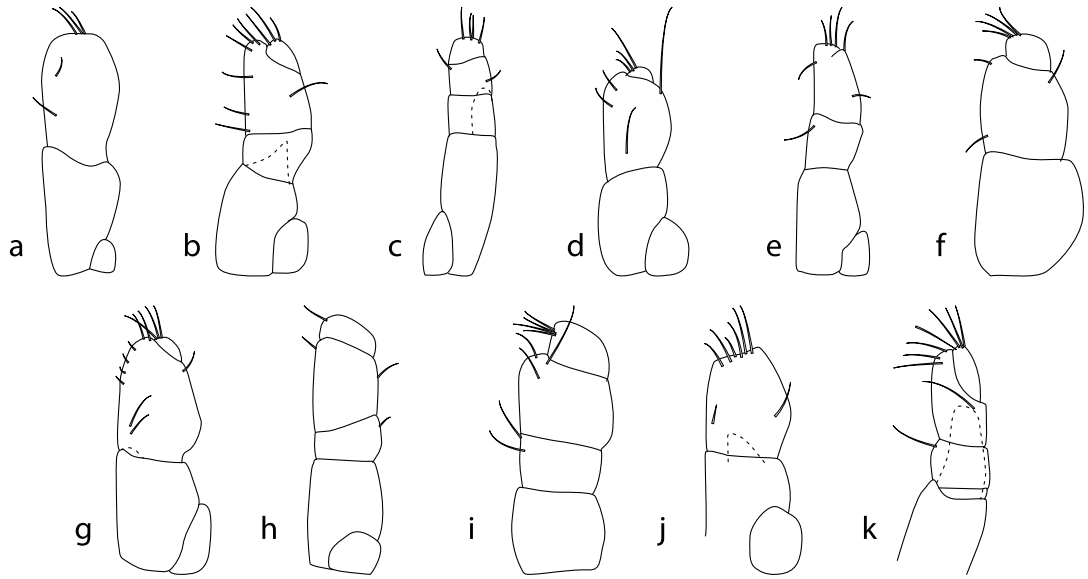


Figure 5.3. Anthuridae. Maxilliped: a, *Anthura*; b, *Apanthura*; c, *Apanthuroides*; d, *Caenanthura*; e, *Cetanthura*; f, *Cyathura*; g, *Haliophasma*; h, *Indanthura*; i, *Mesanthura*; j, *Pendanthura*; k, *Quantanthura*.

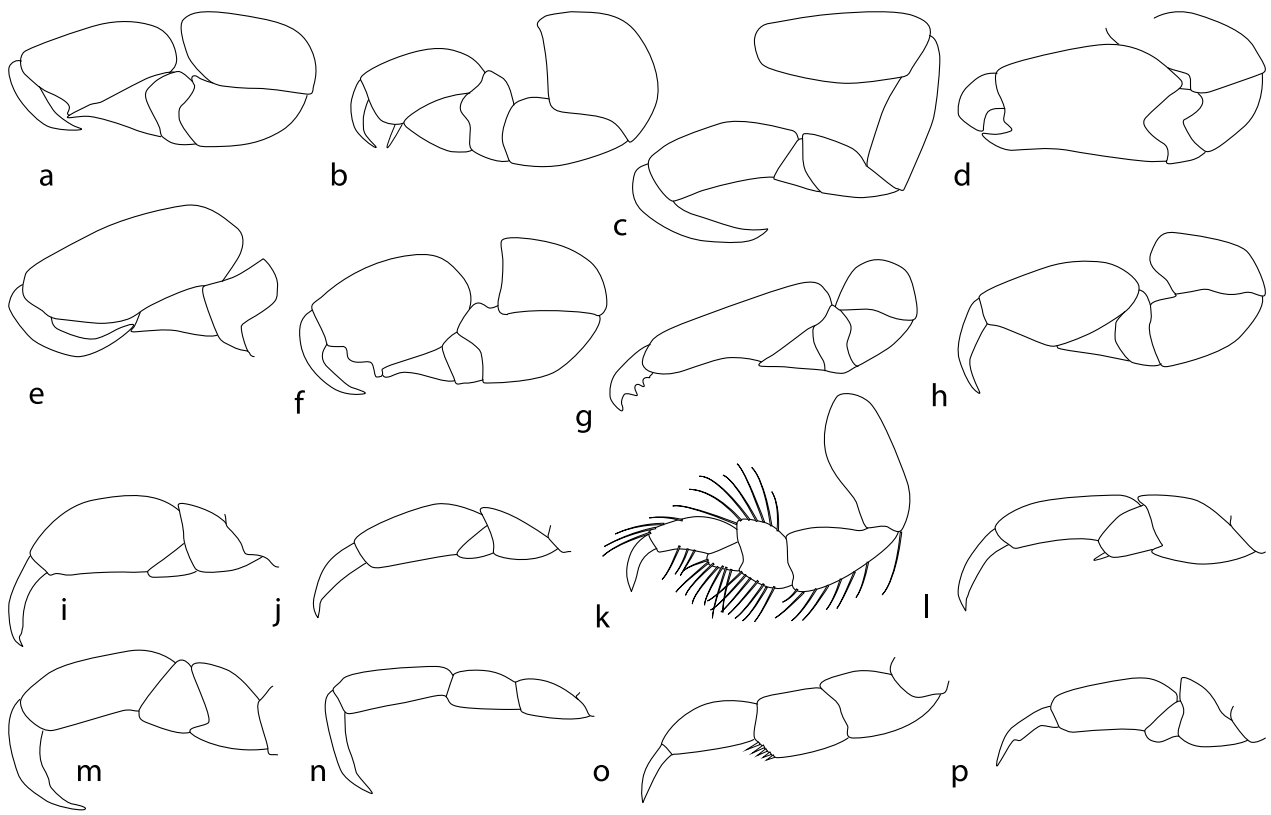


Figure 5.4. Anthuridae. Pereopod 1: a, *Apanthura*; b, *Caenanthura*; c, *Cetanthura*; d, *Chelanthura*; e, *Haliophasma*; f, *Mesanthura*; g, *Nemanthura*; h, *Tinggianthura*. Pereopod 2: i, *Apanthuropsis*; j, *Haliophasma*; k, *Notanthura*. Pereopod 7: l, *Apanthura*; m, *Cyathura*; n, *Haliophasma*; o, *Quantanthura*; p, *Pendanthura*.

Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Maxillipedal endite present as a triangular lobe; palp articles 1–2 fused, 3 free and 4–5 fused; palp article 3 barely produced medially beyond articles 4–5 (if at all); palp terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male). Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin.

Intertidal–bathyal. Temperate Northern and Tropical Atlantic, Indo West-Pacific, Temperate Southern Africa, Temperate Australasia. 46 species (Poore and Lew Ton, 1988a: rediagnosis, key to Australian species; Kim and Yoon, 2021: key to species of Far East).

Apanthuroides Menzies and Glynn 1968

Diagnosis. Body not darkly pigmented, pitted. Pleotelson without indication of posterior margin of pleonite 6. Antennular flagellum of male of 1 basal + 6–7 aestetascs-bearing articles. Antennal flagellum of 7–9 articles, longer than article 5 of peduncle. Mandibular incisor produced anteriorly (beyond palp); molar spike-like on right side, absent on left. Maxillipedal endite reaching palp article 3; palp articles 1–2 fused, 3 free and 4–5 fused; palp article 3 well exceeded by distal articles; palp terminal articles (4–5) subcircular, transverse. Pereopod 1 propodus cylindrical, not in contact with merus. Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin.

Intertidal–bathyal. Temperate Northern and Tropical Atlantic, Indo West-Pacific, Temperate Southern Africa. 9 species (Kensley and Schotte, 2000: rediagnosis, key to Indian Ocean species; Nunomura, 2013).

Apanthuropsis Poore and Lew Ton, 1985

Diagnosis. Body not darkly pigmented. Antennular flagellum of male of 1 basal + c. 20 aesthetasc-bearing articles. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Mandibular molars asymmetrical, left molar with tooth fitting socket of right molar. Maxillipedal palp articles 1–2 fused, 3 free and 4–5 fused; article 3 barely produced medially beyond articles 4–5 (if at all); terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male). Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin.

Shelf. Temperate Australia. 1 species (Poore and Lew Ton, 1985b).

Caenanthura Kensley, 1978

Diagnosis. Body not darkly pigmented. Antennular flagellum of male of 1 basal + c. 20 aesthetasc-bearing articles. Antennal flagellum of 1–2 articles, very short. Mandibular palp of 1 or 2 short article. Maxillipedal palp articles 1–3 fused, 4–5 fused; article 3 produced as lobe beyond distolateral articles 4–5; terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopod 1 palm with strong proximal seta (about as long as unguis). Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin.

Subtidal. Western and Central Indo-Pacific. 6 species (Poore, 2001: rediagnois, synonymy; Song and Min, 2015: key to species).

Cetanthura Kensley, 1982

Diagnosis. Body not darkly pigmented, pitted. Antennular flagellum of male of 1 basal + c. 10 aesthetasc-bearing articles. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Mandibular incisor produced anteriorly (beyond palp). Maxillipedal palp articles 1–2 fused, 3–5 fused. Pereopod 1 propodus cylindrical, not in contact with merus. Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin. Pereopod 7 absent on adults.

Bathyal. Temperate Southern Africa. 1 species (Kensley, 1982).

Chelanthura Poore and Bardsley, 1990

Diagnosis. Body with dark species-specific pigment pattern. Antennular flagellum of male of 1 basal + c. 10 aesthetasc-bearing articles. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Mandibular palp article 3 with row of 10–15 setae on distal oblique margin. Maxillipedal palp articles 1–2 fused, 3 free and 4–5 fused; article 3 well exceeded by distal articles; terminal articles (4–5) at least one third as long as penultimate article (3), almost as long as broad, with a free mesial margin between its suture and distal group of setae. Pereopod 1 chelate, propodus produced posterodistally, dactylus with complexly ridged distal margin, unguis subterminal, carpus and propodus fused. Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin.

Shelf. Temperate Australasia. 4 species (Poore and Bardsley, 1990).

Cortezura Schultz, 1977

Diagnosis. Body not darkly pigmented. Antennular flagellum of male of 1 basal + 1 or 2 short aesthetasc-bearing articles. Antennal flagellum of 1–2 articles, very short. Eyes weakly pigmented. Mandibular molar a triangular blade; palp of 2 articles, second very setose. Maxillipedal endite present as a triangular lobe; palp articles 1–3 fused, 4–5 fused, or 1–5 fused. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male). Pereopods 2–7 merus-propodus bearing long setae on upper and lower margins. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe.

Intertidal, subtidal. Tropical Atlantic, Temperate Northern Pacific. 4 species (Jarquín-Martínez and García-Madrigal, 2021; Kensley, 1978; Schultz, 1977).

Cyathura Norman and Stebbing, 1886

Diagnosis. Body irregularly darkly pigmented, smooth or covered at least in part with setules (fur). Pleonites 1–5 together

shorter than wide. Pleotelson with posterior margin of pleonite 6 indicated dorsally, delineated from telson, or without indication of posterior margin of pleonite 6. Antennular flagellum of male of 4–5 aesthetasc-bearing articles, retractile. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Mandibular palp article 3 with 1–4 setae on distal margin, or with row of 10–15 setae on distal oblique margin. Maxillipedal palp articles 1–3 fused, 4–5 fused; article 3 well exceeded by distal articles; terminal articles (4–5) at least one third as long as penultimate article (3), almost as long as broad, with a free mesial margin between its suture and distal group of setae. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male). Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin, without robust seta on posterior margin or on posterodistal angle.

Freshwater, estuarine, marine intertidal–bathyal. Arctic, Temperate Northern and Tropical Atlantic, Temperate Northern W Pacific, Central Indo-Pacific, Temperate South America, Temperate Southern Africa, Temperate Australasia. 31 species (Bamber, 2008; Cruz et al., 2003; Ferreira et al., 2004). Species of *Cyathura* range from freshwater lakes (Nunomura and Hagino, 2000), through estuaries (e.g. Nunomura, 1977; Poore and Lew Ton, 1985a) to shallow marine sediments (most species) and even to 1000 m depth (Kensley, 1982). The biology of some species has been studied (e.g., Burbanck, 1962; Marques et al., 1994).

Exallanthura Kensley 1980

Diagnosis. Body not darkly pigmented. Antennular flagellum of male of 1 basal + c. 20 aesthetasc-bearing articles. Antennal flagellum of 7–9 articles, longer than article 5 of peduncle. Mandibular palp of 1 article. Maxillipedal palp articles 1–5 fused. Pereopod 1 propodus cylindrical, not in contact with merus. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe. Pereopod 7 absent on adults. Uropodal exopod broad, apically concave.

Shelf. Western Indo-Pacific. 1 species (Kensley, 1980).

Haliophasma Haswell, 1881

Diagnosis. Body not darkly pigmented, pitted. Antennular flagellum of male of 1 basal + c. 20 aesthetasc-bearing articles. Antennal flagellum of 7–9 articles, longer than article 5 of peduncle. Mandibular palp article 3 with row of 10–15 setae on distal oblique margin (sometimes fewer). Maxillipedal endite obsolete or absent; palp articles 1–3 fused, 4–5 fused; palp article 3 barely produced medially beyond articles 4–5 (if at all), or well exceeded by distal articles; palp terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe.

Intertidal–bathyal. Temperate Northern and Tropical Atlantic, Western and Central Indo-Pacific, Temperate Southern Africa, Temperate Australasia, Southern Ocean. 39 species (Poore, 1975: rediagnosis; Poore and Lew Ton, 1988b: key to 16 Australian species).

Indanthura Pillai and Eapen, 1966

Diagnosis. Body not darkly pigmented. Pleonites 1–5 fused, sutures visible only laterally or sutures all indicated dorsally and laterally. Antennular flagellum in juvenile and female of c. 5–7 articles. Antennal flagellum of 7–9 articles, longer than article 5 of peduncle. Mandibular palp article 3 with row of 10–15 setae on distal oblique margin. Maxillipedal palp articles 1–2 fused, 3 free and 4–5 fused; article 3 well exceeded by distal articles; terminal articles (4–5) at least one third as long as penultimate article (3), almost as long as broad, with a free mesial margin between its suture and distal group of setae. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe.

Shelf. Temperate Northern and Tropical Atlantic, Western Indo-Pacific. 4 species (Pillai and Eapen, 1966; Poore, 2001: rediagnosis, synonymy).

Leipanthura Poore, 2009

Diagnosis. Body total length of adult less than 3 mm; irregularly darkly pigmented. Antennal flagellum of 7–9 articles, longer than article 5 of peduncle. Maxillipedal palp articles 1–5 fused. Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin, without robust seta on posterior margin or on posterodistal angle. Pereopod 7 absent on adults. Uropodal exopod cylindrical, articulating distally in same horizontal plane as endopod.

Subtidal (coral reefs). Central Indo-Pacific. 1 species. *Leipanthura* differs from all other anthurids in having a typically "flabelliferan" uropod, the exopod being terminal on the peduncle rather than dorsal as in all others (Poore, 2009).

Malacanthura Barnard, 1925

Diagnosis. Body not darkly pigmented. Antennular flagellum of male of 1 basal + c. 20 aesthetasc-bearing articles. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Maxillipedal endite reaching palp article 3; palp articles 1–2 fused, 3 free and 4–5 fused; palp article 3 barely produced medially beyond articles 4–5 (if at all); palp terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe.

Intertidal–bathyal. Western Indo-Pacific, Temperate South America (S Atlantic), Temperate Southern Africa. 5 species (Bamber, 2000; Barnard, 1925; Kensley and Schotte, 2000).

Mesanthura Barnard, 1914

Diagnosis. Body with dark species-specific pigment pattern. Antennular flagellum of male of 1 basal + c. 10 aesthetasc-bearing articles. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Mandibular palp article 3 with row of 10–15 setae on distal oblique margin. Maxillipedal palp articles 1–2 fused, 3 free and 4–5 fused; article 3 well exceeded by distal articles; terminal articles (4–5) at least one third as long as

penultimate article (3), almost as long as broad, with a free mesial margin between its suture and distal group of setae. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male); dactylus often with complex toothed surface at base of unguis. Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin.

Intertidal–shelf. Tropical Atlantic, Temperate Northern Pacific, Indo West-Pacific, Tropical Eastern Pacific, Temperate Southern Africa, Temperate Australasia, Southern Ocean. 54 species (Poore and Lew Ton, 1986a: rediagnosis; Jarquín-Martínez and García-Madrigal, 2021; Müller, 1993). Species of *Mesanthura* differ from most anthurids in having permanent species-specific colour patterns. One species has been introduced to the Mediterranean (Lorenti et al., 2009).

Nemanthura Wägele, 1981

Diagnosis. Body very slender (c. 20 times as long as wide); not darkly pigmented. Antennal flagellum of 7–9 articles, longer than article 5 of peduncle. Maxillipedal palp articles 1–3 fused, 4–5 fused; article 3 well exceeded by distal articles; terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopod 1 dactylus with tubercular teeth along lower margin. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe.

Shelf. Tropical Atlantic. 1 species (Paul and Menzies, 1971: description of type species as *Haliophasma*; Wägele, 1981).

Notanthura Monod, 1927

Diagnosis. Body not darkly pigmented. Antennular flagellum of male of 4–5 aesthetasc-bearing articles, retractile. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Mandibular molar a triangular blade; palp article 3 with 1–4 setae on distal margin, or with row of 10–15 setae on distal oblique margin. Maxillipedal palp articles 1–3 fused, 4–5 fused; article 3 barely produced medially beyond articles 4–5 (if at all); terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male). Pereopods 2–7 merus-propodus bearing long setae on upper and lower margins. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe. Pleopod 1 endopod tapering to digitiform apex.

Intertidal, subtidal. Temperate Northern and Tropical Atlantic, Temperate Southern Africa. 4 species (Wägele and Platvoet, 1982: as *Monodanthura*; Poore, 2001: rediagnosis, synonymy).

Pendanthura Menzies and Glynn 1968

Diagnosis. Body total length of adult less than 3 mm; irregularly darkly pigmented. Pleonites 1–5 together much shorter than wide. Pleotelson without indication of posterior margin of pleonite 6. Antennular flagellum of male of 4–5 aesthetasc-bearing articles, retractile. Antennal flagellum of 1–2 articles, very short. Mandibular palp of 1 article. Maxillipedal endite present as a triangular lobe; palp articles 1–5 fused. Pereopods 2, 3 carpus without robust seta posterodistally. Pereopods 4–7 carpus triangular, without free anterior margin, without robust seta on posterior margin or on posterodistal angle.

Shelf. Tropical Atlantic, Tropical Eastern Pacific, Indo West-Pacific. 11 species (Kensley and Schotte, 2000; Chew et al., 2016: rediagnosis, key to species; Annisaqois and Wägele, 2021).

Pilosanthura Wägele, 1989

Diagnosis. Body not darkly pigmented, covered at least in part with setules (fur). Pleonites 1–5 sutures all indicated dorsally and laterally. Antennal flagellum of 7–9 articles, longer than article 5 of peduncle. Eyes absent. Maxillipedal endite reaching palp article 3; palp articles 1–2 fused, 3 free and 4–5 fused; palp article 3 barely produced medially beyond articles 4–5 (if at all); palp terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe.

Bathyal. Temperate Northern Atlantic. 2 species (Wägele, 1980b: description of type species; 1989; Negoescu, 2002).

Ptilanthura Harger, 1878

Diagnosis. Body not darkly pigmented. Antennular flagellum of male of 1 basal + c. 10 aesthetasc-bearing articles. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Mandibular palp of 1 article. Maxillipedal palp articles 1–5 fused. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe.

Shelf. Temperate Northern and Tropical Atlantic. 2 species (Kensley, 1996).

Quantanthura Menzies and George, 1972

Diagnosis. Body not darkly pigmented. Antennular flagellum of male of 1 basal + c. 10 aesthetasc-bearing articles; in juvenile and female of c. 5–7 articles. Antennal flagellum of 7–9 articles, longer than article 5 of peduncle. Maxillipedal endite reaching palp article 3; palp articles 1–5 free, or minute article 5 fused with article 4; palp article 3 barely produced medially beyond articles 4–5 (if at all); palp terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopods 4–7 carpus twice width of propodus, rectangular, with obvious free distal margin (usually with row of pectinate setae) defined by stout seta on posterodistal angle, with robust seta on posterior margin and on posterodistal angle. Pereopods 4–7 propodus with 1 robust setae on posterior margin (in addition to posterodistal robust seta).

Subtidal–bathyal. Temperate Northern and Tropical Atlantic, Central Indo-Pacific, Temperate Southern Africa, Temperate Australasia. 13 species (Poore and Lew Ton, 1986b: key to Australian species; Poore, 2001: rediagnosis, synonymy).

Sauranthura Poore and Kensley, 1981

Diagnosis. Body total length of adult less than 3 mm, with dark species-specific pigment pattern. Pleonites 1–5 together shorter than wide. Antennal flagellum of 1–2 articles, very short. Maxillipedal endite present as a triangular lobe; palp articles 1–5 fused. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male). Pereopods 2, 3 carpus with robust seta posterodistally. Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin, without robust seta on posterior margin or on posterodistal angle.

Subtidal (coral reefs). Central Indo-Pacific, Temperate South America. 2 species (Poore and Kensley, 1981; Shiraki et al., 2025).

Skuphonura Barnard, 1925

Diagnosis. Body not darkly pigmented. Head much wider anteriorly in male, with produced chin in males. Antennular flagellum of male of 1 basal + 1 or 2 short aesthetasc-bearing articles. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Maxillipedal palp articles 1–2 fused, 3 free and 4–5 fused; article 3 barely produced medially beyond articles 4–5 (if at all); terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male). Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin.

Shelf. Tropical Atlantic, Temperate South America (W Atlantic). 6 species (Brusca and Müller, 1991; Jarquín-Martínez and García-Madrigal, 2021: comparison of 4 species).

Stygocyathura Botosaneanu and Stock, 1982

Diagnosis. Body not darkly pigmented. Pleonites 1–5 together shorter than wide. Pleotelson without indication of posterior margin of pleonite 6. Antennular flagellum of male of 1 basal + c. 10 aesthetasc-bearing articles. Antennal flagellum of 1–2 articles, very short. Eyes absent. Mandibular palp article 3 with 1–4 setae on distal margin, or with row of 10–15 setae on distal oblique margin. Maxillipedal palp articles 1–2 fused, 3 free and 4–5 fused; article 3 barely produced medially beyond articles 4–5 (if at all); terminal articles (4–5) at least one third as long as penultimate article (3), almost as long as broad, with a free mesial margin between its suture and distal group of setae. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male). Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin, without robust seta on posterior margin or on posterodistal angle. Uropodal exopod linear, articulating transversely.

Freshwater and brackish stygobiont. 23 species (Wägele et al., 1987). Species of *Stygocyathura* are found over a wide ecological range, from subterranean fresh water (Andreev, 1982; Argano, 1972) to brackish water (Botosaneanu, 1987). Some authors have treated the genus as a subgenus of *Cyathura*.

Tinggianthura Chew, Rahim and bin Haji Ross, 2014

Diagnosis. Body not darkly pigmented. Antennular flagellum of male of 1 basal + 1 or 2 short aesthetasc-bearing articles. Antennal flagellum of 1–2 articles, very short. Maxillipedal palp articles 1–3 fused, 4–5 fused; article 3 barely produced medially beyond articles 4–5 (if at all); terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopods 4–7 carpus triangular, without free anterior margin.

Subtidal. Central Indo-Pacific. Malaysia. 2 species (Chew et al., 2014).

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Expanathuridae Poore, 2001

Figures 5.5, 5.6

Expanathurids are distinguished from anthurids, which they resemble superficially, by the absence of statocysts, usually free pleonites, and the primitive condition of the maxilliped (presence of an endite and palp of five articles), anterodistal serrate setae on the propodus of pereopod 7, and the weakly operculiform pleopod 1. Some genera have a highly ornamented telson and uropodal margins not seen in other families (Poore, 2001; Poore and Lew Ton, 2002).

Diagnosis. Body 10–15 times as long as wide, non-males rarely more elongate (pereonite 7 wider than long, much shorter than pereonite 6); pleonites with plumose setae on margins of epimera or posterior margins of pleonite 5 and sometimes pleonite 4; pleonites 1–5 together not more than twice as long as wide; pleonites 1–5 free and articulating, or fused; telson statocysts absent. Antennal flagellum of fewer than 10 articles, shorter than peduncle, or of numerous articles. Mouthparts not produced anteriorly. Mandible tapering and incisor simple, or compact and with weakly-toothed transverse incisor (rarely). Maxillipedal palp narrow and tapering distally to rounded apex (c. 3 times as long as wide), or reduced, digitiform (*Eisothistos*). Pereopods 2–3 carpus not or weakly produced posterodistally. Pereopod 7 propodus anterodistal serrate setae present. Pleopod 1 exopod and endopod together weakly operculiform, or pleopod 1 exopod operculiform alone (*Expanathura* only).

Implicit genric attributes. Body typically elongate (pereonite 1 longer than wide); setation body and limbs not covered by scattered long setae. Pleonites 1–5 free and articulating, together longer than wide in juvenile. Antennular flagellum of male of 6–7 aesthetasc-bearing articles. Mouthparts not produced anteriorly. Maxillipedal palp narrow and tapering distally to apex (at least twice as long as wide); articles 1 and 2 separated by suture. Pereopods 1–3 only slightly differentiated from posterior pereopods, propodi not more swollen than merus. Pereopod 1 palm of dactylus smooth; propodus cylindrical, palm smooth. Pereopod 1 merus narrower than swollen propodus. Pereopods 1–7 merus without robust seta on anterior margin. Pereopods 4–7 propodus with 1 distal robust seta on cutting edge. Distal palmar robust setae on pereopods 2–7 propodus and 4–7 carpus simple or flagellate. Apices of rami without serrate robust seta.

Key to genera of Expanathuridae

1. Pereopods 1–3 only slightly differentiated from posterior pereopods, propodi not swollen (fig. 5.6a–c). Pleopod 1 rami fused in juveniles (fig. 5.6h). Female pereon and pereopods covered with long setae, body becoming extremely elongate after spawning (fig. 5.5b, c) ..... *Eisothistos*

– Pereopods 1–3 well differentiated from posterior pereopods, propodi swollen. Pleopod 1 rami free. Female pereon and pereopods not covered with long setae, never elongate 2

2. Pleonites 5 and 6 not longer than pleonites 1–4; pleonite 6 clearly fused dorsally to telson. Uropodal exopod a simple narrow leaf (fig. 5.5a) ..... *Coralanthura*

– Pleonites 5 and 6 longer than pleonites 1–4 or all pleonites fused. Pleonite 6 usually marked off dorsally from telson. Uropodal exopod broad or complex 3

3. Uropodal exopod with spike-like dorsal lobe, rami and telson with dentate margins (fig. 5.5h–j) 4

– Uropodal exopod with obsolete dorsal lobe, rami and telson with entire or dentate margins (fig. 5.5f, g) 6

4. Uropodal exopod spike shorter than proximal plate (fig. 5.5i). Mandibular palp with 3 articles (fig. 3.0). Maxillipedal endite short or absent (fig. 5.5p) ..... *Heptanthura*

– Uropodal exopod spike shorter or longer than proximal plate (fig. 5.5h, j). Mandibular palp with fewer than 3 articles (fig. 5.5m). Maxillipedal endite prominent (fig. 5.5q, r) 5

5. Telsonic apex tapering to point from midpoint (fig. 5.5g). Mandibular palp of 2 articles (fig. 5.5n). Maxillipedal palp broad (fig. 5.5r) ..... *Rhiganthura*

– Telsonic apex apically rounded (fig. 5.5h). Mandibular palp of one seta only (fig. 5.5m). Maxillipedal palp acute (fig. 5.5q) ..... *Minyanthura*

6. Pereopod 1 propodus broader than that of pereopod 2, strongly tapering, obscurely dentate proximally (fig. 5.6d, e). Antennular flagellum of male with basal article short, with numerous aesthetascs (fig. 5.5d) ..... *Expanathura*

– Pereopod 1 propodus similar to that of pereopod 2, scarcely tapering, palm smooth (fig. 5.6f, g). Antennular flagellum of male with rows of aesthetascs on all articles (fig. 5.5e) ..... *Panathura*

Coralanthura Poore and Kensley, 1981

Diagnosis. Pleonites of similar lengths, with plumose setae on ventral margins of all epimera; pleotelson without indication of posterior margin of pleonite 6. Palp of 3 articles. Maxillipedal endite apically rounded, reaching to palp article 3; palp broad (1.5–2 times as wide as long), article 4 semicircular. Pereopod 1 palm of dactylus tuberculate. Pereopods 1–7 merus with robust seta on anterior margin. Pleopod 1 weakly operculiform in both sexes, with exopod slightly wider than endopod but not enclosing it totally. Uropodal exopod a narrow leaf articulating proximally. Apices of rami without serrate robust seta. Telson with smooth distal margin.

Subtidal (coral reef). Central Indo-Pacific. 1 species (Poore and Kensley, 1981; Poore and Lew Ton, 2002).

Eisothistos Haswell, 1884

Diagnosis. Body of postspawning female grossly elongate; of juvenile and male of usual proportions; setation areas of body and bases of some limbs of female covered with scattered long setae. Pleonites 1–5 free and articulating and fused in postspawning female, together longer than wide in male and much wider than long in juvenile and prespawning female, pleonites 1–3 longer than 4 and 5 in male and manca, all of similar lengths in juvenile and female, with plumose setae on ventral margins of all epimera; pleotelson with posterior margin of pleonite 6 indicated dorsally, delineated from telson, or without indication of posterior margin of pleonite 6. Antennular flagellum of male of 1 very short basal article bearing numerous aesthetascs and c. 7 longer articles each with 1–2 aesthetascs (or 7 longer articles, second with bunches of aesthetascs). Mandible and maxilla produced anteriorly beyond rostrum. Palp absent. Maxillipedal endite obsolete or absent; palp of 1–5 weakly differentiated narrow articles. Pereopods 1–3 only slightly differentiated from posterior pereopods, propodi not more swollen than merus. Pereopod 1 merus as wide as narrow propodus. Pleopod 1 weakly operculiform, with rami fused in juvenile and prespawning female. Uropodal exopod with strong apical spike, with serrate margin; with serrate lateral lobe between articulation and apical spike. Endopod and spike of exopod with apical serrate robust seta. Telson with dentate distal margin.

Intertidal–bathyal. Temperate Northern and Tropical Atlantic, Temperate Northern W Pacific, Indo West-Pacific, Temperate South America, Temperate Southern Africa, Temperate Australasia, Southern Ocean. 31 species (Knight-Jones and Knight-Jones, 2002; Poore and Lew Ton, 2002; Wägele, 1979).

Expanathura Wägele, 1981

Diagnosis. Pleonites 5 and 6 longer than pleonites 1–4, with plumose setae on dorsal and lateral margins of pleonite 5 (at least in some life stages); pleotelson with posterior margin of pleonite 6 indicated dorsally, delineated from telson. Antennular flagellum of male of 1 very short basal article bearing numerous aesthetascs and c. 7 longer articles each with 1–2 aesthetascs (or 7 longer articles, second with bunches of aesthetascs). Palp of 3 articles. Maxillipedal endite tapering to acute apex, reaching to at least palp article 4; palp articles 1 and 2 separated by suture. Pereopod 1 propodus as broad as long, triangular, palm dentate proximally. Pereopods 4–7 propodus with row of robust setae along cutting edge (at least 1 in addition to distal seta). Pleopod 1 exopod operculiform alone and enclosing narrower endopod in both sexes. Uropodal exopod a broad leaf articulating longitudinally, with smooth margin; without serrate lateral lobe. Telson with smooth distal margin.

Intertidal–shelf. Indo West-Pacific, Southern Ocean. 8 species (Poore and Lew Ton, 2002: rediagnosis, key to 6 species; Annisaqois and Wägele, 2021: differences between species; Shiraki et al., 2021: key to 7 species).

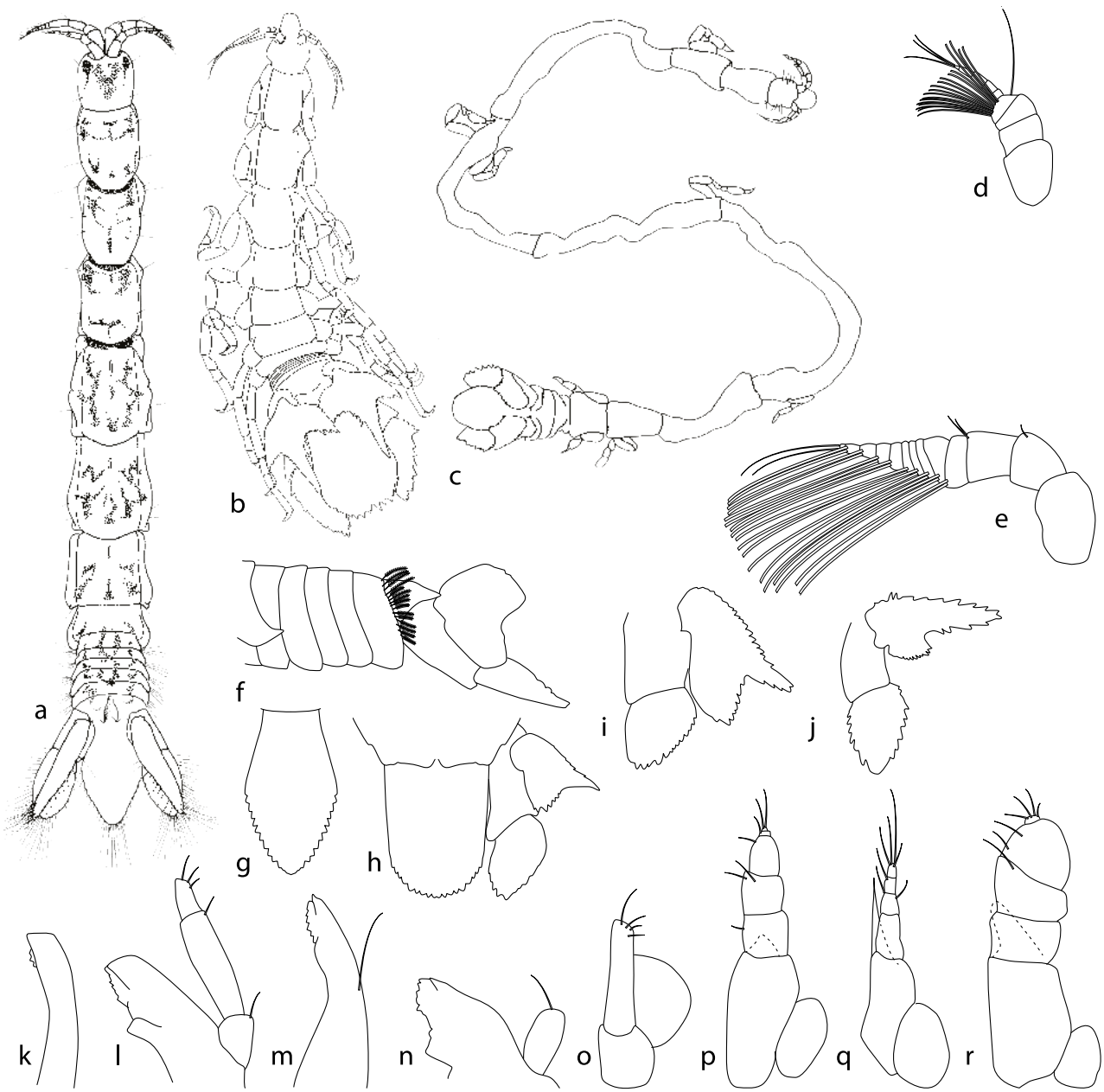


Figure 5.5. Expanthuridae. a, *Coralanthura endeavourae* Poore and Kensley, 1981; b, *Eisothistos bellonae* Poore and Lew Ton, 2002; c, *Eisothistos* sp. (post-spawning female). Male antennula: d, *Expanathura*; e, *Panathura*; f, pleon, uropod, *Expanathura*; g, telson, *Rhiganthura*; h, telson, uropod, *Minyanthura*. Uropod: i, *Heptanthura*; j, *Rhiganthura*. Mandible: k, *Eisothistos*; l, *Heptanthura*; m, *Minyanthura*; n, *Rhiganthura*. Maxilliped: o, *Eisothistos*; p, *Heptanthura*; q, *Minyanthura*; r, *Rhiganthura*.

Heptanthura Kensley, 1978

Diagnosis. Pleonites 1–5 free and articulating or fused, pleonites 5 and 6 longer than pleonites 1–4, with plumose setae on dorsal and lateral margins of pleonite 5 (at least in some life stages); pleotelson with posterior margin of pleonite 6 indicated dorsally, delineated from telson. Palp of 3 articles, or absent. Maxillipedal endite short or absent; palp articles 1–2 fused. Pereopods 1–3 only slightly differentiated from posterior pereopods, propodi not more swollen than merus. Distal palmar robust setae on pereopods 2–7 propodus and 4–7 carpus bifid and blade-like. Pleopod 1 weakly operculiform in both sexes, with exopod slightly wider than endopod but not enclosing it totally. Uropodal exopod with strong apical spike, with serrate margin; without serrate lateral lobe. Telson with dentate distal margin.

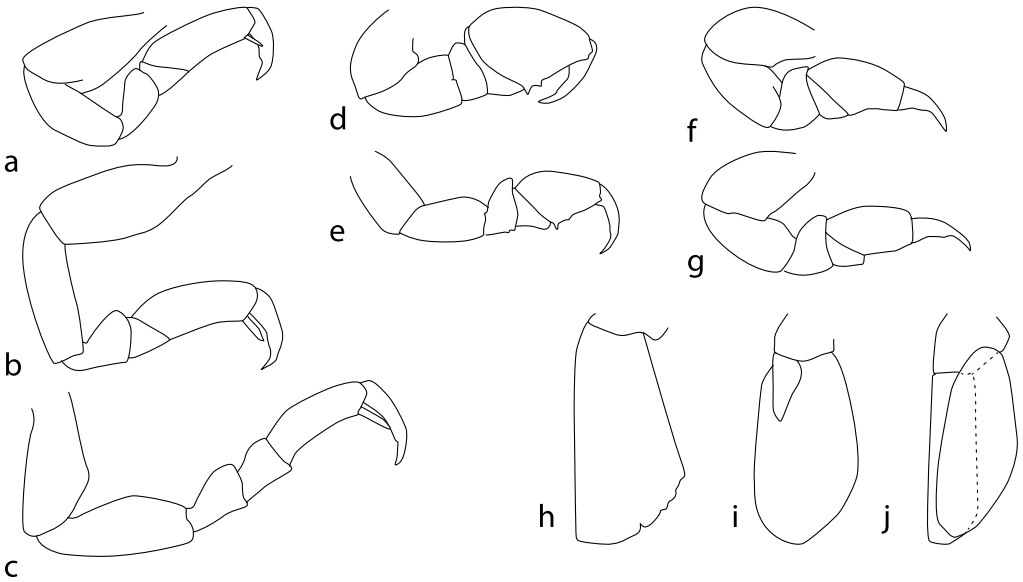


Figure 5.6. Expanthuridae. a, b, c, pereopods 1, 2, 4, *Eisothistos*. d, e, pereopods 1, 2, *Expanathura*. f, g, pereopods 1, 2, *Panathura*. Pleopod 1: h, *Eisothistos*; i, *Expanathura*; j, *Heptanthura*.

Intertidal–shelf. Temperate Northern and Tropical Atlantic, Central Indo-Pacific, Temperate Australasia. 10 species (Kensley and Schotte, 2000: rediagnosis; Poore and Lew Ton, 2002: synonymy).

Minyanthura Kensley, 1982

Diagnosis. Body compact (pereonite 1 shorter than wide) and total length less than 4 mm. Pleonites 1–5 fused, together wider than long in both sexes, with plumose setae on dorsolateral and lateral margins of pleonites 4 and 5; pleotelson without indication of posterior margin of pleonite 6. Palp of 1 seta. Maxillipedal endite tapering to acute apex, reaching to at least palp article 4. Pleopod 1 weakly operculiform in both sexes, with exopod slightly wider than endopod but not enclosing it totally. Uropodal exopod with strong apical spike, with serrate margin; without serrate lateral lobe. Telson with dentate distal margin.

Intertidal, subtidal. Tropical Atlantic, Eastern Indo-Pacific, Temperate Southern Africa. 3 species (Kensley, 1982; Müller, 1993).

Panathura Barnard, 1925

Diagnosis. Pleonites 5 and 6 longer than pleonites 1–4, with plumose setae on dorsolateral and lateral margins of pleonites 4 and 5; pleotelson with posterior margin of pleonite 6 indicated dorsally, delineated from telson. Palp of 3 articles. Maxillipedal endite apically rounded, reaching to palp article 3. Pereopod 1 merus as wide as narrow propodus. Pleopod 1 weakly operculiform in both sexes, with exopod slightly wider than endopod but not enclosing it totally. Uropodal exopod a broad leaf articulating longitudinally, with smooth margin; without serrate lateral lobe. Telson with smooth distal margin.

Subtidal–slope. Western and Central Indo-Pacific, Temperate Southern Africa, Temperate Australasia, Southern Ocean. 6 species (Poore and Lew Ton, 2002: rediagnosis, key to 5 species).

Rhiganthura Kensley, 1978

Diagnosis. Body compact (pereonite 1 shorter than wide) and total length less than 4 mm. Pleonites 1–5 together wider than long in both sexes, pleonites 5 and 6 longer than pleonites 1–4 and pleonite 1 very short, concealed dorsally, with plumose setae on dorsal and lateral margins of pleonite 5 (at least in some life stages); pleotelson without indication of posterior margin of pleonite 6. Palp of 1 or 2 articles. Maxillipedal endite apically rounded, reaching to palp article 3; palp broad (1.5–2 times as wide as long), article 4 semicircular; palp articles 1–2 fused. Pereopod 1 palm of dactylus tuberculate and sometimes carpus and propodus tuberculate. Pereopods 4–7 propodus with row of robust setae along cutting edge (at least 1 in addition to distal seta). Pleopod 1 weakly operculiform in both sexes, with exopod slightly wider than endopod but not enclosing it totally. Uropodal exopod with strong apical spike, with serrate margin; with serrate lateral lobe between articulation and apical spike. Telson with dentate distal margin.

Intertidal–shelf. Central Indo-Pacific, Temperate Australasia. 2 species (Poore and Lew Ton, 2002).

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Hyssuridae Wägele, 1981

Figure 5.7

Members of the Hyssuridae are distinguished from other anthuroids by the absence of a telsonic statocyst, free pleonites, non-operculiform first pleopods (all pleopods are similar) and small size (Müller, 1990; Poore, 2001; Poore and Lew Ton, 1988; Wägele, 1981).

Diagnosis. Body slender (pereonite 7 longer than wide, little or no shorter than pereonite 6); pleonites without marginal plumose setae on pleonal epimera or posterior borders of pleonites 4 and 5; pleonites 1–5 together 3 times as long as wide; pleonites 1–5 free and articulating; telson statocysts absent. Antennal flagellum of fewer than 10 articles, shorter than peduncle. Mouthparts not produced anteriorly. Mandible compact and with weakly-toothed transverse incisor. Maxillipedal palp broad (c. twice as long as wide). Pereopods 2–3 carpus strongly produced posterodistally. Pereopod 7 propodus anterodistal serrate setae absent. Pleopods 1–5 similar, none operculiform.

Implicit generic attributes. Eyes absent. Antennular flagellum article 1 shorter than wide. Antenna flagellum of more than 6 articles, first shorter than others together. Mandibular palp of 3 articles. Maxillipedal endite a short triangular lobe with distal seta(e). Pereopod 2 carpus acutely produced, smooth; propodal palm axial or slightly oblique. Pereopod 3 merus and carpus without tufts of long marginal setae; carpus bluntly produced posterodistally, as in pereopod 2. Pereopods 4–7 propodi without pectinate setae along mesiodistal margin; carpus triangular, with 1 marginal robust or simple seta. Pereopod 7 dactylus narrow, almost as long as propodus. Pleopodal endopods with several marginal setae; pleopod 1 endopod longer and broader than exopod, marginal setae shorter than endopod length. Uropodal endopod free.

Key to genera of Hyssuridae

1. Uropodal exopod as broad or broader than long, endopod fused to peduncle (fig. 5.7b, e). Pleopodal endopods with single apical seta (fig. 5.7m). Mandibular palp of 1 article with seta (fig. 5.7h) 2

– Uropodal exopod longer than wide, endopod free (fig. 5.7c, d). Pleopodal endopods with several marginal setae (fig. 5.7k, l). Mandibular palp of 3 articles (fig. 5.7f, g) 3

2. Pereopod 3 merus and carpus with tufts of long setae (fig. 5.7q). Telson short, excavate apically (fig. 5.7e). Eyes present ..... *Xenanthura*

– Pereopod 3 merus and carpus acutely produced posterodistally (fig. 5.7n). Telson with apical projection (fig. 5.7b). Eyes absent ..... *Belura*

3. Uropodal exopod linear, its mesial margin and lateral margins of telson with cuticular spines (fig. 5.7d) ..... *Neohyssura*

– Uropodal exopod linear or with lateral lobe, unarmed. Telson unarmed (fig. 5.7c) 4

4. Pereopods 4–7 with carpus quadrangular, with 2–3 marginal spiniform setae (fig. 5.7o). Mandibular molar acute (fig. 5.7f) ..... *Hyssura*

– Pereopods 4–7 with carpus triangular, with l marginal spiniform seta (fig. 5.7p). Mandibular molar blunt (fig. 5.7g) 5

5. Pleopod 1 endopod about as long and broad as exopod (fig. 5.7l). Maxillipedal endite prominent (fig. 5.7j) ..... *Kupellonura*

– Pleopod 1 endopod shorter and narrower than exopod (fig. 5.7k). Maxillipedal endite absent (fig. 5.7i) ..... *Galziniella*

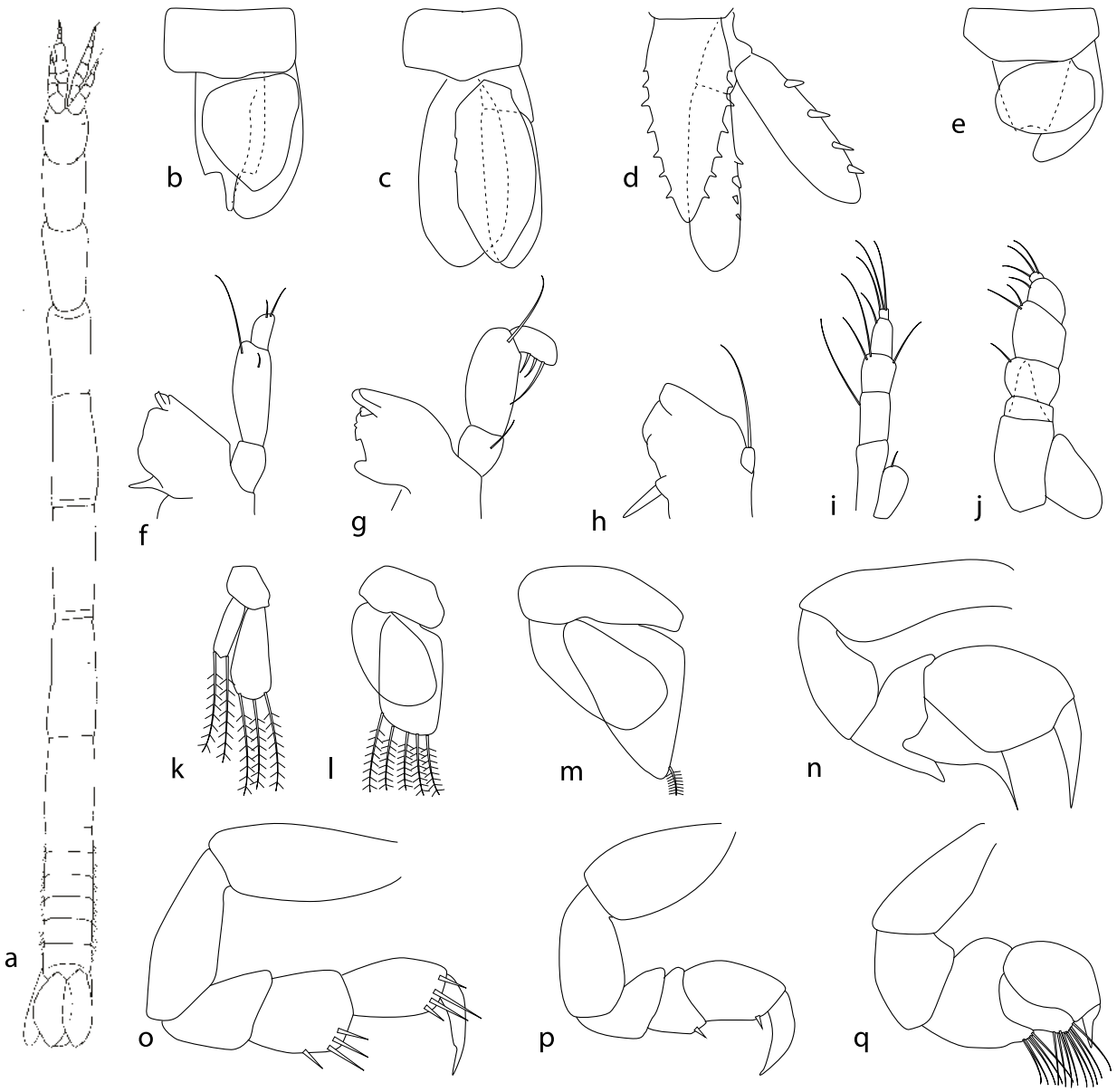


Figure 5.7. Hyssuridae. a, *Kupellonura biriwa* Poore and Lew Ton 1988. Pleonite 6, telson, right uropod: b, *Belura*; c, *Kupellonura*; d, *Neohyssura*; e, *Xenanthura*. Mandible: f, *Hyssura*; g, *Kupellonura*; h, *Xenanthura*. Maxilliped: i, *Galziniella*; j, *Kupellonura*. Pleopod 1: k, *Galziniella*; l, *Kupellonura*; m, *Xenanthura*. n, pereopod 3, *Belura*. o, pereopod 7, *Hyssura*. p, pereopod 4, *Kupellonura*. q, pereopod 3, *Xenanthura*.

Belura Poore and Lew Ton, 1988

Diagnosis. Antenna flagellum of 5 articles, first longer than remaining 4. Mandibular molar an articulating cirolanid-type blade; palp of 1 article with 1 seta or of seta alone. Maxillipedal palp of single fused article. Pereopod 2 carpus a bluntly produced blade, weakly to strongly crenulate; propodus without robust setae on cutting edge. Pereopod 3 carpus acutely produced posterodistally, different from pereopod 2. Pereopods 4–7 propodi with 1 distal robust seta on cutting edge. Pereopod 7 dactylus stout, less than two thirds length of propodus. Pleopodal endopods with single apical seta. Uropodal endopod fused to peduncle; exopod ovoid; rami and telson margins with cuticular spines (especially exopod mesial margin); telson with medial projection on excavate apex.

Subtidal, shelf. Temperate Australasia, Southern Ocean. 2 species (Poore and Lew Ton, 1988).

Galziniella Müller, 1991

Diagnosis. Mandibular molar obsolete, with strong seta reaching near tip of incisor. Maxillipedal endite absent; palp with articles 1 and 2 fused, 3–5 free. Pereopod 2 propodus without robust setae on cutting edge. Pereopods 4–7 propodi with at least 3 robust setae along cutting edge. Pleopod 1 endopod shorter and narrower than exopod, marginal setae longer than endopod length. Uropodal exopod narrowly leaf-shaped; rami and telson margins entire; telson ovoid, with rounded apex.

Intertidal. Eastern Indo-Pacific. (French Polynesia). 1 species (Müller, 1991).

Hyssura Norman and Stebbing, 1886

Diagnosis. Mandibular molar spike-like. Maxillipedal palp of 5 free articles. Pereopod 2 propodus with robust flagellate setae along cutting edge. Pereopods 4–7 propodi with 1 distal robust seta on cutting edge; with short transverse row of 1–3 pectinate setae along mesiodistal margin; carpus quadrangular, wider than propodus, with or without 2 or more pectinate setae along free distal margin. Uropodal exopod with lateral lobe; rami and telson margins entire, or dentate; telson triangular, or ovoid, with rounded apex.

Bathyal. Tropical Atlantic, including Mediterranean, Central Indo-Pacific. 7 species (Kensley, 1978; 1982a: as *Ocsanthura*; Poore and Lew Ton, 1988: rediagnosis).

Kupellonura Barnard, 1925

Diagnosis. Eyes present. Mandibular molar blunt. Maxillipedal palp of 5 free articles. Pereopod 2 propodus with robust flagellate setae along cutting edge. Pereopods 4–7 propodi with 1 distal robust seta on cutting edge. Uropodal exopod narrowly leaf-shaped, or with lateral lobe; rami and telson margins entire, or dentate; telson ovoid, with rounded apex.

Intertidal–bathyal. Temperate Northern and Tropical Atlantic, North W Pacific, Central and Eastern Indo-Pacific, Temperate Southern Africa, Temperate Australasia, Southern Ocean. 19 species (Kensley, 1982b; Poore and Lew Ton, 1988: rediagnosis; Shiraki et al., 2022).

Neohyssura Amar, 1953

Diagnosis. Mandibular molar spike-like. Maxillipedal palp of 5 free articles. Pereopod 2 propodus with robust flagellate setae along cutting edge. Pereopods 4–7 propodi with 1 distal robust seta on cutting edge. Uropodal exopod narrowly leaf-shaped; rami and telson margins with cuticular spines (especially exopod mesial margin); telson triangular.

Intertidal–bathyal. Temperate Northern and Tropical Atlantic, Western and Central Indo-Pacific, Temperate Southern Africa. 6 species (Wägele, 1987; Poore and Lew Ton, 1988: rediagnosis).

Xenanthura Barnard, 1925

Diagnosis. Eyes present. Antennular flagellum article 1 twice as long as wide. Antenna flagellum of 5 articles, first longer than remaining 4. Mandibular molar an articulating cirolanid-type blade; palp of 1 article with 1 seta or of seta alone. Maxillipedal palp of single fused article. Pereopod 2 carpus a bluntly produced blade, weakly-strongly crenellate; propodal palm transverse, crenellate; propodus without robust setae on cutting edge. Pereopod 3 merus and carpus with tufts of long marginal setae; carpus not produced. Pereopods 4–7 propodi without robust setae on cutting edge (few tubercles on merus-propodus instead); with short transverse row of 1–3 pectinate setae along mesiodistal margin. Pereopod 7 dactylus stout, less than two thirds length of propodus. Pleopodal endopods with single apical seta. Uropodal endopod fused to peduncle; exopod ovoid; rami and telson margins entire; telson short, excavate apically (without medial projection).

Intertidal–shelf. Tropical Atlantic, Western and Central Indo-Pacific, Temperate South America, Temperate Australasia. 7 species (Poore and Lew Ton, 1988: rediagnosis; Müller, 1990).

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Leptanthuridae Poore, 2001

Figures 5.8, 5.9

Leptanthurids have a single telsonic statocyst and an even row of robust setae, often complex, along the palm of pereopod 1, which is usually defined proximally by a square angle or a protruding tooth (Poore, 2001). Leptanthurids are probable predators (Wägele, 1981, 1985a).

Diagnosis. Body 10–15 times as long as wide, non-males rarely more elongate (pereonite 7 wider than long, much shorter than pereonite 6); pleonites without marginal plumose setae on pleonal epimera or posterior borders of pleonites 4 and 5; pleonites 1–5 together not more than twice as long as wide; pleonites 1–5 free and articulating, or fused; telson statocyst single. Antennal flagellum of fewer than 10 articles, shorter than peduncle, or of numerous articles. Mouthparts acutely produced anteriorly. Mandible with acute anteriorly directed incisor. Maxillipedal palp narrow, tapering to acute apex, of fewer than 4 articles (c. 3 times as long as wide). Pereopods 2–3 carpus not or weakly produced posterodistally. Pereopod 7 propodus anterodistal serrate setae absent. Pleopod 1 exopod operculiform alone.

Implicit generic attributes. Pleonites 1–5 free and articulating; pleotelson with posterior margin of pleonite 6 indicated dorsally, delineated from telson. Eyes well developed. Antennular and antennal peduncle articles compact. Antennal peduncle without sucker-like cuticular structures; flagellum of 5–8 articles, shorter than peduncle; flagellum articles cylindrical and free. Mandibular palp of 3 articles; article 3 with row of 7 or more setae on oblique apex. Maxillipedal palp almost as long as basis. Pereopods 1–3 propodi without rolled tessellated margin. Pereopod 1 carpus, posterior margin without short robust setae; propodus significantly larger than propodus of pereopods 2 and 3; palm axial or oblique; palm with proximal tooth (defined by clear angle to palm). Pereopods 2 and 3 carpus margin without robust setae. Pereopodal propodi 2 and 3 ovate, 4–7 linear. Pereopods 4–7 carpus quadrangular or elongate, with free anterior margin. Pereopod 7 present on adults.

Key to genera of Leptanthuridae

1.	Pereopod 7 absent on adults. Pereopodal propodi 2–6 similar, much narrower than long (fig. 5.9i, j)	*Curassanthura*
–	Pereopod 7 present on adults. Pereopodal propodi 2 and 3 differentiated from 4–7, even slightly	2
2.	Maxillipedal endite reaching at least end of first palp article (fig. 5.8i–k)	3
–	Maxillipedal endite absent or obsolete (fig. 5.8l, m)	9
3.	Pleonites 1–5 fused; pleonite 6 not distinguishable from telson (fig. 5.8n). Pereopods 1–3 similar, propodus with rolled tessellated palm and strong proximal thumb (fig. 5.9a)	*Aenigmathura*
–	Pleonites free and articulating (rarely 1–5 fused); pleonite 6 marked off dorsally from telson (fig. 5.8a, b). Pereopods 2 and 3 or 3 only differentiated from pereopod 1, none with rolled tessellated propodal palm	4
4.	Antennae 1 and 2 flagella of >12 articles, longer than or equal to peduncles (fig. 5.8a, b)	5
–	Antennae 1 and 2 flagella of c. 12 articles, shorter than peduncles (fig. 5.8c, d, e)	6
5.	Antennal peduncle with sucker-like cuticular structures (fig. 5.8e)	*Negoescuanthura*
–	Antennal peduncle without sucker-like cuticular structures	*Accalathura*
6.	Pereopods 4–7 carpus triangular, enclosed anteriorly by surrounding articles (fig. 5.9o, q)	*Albanthura*
–	Pereopods 4–7 carpus quadrangular or elongate, with free anterior margin (fig. 5.9p)	7
7.	Maxillipedal palp of 5 articles (fig. 5.8j). Pereopod 2 much more elongate than pereopod 1 (fig. 5.9b, c)	*Bourbonanthura*

– Maxillipedal palp of 3 articles (fig. 5.8k). Pereopod 2 similar to but smaller than pereopod 1 8

8. Eyes poorly developed. Pereopod 1 carpus without robust setae on posterior margin; palm with row of similar simple robust setae (fig. 5.9h) ..... *Calathura*

– Eyes well developed. Pereopod 1 carpus with robust setae on posterior margin; palm with row of complex robust setae and distinctive seta on tooth (fig. 5.9n) ..... *Virganthura*

9. Mandibular palp of 3 articles 10

– Mandibular palp of 1 article 12

10. Maxillipedal palp fused to basis and all articles (except sometimes for minute distal article) (fig. 5.8m) ..... *Neoanthura*

– Maxillipedal palp free from basis, with articles 1–3 or 1–4 fused, article 5 minute if visible (fig. 5.8l) 11

11. Antennular and antennal peduncles articles elongate (fig. 5.8c). Pereopods 1 and 2 both with strong proximal thumb on propodal palm (fig. 5.9f, g) ..... *Bunderanthura*

– Antenna 1 and 2 peduncles articles compact (fig. 5.8d). Pereopods 1 and 2 with short proximal thumb on propodal palm (fig. 5.9k, j) ..... *Leptanthura*

12. Pereopod 1 propodus much larger than that of pereopod 2 (fig. 5.9d, e). Mandibular palp of one article with one seta (fig. 5.8f) ..... *Bullowanthura*

– Pereopods 1 and 2 or 1–3 similar. Mandibular palp of one article without seta or absent 13

13. Pereopods 1 and 2 similar, enlarged, propodus grossly produced at proximal end of palm so that palm is transverse (fig. 5.9m). Pereopods 4–7 with merus not distally lobed on flexor margin. Mandibular palp absent (fig. 5.8g) ..... *Psittanthura*

– Pereopods 1–3 similar, propodus with small thumb at proximal end of axial palm. Pereopods 4–7 with merus lobed (fig. 5.9q). Mandibular palp a simple article (fig. 5.8h) ..... *Ulakanthura*

Accalathura Barnard, 1925

Diagnosis. Antennal flagellum of 13–20 articles, longer than or slightly shorter than peduncle. Maxillipedal endite reaching middle of second fused segment; palp free from basis, with articles 1–2 fused and 3–5 fused. Pereopod 1 palm with even marginal row of short complex robust setae along length; without distinctive robust setae on proximal tooth.

Intertidal–bathyal. Tropical Atlantic, Western and Central Indo-Pacific, Temperate Southern Africa, Temperate Australasia, Southern Ocean (Wägele, 1985a; Poore and Lew Ton, 1990: rediagnosis, key to 13 Australian species; King, 2008: redescription of type species).

Aenigmathura Thomson, 1951

Diagnosis. Pleonites 1–5 fused (or sutures immoveably indicated); pleotelson without indication of posterior margin of pleonite 6. Antennal flagellum articles short and fused. Maxillipedal endite reaching at least article 3; palp free from basis, with articles 1–2 fused and 3–5 fused. Pereopods 1–3 propodi with rolled tessellated margin. Pereopod 1 palm with even marginal row of short complex robust setae along length; with 1–2 distinctive robust setae on tooth.

Intertidal–bathyal. Temperate Australia. 4 species (Poore and Lew Ton, 1986).

Albanthura Wägele, 1985

Diagnosis. Eyes absent. Mandibular palp article 3 with fewer than 4 terminal setae. Maxillipedal endite reaching at least article 3; palp free from basis, with articles 1–2 fused, 3–4 and 5 free. Pereopod 1 palm defined proximally by angle distant from palm of carpus; with even marginal row of short complex robust setae along length; with 1 larger simple robust seta on proximal angle. Pereopods 2 and 3 carpus margin with 1–2 robust setae (as in propodus). Pereopods 4–7 carpus triangular, enclosed anteriorly by surrounding articles.

Shelf–bathyal. New Zealand. 2 species (Wägele, 1985b).

Bourbonanthura Müller, 1990

Diagnosis. Eyes poorly developed, or absent. Maxillipedal endite reaching at least article 3; palp free from basis, of 5 free articles. Pereopod 1 palm with even marginal row of short complex robust setae along length; without distinctive robust setae on proximal tooth.

Intertidal, subtidal. Eastern Indo-Pacific, Temperate Southern Africa. 2 species (Müller, 1990, 1993).

Bullowanthura Poore, 1978

Diagnosis. Eyes absent. Antennal flagellum rudimentary (fewer than 5 articles), shorter than last article of peduncle. Mandibular

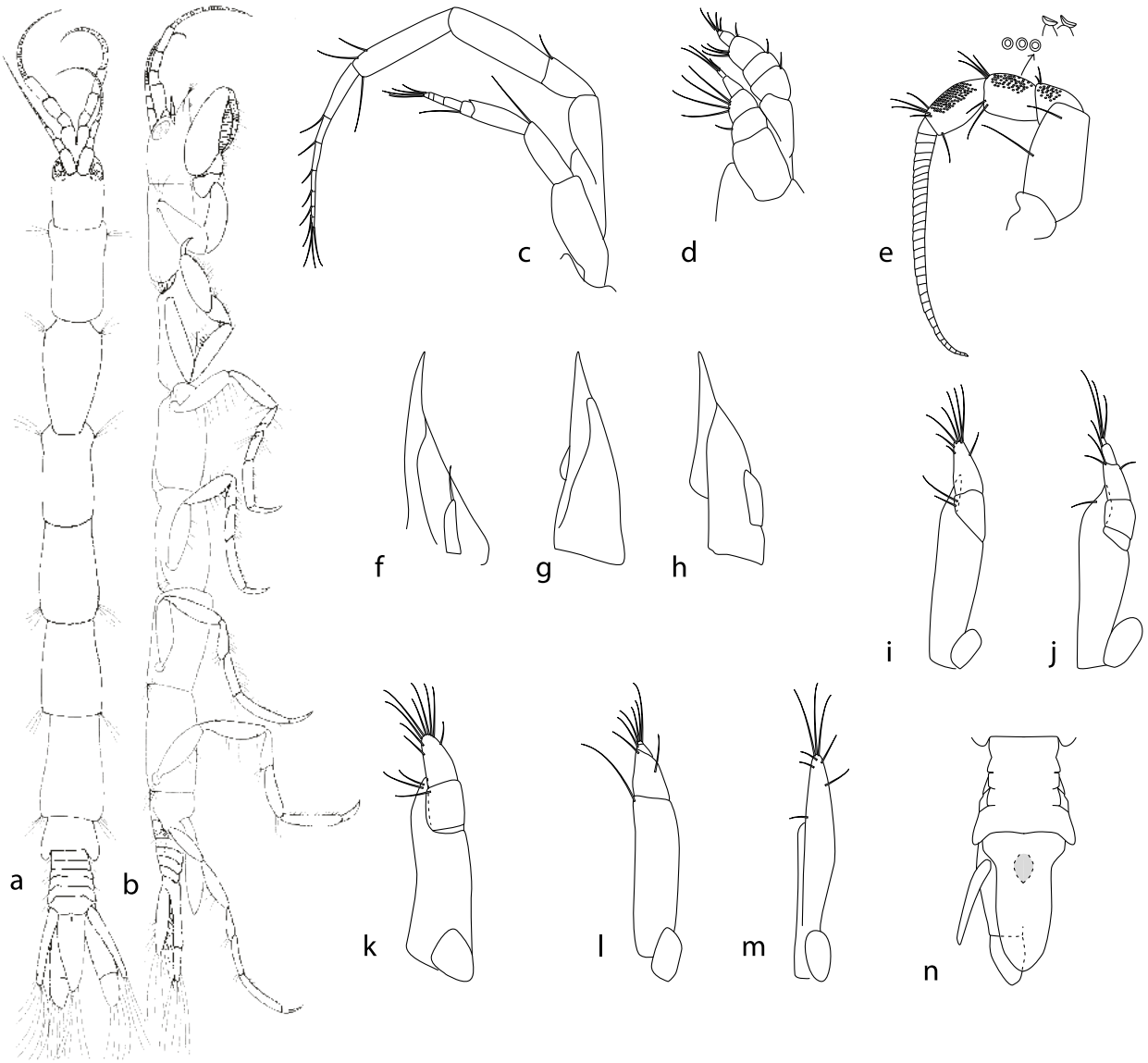


Figure 5.8. Leptanthuridae. a, b, *Accalathura themeda* Poore and Lew Ton, 1990. Left antennula, antenna: c, *Bunderanthura*; d, *Leptanthura*. e, antenna with detail of sucker-like cuticular structures, *Negoescuanthura*. Mandible: f, *Bullowanthura*; g, *Psittanthura*; h, *Ulakanthura*. Maxilliped: i, *Aenigmathura*; j, *Bourbonanthura*; k, *Calathura*; l, *Leptanthura*; m, *Neoanthura*. n, pleon, telson, uropod, *Aenigmathura*.

palp of 1 article. Maxillipedal endite absent or obsolete; palp one-third as long as basis, palp free from basis, with articles 1–2 fused and 3–5 fused. Pereopod 1 carpus, posterior margin with short robust setae (as on propodus); palm with even marginal row of short complex robust setae along length; palm with 1–2 distinctive robust setae on tooth. Pereopods 2 and 3 carpus margin with 1–2 robust setae (as in propodus). Pereopods 4–7 carpus triangular, enclosed anteriorly by surrounding articles.

Subtidal–bathyal. Temperate Northern Atlantic, Temperate Australasia. 5 species (Negoescu, 2005; Poore, 1978).

Bunderanthura Poore and Humphreys, 2013

Diagnosis. Antennular and antennal peduncle articles longer than wide. Maxillipedal endite absent or obsolete; palp one third as long as basis, palp free from basis, with articles 1–2 fused, articles 3–5 minute, free. Pereopod 1 palm and peropod 2 palm with proximal tooth; with even marginal row of short complex robust setae along length; with 1 larger simple robust seta on proximal angle.

Anchialine sinkhole near coast. NW Australia. 1 species (Poore and Humphreys, 2013).

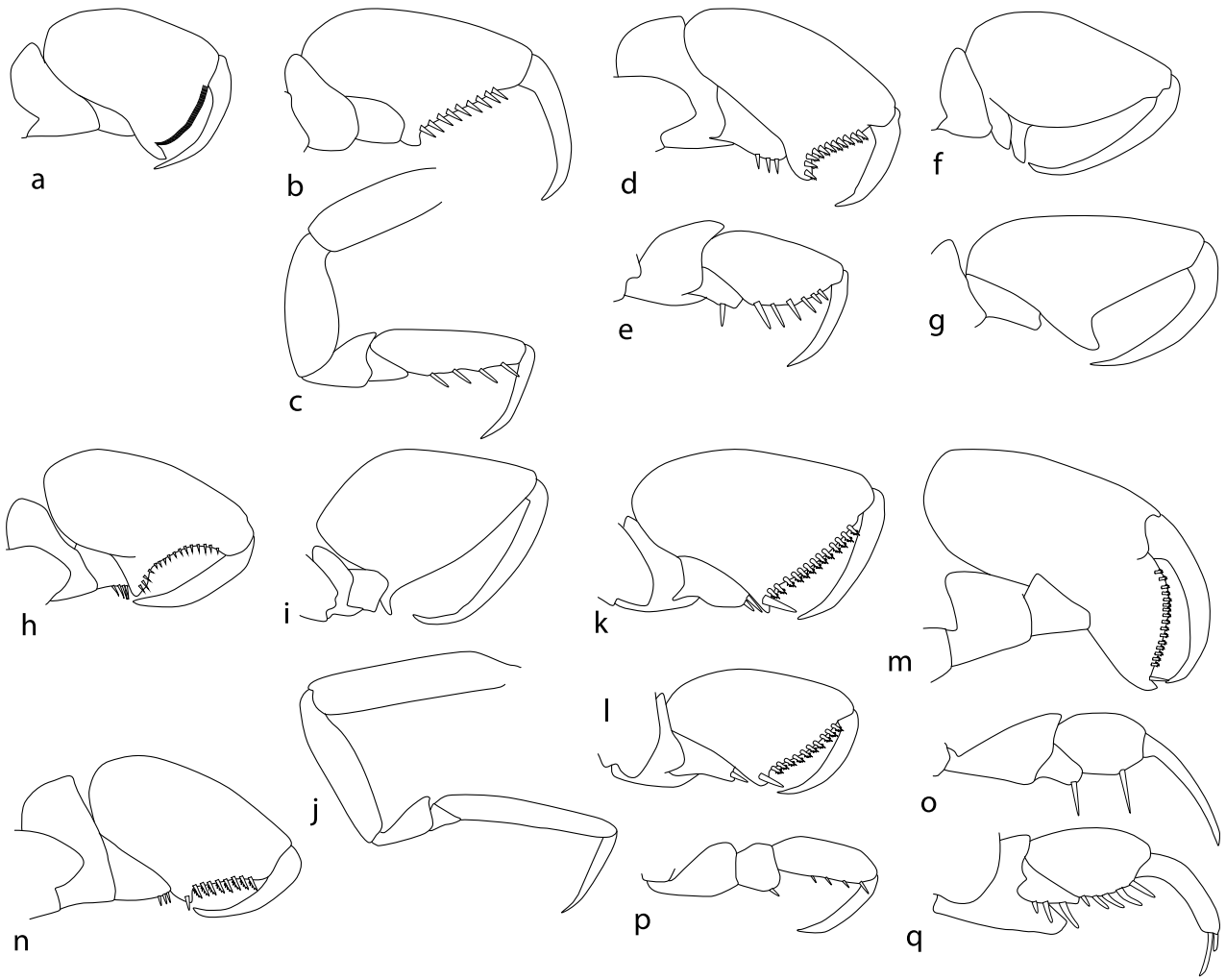


Figure 5.9. Leptanthuridae. Pereopod 1 or 1 and 2: a, *Aenigmathura*; b, c, *Bourbonanthura*; d, e, *Bullowanthura*; f, g, *Bunderanthura*; h, *Calathura*; i, j, *Curassanthura*; k, l, *Leptanthura*; m, *Psittanthura*; n, *Virganthura*. Pereopod 4: o, *Albanthura*; p, *Calathura*; q, *Ulakanthura*.

Calathura Norman and Stebbing, 1886

Diagnosis. Maxillipedal endite reaching at least article 3; palp one third as long as basis, palp free from basis, of 5 free articles. Pereopod 1 palm with even marginal row of closely set simple robust setae; without distinctive robust setae on proximal tooth.

Subtidal–bathyal. Temperate Northern Atlantic. 2 species (Brandt and Negoescu, 1997: redescription of type species).

Curassanthura Kensley, 1981

Diagnosis. Eyes poorly developed. Mandibular palp article 3 with fewer than 4 terminal setae. Maxillipedal endite reaching at least article 3; palp free from basis, of 5 free articles. Pereopod 1 palm with even marginal row of short complex robust setae along length; without distinctive robust setae on proximal tooth, or with 1–2 distinctive robust setae on tooth. Pereopodal propodi 2–6 similar, much narrower than long. Pereopod 7 absent on adults.

Hypogean in beach sand. Tropical Atlantic. 5 species (Wägele, 1985c; Wägele and Brandt, 1985).

Leptanthura Sars, 1897

Diagnosis. Eyes poorly developed, or absent. Antennal flagellum rudimentary (fewer than 5 articles), shorter than last article of peduncle. Mandibular palp article 3 with fewer than 4 terminal setae. Maxillipedal endite absent or obsolete; palp one third as long as basis, palp free from basis, with articles 1–3 fused, 5 minute if visible or free from basis, with articles 1–4 fused and 5 minute if visible. Pereopod 1 carpus, posterior margin with short robust setae (as on propodus); palm defined proximally by angle distant from palm of carpus; palm with even marginal row of short complex robust setae along length, with 1 larger simple robust seta on proximal angle. Pereopods 2 and 3 carpus margin with 1–2 robust setae (as in propodus). Pereopods 4–7 carpus triangular, enclosed anteriorly by surrounding articles.

Intertidal–bathyal. Arctic, Temperate Northern and Tropical Atlantic, Temperate Northern Pacific, Western and Central Indo-Pacific, Temperate Southern Africa, Temperate Australasia. 43 species (Kensley and Schotte, 2000; Müller, 1992; Negoescu, 2007).

Negoescuanthura Jarquín-Martínez and García-Madrigal, 2021

Diagnosis. Antennal peduncle with sucker-like cuticular structures; flagellum of more than 30 articles, longer than peduncle. Maxillipedal endite reaching middle of second fused segment; palp free from basis, with articles 1–2 fused and 3–5 fused. Pereopod 1 palm with even marginal row of short complex robust setae along length; without distinctive robust setae on proximal tooth.

Subtidal. Tropical Eastern Pacific. 2 species (Jarquín-Martínez and García-Madrigal, 2021).

Neoanthura Menzies, 1956

Diagnosis. Eyes absent. Antennal flagellum rudimentary (fewer than 5 articles), shorter than last article of peduncle. Maxillipedal endite absent or obsolete; palp one third as long as basis, palp fused to basis and all articles (except sometimes for minute distal article).

Bathyal. Tropical Atlantic. 1 species (Menzies, 1956).

Psittanthura Wägele, 1985

Diagnosis. Eyes absent. Mandibular palp absent. Maxillipedal endite absent or obsolete; palp one third as long as basis, palp free from basis, with articles 1–4 fused and 5 minute if visible. Pereopod 1 propodus narrower than on similarly shaped pereopod 2; palm transverse, its proximal angle strongly produced away from carpus; palm defined proximally by angle distant from palm of carpus; palm with even marginal row of short complex robust setae along length; palm with 1 larger simple robust seta on proximal angle. Pereopodal propodus 2 similar to propodus of pereopod 1, propodus 3 smaller, with transverse palm. Pereopods 4–7 carpus triangular, enclosed anteriorly by surrounding articles.

Bathyal. New Zealand. 1 species (Wägele, 1985b).

Ulakanthura Poore, 1978

Diagnosis. Pleonites 1–5 free and articulating. Eyes absent. Antennal flagellum rudimentary (fewer than 5 articles), shorter than last article of peduncle. Mandibular palp of 1 article. Maxillipedal endite absent or obsolete; palp one third as long as basis, palp free from basis, with articles 1–3 fused, 5 minute if visible. Pereopod 1 carpus, posterior margin with short robust setae (as on propodus); propodus narrower than on similarly shaped pereopod 2; palm defined proximally by angle distant from palm of carpus; palm with even marginal row of short complex robust setae along length; palm with 1 larger simple robust seta on proximal angle. Pereopodal propodi 2 and 3 similar to propodus 1 (bases of these limbs much longer and broader than in pereopod 1). Pereopods 4–7 carpus triangular, enclosed anteriorly by surrounding articles.

Subtidal. Temperate Australasia. 7 species (Poore, 1978).

Virganthura Kensley, 1987

Diagnosis. Mandibular palp article 3 with c. 5 setae in longitudinal row. Maxillipedal endite reaching at least article 3; palp free from basis, with articles 1–2 fused, 3–4 and 5 free. Pereopod 1 carpus, posterior margin with short robust setae (as on propodus); palm with even marginal row of short complex robust setae along length; palm with 1–2 distinctive robust setae on tooth.

Shelf. Tropical Atlantic. 1 species (Kensley, 1987).

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Paranthuridae Menzies and Glynn, 1968

Figure 5.10

The family Paranthuridae was introduced to include all anthuroids with "piercing" mouthparts, that is, with the labrum, mandible and maxilliped produced forward as cone comprising acute stylets (Menzies and Glynn, 1968). Poore (2001) separated most of these as Leptanthuridae, retaining Paranthuridae for six genera lacking statocysts and without complex robust setae along the palm of pereopod 1. Shiraki et al. (2022) added another genus. Shiraki et al. (2026) provided a key to genera. Many species are darkly pigmented. The family includes one endemic New Zealand species from interstitial fresh water, *Cruregens fontanus* Chilton, 1882.

Diagnosis. Body 10–15 times as long as wide, non-males rarely more elongate (pereonite 7 wider than long, much shorter than pereonite 6); pleonites without marginal plumose setae on pleonal epimera or posterior borders of pleonites 4 and 5; pleonites 1–5 together not more than twice as long as wide; pleonites 1–5 free and articulating, or fused; telson statocysts absent. Antennal flagellum rudimentary (fewer than 5 fused articles), shorter than last article of peduncle. Mouthparts acutely produced anteriorly. Mandible with acute anteriorly directed incisor (often secondarily blunt). Maxillipedal palp narrow, tapering to acute apex, of fewer than 4 articles (c. 3 times as long as wide). Pereopods 2–3 carpus not or weakly produced posterodistally. Pereopod 7 propodus anterodistal serrate setae absent. Pleopod 1 exopod operculiform alone.

Implied generic characters. Body pigmented; pleonite 1 mid-dorsal length as long as pleonite 2; pleonites articulating; pleonite 6 posterior margin indicated dorsally, delineated from telson; pleotelson oval. Eyes well developed. Antennal flagellum articles cylindrical and free. Mandibular palp absent. Pereopod 1 palm without proximal tooth (palm more or less continuous with that of carpus). Pereopodal propodi 2 and 3 ovate, 4–7 linear. Pereopod 7 absent in adults.

Key to genera of Paranthuridae

1. Pereopod 7 present in adults. Pereopod l propodus without proximal row of closely set setae on mesial surface (fig. 5.10p). Mandible with 3-articled palp (fig. 5.10m) 2
– Pereopod 7 absent in adults. Pereopod 1 propodus without or with row of closely set setae on mesial surface (fig. 5.10o). Mandible without palp (fig. 5.10l) 4
2. Pleonites free or fused; pleonite 6 articulating with pleon, usually distinct from telson; telson oval. Uropodal exopod linear or leaf-shaped (fig. 5.10a). Antenna flagellum plate-like, of short fused articles (fig. 5.10j) ..... *Paranthura*
– Pleonites fused but with sutures visible; pleonite 6 not articulating with pleon; telson triangular. Uropodal exopod reduced (fig. 5.10g, h). Antenna flagellum articles cylindrical (fig. 5.10j) 3
3. Eyes present. Pleonites 1–5, pleotelson fused (sutures visible; fig. 5.10g) ..... *Deltanthura*
– Eyes absent. Pleonites 1–5, pleotelson fused (sutures barely visible; fig. 5.10h) ..... *Pseudanthura*
4. Pereonite 7 very short, not visible laterally (fig. 5.10b–d). Head as long as wide 5

– Pereonite 7 one third as long as pereonite 6 (fig. 5.10e, f). Head longer than wide 6

5. Pleonites 1–5 separated by integumental folds dorsally; pleonite 1 twice as long as pleonite 2 (fig. 5.10d) ..... *Colanthura*

– Pleonites 1–5 fused, rarely with integumental folds dorsally; pleonites of similar lengths (fig. 5.10b, c) ..... *Califanthura*

6. Pleonites 2–5 only fused (fig. 5.10d). Marine or estuarine. Eyes present ..... *Cruranthura*

– Pleonites all free (fig. 5.10f). Hypogean freshwater. Eyes absent ..... *Cruregens*

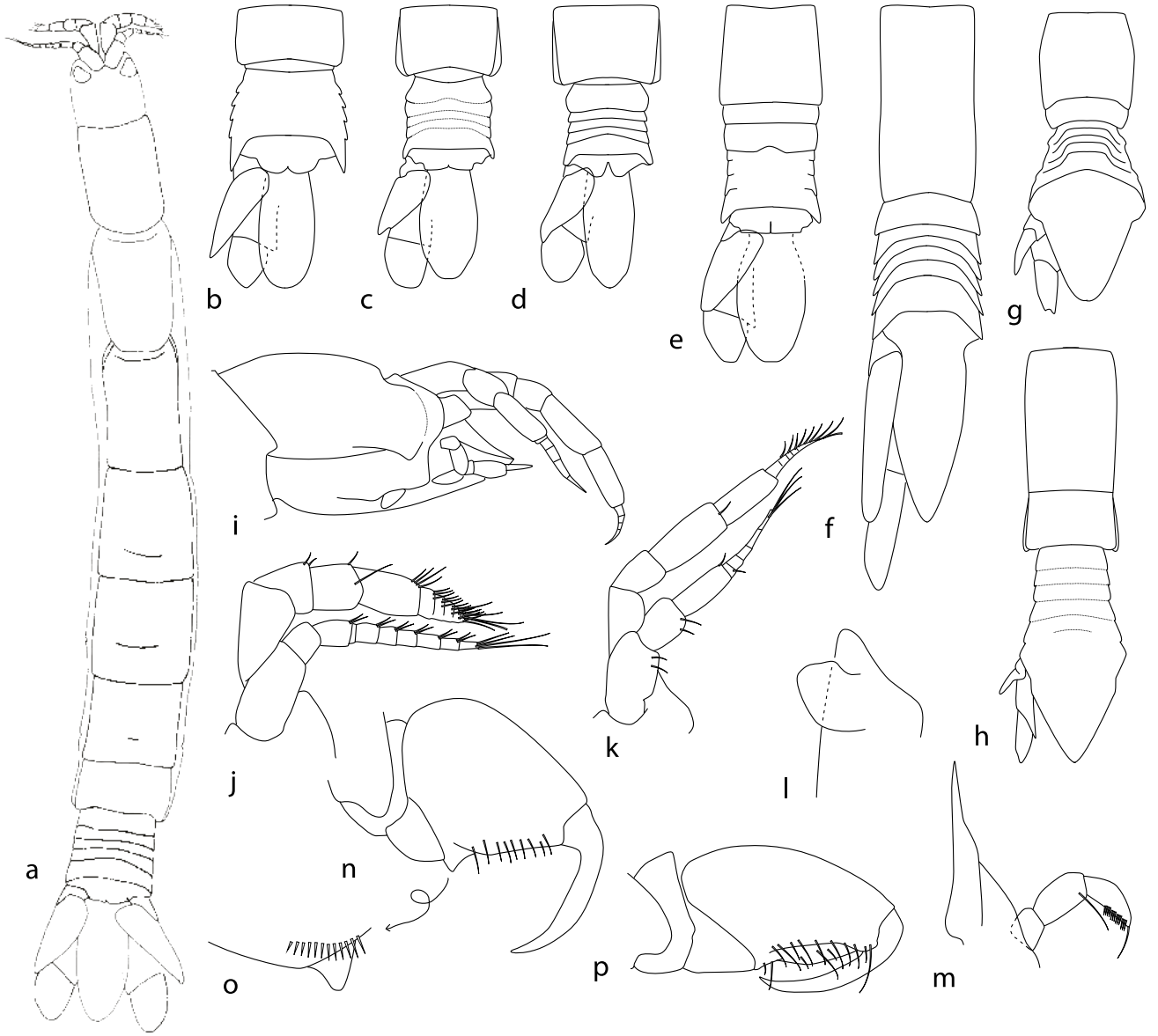


Figure 5.10. Paranthuridae. a, *Paranthura acacia* Poore, 1984. Pereonites 6, 7, pleon, pleotelson, uropod: b, c, *Califanthura*; d, *Colanthura*; e, *Cruranthura*; f, *Cruregens*; g, *Deltanthura*; h, *Pseudanthura*. i, head, mouthparts, antennula, antenna, lateral, *Pseudanthura*. Antennula, antenna: j, *Paranthura*; k *Pseudanthura*. Mandible: l, *Califanthura*; m, *Pseudanthura*. n, o, *Califanthura*, pereopod 1 palm with thumb and row of setae. p, *Paranthura*.

Califanthura Schultz, 1977

Diagnosis. Pereonite 7 extremely reduced, hidden except dorsally; pleonites 1–5 fused (or sutures immoveably indicated). Pereopod 1 propodus with row of closely set setae confined proximally on mesial surface. Uropodal exopod narrowly leaf-shaped.

Intertidal–bathyal. Tropical Atlantic, Temperate South America, Temperate Australasia, Southern Ocean. 9 species (Poore, 1984a: rediagnosis).

Colanthura Richardson, 1902

Diagnosis. Pereonite 7 extremely reduced, hidden except dorsally; pleonites 1–5 fused but indicated by folds dorsally and laterally; pleonite 1 middorsal length longer than pleonite 2, swollen laterally. Pereopod 1 propodus with row of closely set setae confined proximally on mesial surface. Uropodal exopod narrowly leaf-shaped.

Intertidal–bathyal. Temperate Northern and Tropical Atlantic, Temperate Northern Pacific, Indo West-Pacific, Temperate Southern Africa. 14 species (Poore, 1984a: rediagnosis).

Cruranthura Thomson, 1946

Diagnosis. Pereonite 7 one third as long as pereonite 6; pleonites 1 free, 2–5 not indicated by folds dorsally. Pereopod 1 propodus with row of closely set setae confined proximally on mesial surface. Uropodal exopod narrowly leaf-shaped.

Intertidal, subtidal. Temperate Northern Atlantic, Central Indo-Pacific, Temperate Australasia. 4 species (Poore, 1984a: rediagnosis).

Cruregens Chilton, 1882

Diagnosis. Body not pigmented; pereonite 7 one third as long as pereonite 6; pleonites 1–5 free and articulating; pleonites fused; pleonite 6 not delineated from pletelson. Eyes absent. Pereopod 1 propodus with setae on mesial surface evenly spaced along palm; palm with proximal tooth (defined by clear angle to palm). Pereopodal propodi 2–6 similar, much narrower than long. Uropodal exopod linear, apically rounded.

Freshwater stygobiont. New Zealand endemic. 1 species (Wägele, 1982: redescription of type species).

Deltanthura Shiraki, Shimomura and Kakui, 2022

Diagnosis. Body not pigmented; pereonite 7 half as long as pereonite 6; pleonites 1–5 fused (sutures visible); pleonites fused; pleonite 6 not delineated from pletelson; pleotelson triangular. Mandibular palp of 3 articles. Pereopod 1 propodus with setae on mesial surface evenly spaced along palm. Pereopodal propodi 2–6 similar, much narrower than long. Pereopod 7 present on adults. Uropodal exopod elongate-triangular, reaching beyond end of peduncle.

Slope. Temperate Northern Pacific. 1 species (Shiraki et al., 2022, 2026).

Paranthura Bate and Westwood, 1866

Diagnosis. Pereonite 7 half as long as pereonite 6; pleonites 1–5 free and articulating, or 1–5 fused (or sutures immoveably indicated), or 1 free, 2–5 not indicated by folds dorsally. Antennal flagellum articles plate-like, of short fused articles. Mandibular palp of 3 articles. Pereopod 1 propodus with setae on mesial surface evenly spaced along palm. Pereopod 7 present on adults. Uropodal exopod narrowly leaf-shaped, or broad and more or less notched.

Intertidal–bathyal. Cosmopolitan except Arctic. 68 species (Poore, 1984b: key to 13 species from SE Australia).

Pseudanthura Richardson, 1911

Diagnosis. Body not pigmented; pereonite 7 half as long as pereonite 6; pleonites 1–5 fused (or sutures immoveably indicated); pleonites fused; pleonite 6 not delineated from pletelson; pleotelson triangular. Eyes absent. Mandibular palp of 3 articles. Pereopod 1 propodus with setae on mesial surface evenly spaced along palm. Pereopod 7 present on adults. Uropodal exopod linear, tapering, as long as or shorter than peduncle.

Shelf–abyssal. Tropical Atlantic, Indo West-Pacific, Temperate South America, Temperate Australasia. 5 species (Poore and Lew Ton, 1986: rediagnosis, key to species).

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Remaining Cymothoida Wägele, 1989

The remaining Cymothoida is a polyphyletic grouping that includes all predatory, parasitic, blood-sucking or scavenging cymothoidan isopods except anthuroids. They are best defined by the absence of the extreme mouthpart modifications and reductions seen in Anthuroidea. Brandt and Poore (2003) treated them as two superfamilies, Cirolanoidea and "Cymothooidea". They include the former suborder Gnathiidea, now treated as a derived and specialised family (Brandt and Poore, 2003; Brusca and Wilson, 1991).

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Aegidae White, 1850

Figures 5.11, 5.12

Aegidae are associates of fishes, almost exclusively attaching temporarily to the external skin surface. A few species are associated with other invertebrates, notably sponges, which might be used as refugia. Aegids are regarded as micropredators rather than parasites, feeding on blood or mucus temporarily and never attaching permanently (Bruce, 2009). Many species are relatively large (1–7 cm) and can be recognised as belonging to this family by the prehensile dactyli on pereopods 1–3 and the large dark eyes, sometimes meeting, or almost meeting, at the midline of the head. Species of the family are occasionally pests of aquaculture fishes. The family is almost exclusively marine, with the monotypic *Alitropus* H. Milne Edwards, 1840 the only genus occurring in fresh water.

Earlier keys to genera included *Barybrotes* Schioedte and Meinert, 1879, now in its own family Barybrotidae Hansen, 1890 (Bruce, 2009), or were limited to seven marine genera.

Diagnosis. Eyes large, often medially united. Mouthparts forming buccal cone; maxillula styliform, with terminal and mesial robust setae; maxilla with single distomesial basal endite; maxilliped palp with conspicuous recurved ("hooked") robust setae. Pereopods 1–3 robust, with dactylus as long as or longer than propodus, usually strongly recurved.

Implicit generic attributes. Head overlapped laterally by anterior angles of pereonite 1. Antennulae and antennae well developed; division between peduncle and flagellum distinct. Frontal lamina present, varied in shape, occasionally absent, usually not abutting clypeus. Clypeus and labrum present, often indistinct. Mandible incisor narrow, small molar process present, occasionally absent, laminar and triangular when present; lacinia mobilis and spine row absent. Maxillula styliform, with flattened terminal robust setae, may be distally hooked. Maxilliped endite present (*Aega* group of genera and *Rocinela*) or absent (*Syscenus* and *Xenuraega*); palp with 3–5 articles, at least articles 3 and 4 with large, hooked robust setae. Penial processes flush.

Key to genera of Aegidae

1. Pleonite 1 abruptly narrower than pereonite 7. Pleonite 5 lateral margin entirely free. Eyes usually absent (fig. 5.11f–h) 2

– Pleonite 1 not abruptly narrower than pereonite 7. Pleonite 5 lateral margin partly or entirely overlapped by pleonite 4. Eyes present, often large (fig. 5.11a–e) 3

2. Frontal lamina present (fig. 5.11u). Uropodal rami both laminar (fig. 5.11f) ..... *Syscenus*

– Frontal lamina absent (fig. 5.11v). Uropodal endopod stub-like, exopod filamentous or both rami elongate (fig. 5.11h) ..... *Xenuraega*

3. Body dorsally compressed (fig. 5.11e). Frontal lamina slender, lanceolate (fig. 5.11q). Rostrum anteriorly widely rounded or truncate (fig. 5.11q, s, t). Maxilliped palp 3-articled (fig. 5.12p, q) 4

– Body dorsally moderately to strongly vaulted (fig. 5.11b). Frontal lamina wide (fig. 5.11n, o). Rostrum narrowly rounded, subtruncate or acute (fig. 5.11a, b, r). Maxilliped palp 5-articled; article 5 may be minute or fused to article 4 (fig. 5.12k–n) 5

4. Coxae of pereonites 5–7 as long or longer than respective segment (fig. 5.11d, e). Frontal lamina small but obvious (fig. 5.11t). Maxilliped endite present (fig. 5.12p). Plane of uropodal endopod set oblique to exopod. Marine ..... *Rocinela*

– Coxae of pereonites 5–7 distinctly shorter than respective segment (fig. 5.11c). Frontal lamina minute (fig. 5.11q). Maxilliped endite absent. Uropodal rami coplanar. Estuarine and freshwater, Australasia ..... *Alitropus*

5. Frontal lamina ventrally flat, not strongly narrowed posteriorly. Antennula peduncle articles 1 and 2 flattened (fig. 5.11n, o) 6

– Frontal lamina with free posterior margin and/or narrowed posteriorly (fig. 5.11p r). Antennula peduncle articles 1 and 2 not flattened or expanded (fig. 5.11p r) 7

6. Uropodal rami coplanar, extending to or beyond pleotelson apex; uropodal endopod lateral margin usually without distinct excision. Pleotelson posterior margin not distinctly produced, with or without median point, may be concave or truncate (fig. 5.11a) ..... *Aega*

– Uropodal endopod at oblique angle to exopod, rami usually not extending to pleotelson apex; uropodal endopod lateral margin usually with distinct excision. Pleotelson apex forming distinct point, usually produced (fig. 5.11i, j) ..... *Aegapheles*

7. Rostrum bent ventrally or ventroposteriorly (fig. 5.11l, p). Maxilliped palp article 5 longer than wide, not fused to article 4 (fig. 5.12m, n) ..... *Aegiochus*

– Rostrum minute, not projecting, not visible in dorsal view (fig. 5.11m, r). Maxilliped palp article 5 minute, less than 0.3 width of article 4 (fig. 5.12o) ..... *Epulaega*

Aega Leach, 1815

Diagnosis. Body dorsally vaulted; rostral point large, dorsal, rostral point apex shape acute. Coxae 5–7 as long or longer than respective pereonite. Pleon not distinctly narrower than pereonite 7; pleonite 5 lateral margins largely or wholly overlapped by pleonite 4. Eyes large, occupying 50% or more of head. Antennula peduncle article 1 close-set or together, articles 1 and 2 short, dorsoventrally flattened. Antennal peduncle articles 1–3 short, 4 and 5 longest, articles 4 or 4 and 5 without long plumose setae. Frontal lamina posteriorly wide, separate from clypeus. Mandible incisor bicuspid. Maxilliped endite present; palp 5-articled, article 1 present. Pleopod 2 appendix masculina inserted basally; pleopods 3 and 4 endopods same size as exopod, with few plumose marginal setae at distolateral angle only. Uropodal rami with distinct apex, rami coplanar.

Subtidal–abyssal (to 2148 m). Cosmopolitan. 37 species (Brusca, 1983: key to 11 species of eastern Pacific; Bruce, 2009: rediagnosis, key to 7 New Zealand species).

Aegapheles Bruce, 2009

Diagnosis. Body dorsally vaulted; head overlapped laterally by anterior angles of pereonite 1; rostral point large, dorsal, rostral point apex shape acute. Coxae 5–7 as long or longer than respective pereonite. Pleon not distinctly narrower than pereonite 7; pleonite 5 lateral margins largely or wholly overlapped by pleonite 4. Eyes large, occupying 50% or more of head. Antennula peduncle article 1 close-set or together, articles 1 and 2 short, articles 1 and 2 dorsoventrally flattened. Antennal peduncle articles 1–3 short, 4 and 5 longest, articles 4 or 4 and 5 without long plumose setae. Frontal lamina posteriorly wide, separate from clypeus. Mandible incisor bicuspid. Maxilliped endite present; palp 5-articled, article 1 present. Pleopod 2 appendix masculina inserted basally; pleopods 3 and 4 endopods same size as exopod, with few plumose marginal setae at distolateral angle only. Uropodal rami with distinct apex, rami exopod at oblique angle to endopod.

Subtidal–bathyal (70–1140 m). Cosmopolitan. 17 species (Bruce, 2004: description of 21 species as "*Aega deshaysiana* (Milne Edwards, 1840) group"; Bruce, 2009: diagnosis, key to 7 New Zealand species).

Aegiochus Bovallius, 1885

Diagnosis. Body dorsally vaulted; rostral point large, dorsal, rostral point apex shape narrowly rounded. Coxae 5–7 as long or longer than respective pereonite. Pleon not distinctly narrower than pereonite 7; pleonite 5 lateral margins largely or wholly overlapped by pleonite 4. Eyes often large, sometimes medially united. Antennula peduncle article 1 separated by rostrum, articles 1 and 2 short, cylindrical. Antennal peduncle articles 1–3 short, 4 and 5 longest, articles 4 or 4 and 5 without long plumose setae. Frontal lamina wide, posteriorly narrow, forming stem. Mandible incisor bicuspid. Maxilliped endite present; palp 5-articled, article 1 present. Pleopod 2 appendix masculina inserted basally; pleopods 3 and 4 endopods same size as exopod, with plumose marginal setae. Uropodal rami with distinct apex, rami coplanar.

Subtidal–abyssal (shallow–3461 m). Cosmopolitan. 38 species (Brusca, 1983: description of 5 species as *Aega* (*Rhamphion*) Brusca, 1983), junior synonym; Bruce, 2009: rediagnosis, key to 15 NZ species).

Alitropus H. Milne Edwards, 1840

Diagnosis. Body dorsally depressed; rostral point small, dorsal, rostral point apex shape acute. Coxae 5–7 shorter than

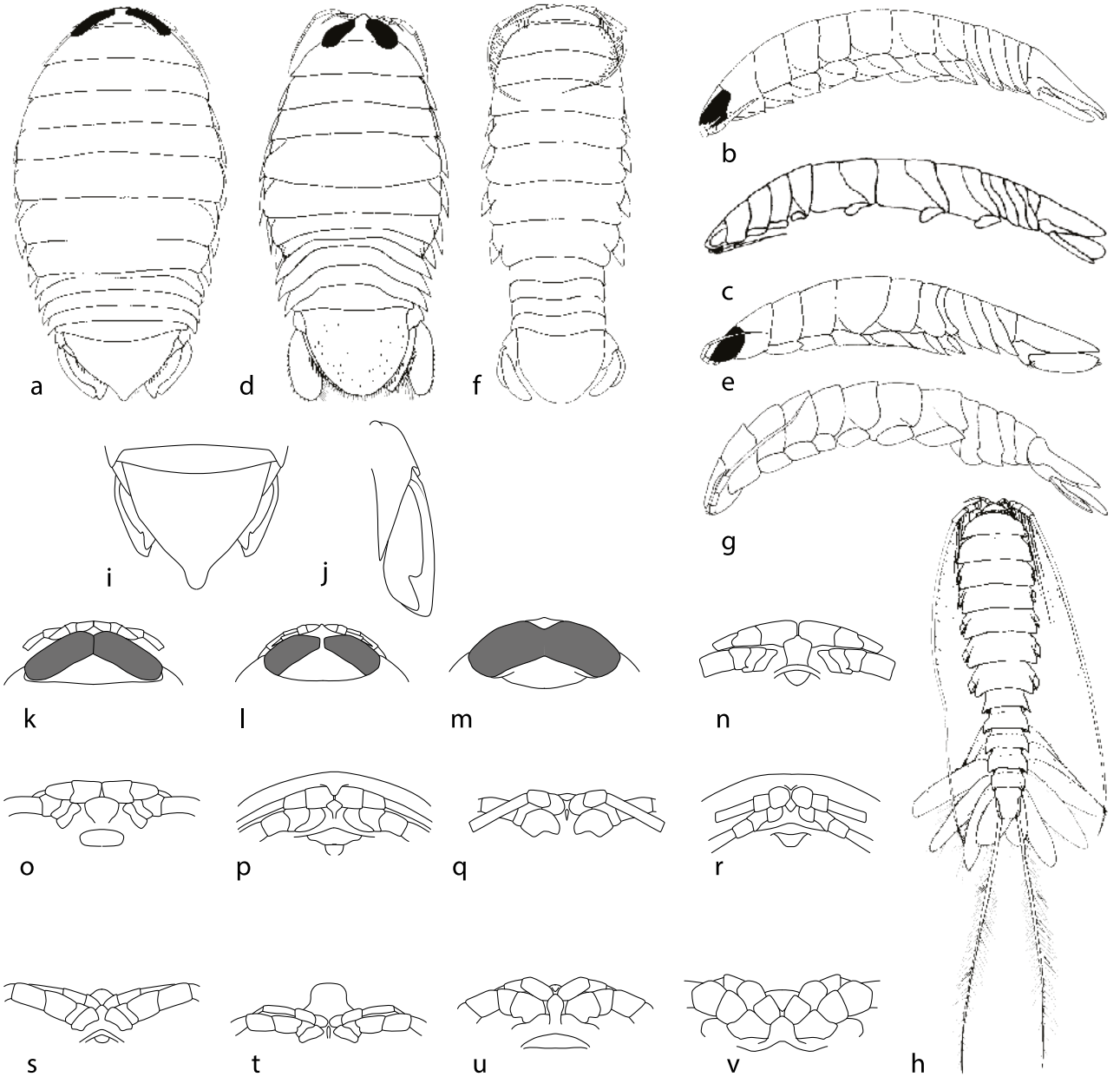


Figure 5.11. Aegidae. a, b, *Aega falklandica* Kussakin, 1967; c, *Alitropus typus* H. Milne Edwards, 1840; d, e, *Rocinela bonita* Bruce, 2009; f, g, *Syscenus kapoo* Bruce, 2009; h, *Xenuraega ptilocera* Tattersall, 1909. i, j, pleonite 5, pleotelson, uropods, *Aegapheles*. Head, eyes, antennae, dorsal: k, *Aegapheles*; l, *Aegiochus*; m, *Epulaega*. Antennulae, antennae, frontal lamina: n, *Aega*; o, *Aegapheles*; p, *Aegiochus*; q, *Alitropus*; r, *Epulaega*; s, t, *Rocinela*; u, *Syscenus*; v, *Xenuraega*.

respective pereonite. Pleon not distinctly narrower than pereonite 7; pleonite 5 lateral margins largely or wholly overlapped by pleonite 4. Eyes large, occupying 50% or more of head. Antennula peduncle article 1 close-set or together, articles 1 and 2 short, articles 1 and 2 cylindrical. Antennal peduncle articles 1–3 short, 4 and 5 longest, articles 4 or 4 and 5 without long plumose setae. Frontal lamina slender, elongate, posteriorly narrow, forming stem. Mandible incisor unicuspid. Maxilliped endite absent; palp articles 3-articled, article 1 indivisibly fused. Pleopod 2 appendix masculina inserted subbasally; pleopods 3 and 4 endopods smaller than exopod, without plumose marginal setae. Uropodal rami rounded, without distinct apex, rami exopod at oblique angle to endopod.

Freshwater, estuarine. Central Indo-Pacific (S and SE Asia, tropical Australia). 1 species (Ho and Tonguthai, 1992: figures of only species). *Alitropus typus* H. Milne Edwards, 1840 is an ectoparasitic pest on cultured fish in SE Asia (Bhakta et al., 2021; Shah et al., 2017; Wang et al., 2008).

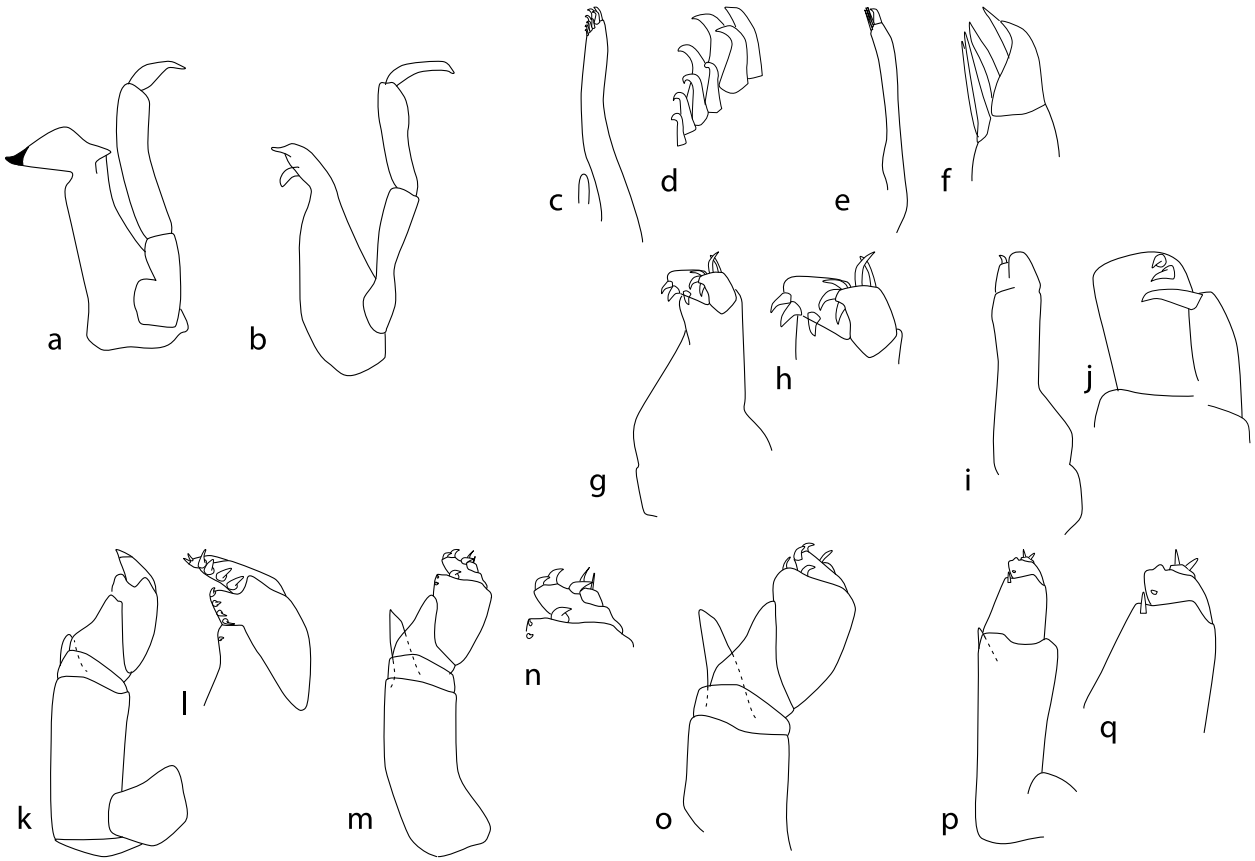


Figure 5.12. Aegidae. Mandible: a, *Aega*; b, *Rocinela*. Maxillula, detail of apex: c, d, *Aega*; e, f, *Rocinela*. Maxilla, detail of apex: g, h, *Aega*; i, j, *Rocinela*. Maxilliped, detail of apex: k, l, *Aega*; m, n, *Aegiochus*; o, *Epulaega*; p, q, *Rocinela*.

Epulaega Bruce, 2009

Diagnosis. Body dorsally vaulted; rostral point small, anteroventral, rostral point apex shape acute. Coxae 5–7 as long or longer than respective pereonite. Pleon not distinctly narrower than pereonite 7; pleonite 5 lateral margins largely or wholly overlapped by pleonite 4. Eyes large, occupying 50% or more of head. Antennula peduncle article 1 close-set or together, articles 1 and 2 short, cylindrical. Antennal peduncle articles 1–3 short, 4 and 5 longest, articles 4 or 4 and 5 without long plumose setae. Frontal lamina wide, posteriorly narrow, forming stem. Mandible incisor bicuspid. Maxilliped endite present; palp 5-articled, article 1 present. Pleopod 2 appendix masculina inserted basally; pleopods 3 and 4 endopods same size as exopod, with plumose marginal setae. Uropodal rami with distinct apex, rami coplanar.

Subtidal–slope (to 500 m); associated with sponges. Central Indo-Pacific, Temperate Southern Africa, Temperate Australasia. 5 species (Bruce, 2009).

Rocinela Leach, 1818

Diagnosis. Body dorsally depressed; rostral point large, dorsal, rostral point apex shape broadly to narrowly rounded. Coxae 5–7 as long or longer than respective pereonite. Pleon not distinctly narrower than pereonite 7; pleonite 5 lateral margins largely or wholly overlapped by pleonite 4. Eyes large, occupying 50% or more of head. Antennula peduncle article 1 close-set or together, articles 1 and 2 elongate, cylindrical. Antennal peduncle articles 1 and 2 short, 5 longest, articles 4 or 4 and 5 without long plumose setae. Frontal lamina slender, elongate, posteriorly narrow, forming stem. Mandible incisor unicuspid. Maxilliped endite present, or absent; palp articles 3-articled, article 1 indivisibly fused. Pleopod 2 appendix masculina inserted sub-basally; pleopods 3 and 4 endopods smaller than exopod, without plumose marginal setae. Uropodal rami rounded, without distinct apex, exopod at oblique angle to endopod.

Subtidal–abyssal (103–1976 m). Cosmopolitan. 42 species (Brusca and France, 1992: key to eastern Pacific species; Bruce, 2009: rediagnosis, key to 7 New Zealand species).

Syscenus Harger, 1880

Diagnosis. Body dorsally vaulted; head not overlapped laterally by anterior angles of pereonite 1; rostral point small, anteroventral, rostral point apex shape narrowly rounded.

Coxae 5–7 shorter than respective pereonite. Pleon distinctly narrower than pereonite 7; pleonite 5 lateral margins free. Eyes usually absent (present in 2 species). Antennula peduncle article 1 close set or together, articles 1 and 2 elongate, articles 1 and 2 cylindrical. Antennal peduncle articles 1 and 2 short, 5 longest, articles 4 or 4 and 5 with long plumose setae. Frontal lamina wide, posteriorly wide, separate from clypeus. Mandible incisor unicuspid. Maxilliped endite absent; palp 3-articled or 2-articled, article 1 indivisibly fused. Penial processes flat lobes. Pleopod 2 appendix masculina inserted subproximally; pleopods 3 and 4 endopods smaller than exopod, without plumose marginal setae. Uropodal rami coplanar.

Mesopelagic (704–4609 m). Cosmopolitan. 9 species (Brandt and Andres, 2008; Bruce, 2009).

Xenuraega Tattersall, 1909

Diagnosis. Body dorsally vaulted; head not overlapped laterally by anterior angles of pereonite 1; rostral point small, anteroventral, apex narrowly rounded. Coxae 5–7 shorter than respective pereonite. Pleon distinctly narrower than pereonite 7; pleonite 5 lateral margins free. Eyes absent. Antennula peduncle article 1 close set or together, articles 1 and 2 elongate, articles 1 and 2 cylindrical. Antennal peduncle articles 1 and 2 short, 5 longest, articles 4 or 4 and 5 with long plumose setae. Frontal lamina wide, posteriorly wide, separate from clypeus. Mandible incisor unicuspid. Maxilliped endite absent; palp 3-articled or 2-articled, article 1 indivisibly fused. Penial processes flat lobes. Pleopod 2 appendix masculina inserted sub-basally; pleopods 3 and 4 endopods smaller than exopod, without plumose marginal setae. Uropod with one or both rami elongate (0.2–0.8 body length) or filamentous.

Mesopelagic (310–1250 m). Temperate Northern Atlantic, Temperate Northern Pacific. 2 species (Bruce, 1993; Shimomura and Bruce, 2019).

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Anuropidae Stebbing, 1893

Figure 5.13

Anuropids are unique in having the uropods concealed by the pleotelson, almost identical to pleopods 1–5 and presumably performing a respiratory function. The uropods do, however, move laterally as is typical in cymothoidans (Jansen, 1982). All species have been taken from midwater oceanic environments or at the surface from the guts of oceanic albatrosses and petrels (Lincoln and Jones, 1973; Sivertsen and Holthuis, 1980). Anuropids are probable symbionts of scyphozoans (Barham and Pickwell, 1969). Individuals are large isopods, up to 70 mm long.

Diagnosis. Eyes widely separated, lateral, sometimes small or absent. Antennula of 2 articles with second article expanded and scalloped. Mandibular incisor blade-like; lacinia mobils and spine row present; molar blade-like. Maxillipedal endite absent; palp of 1 article. Pereopod 1 subchelate, pereopods 2–7 ambulatory. Uropod folded ventrally below pleotelson, resembling pleopods.

Anuropus Beddard, 1893

Meso- and bathypelagic. Arctic, Temperate Northern Pacific, Western Indo-Pacific, Tropical Eastern Pacific, Temperate South America, Temperate Australasia, Southern Ocean. 10 species (Jansen, 1982: key to 7 species; Brandt and Retzlaff, 2002).

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Figure 5.13. Anuropidae. a, *Anuropus pacificus* Lincoln and Jones, 1973. *Anuropus*: b, pleotelson, uropods, ventral view; c, maxilliped.

Barybrotidae Hansen, 1890

Figure 5.14

The only species *Barybrotes indus* Schioedte and Meinert, 1879 has long been considered a member of Aegidae but shares few characters with this family (Bruce, 2009). While the mouthparts are similar, they are not homologous. The maxilla is minute and the maxilliped palp has only four articles. The species is a probable micropredator of fishes.

Diagnosis. Eyes widely separated. Mouthparts forming buccal cone. Mandibular incisor broad, tridentate; lacinia mobils and spine row absent; molar bladelike. Maxillula outer endite styliform, with flattened terminal robust setae. Maxilla with 1 endite with terminal sharp recurved robust setae. Maxillipedal endite absent; palp of 4 articles, article 2–4 with hooked robust setae. Pereopods 1–3 with prehensile dactylus, 4–7 natatory, with flattened bases with fringe of plumose setae.

Barybrotes Schioedte and Meinert, 1879

Slope. Western and Central Indo-Pacific. 1 species (Pillai, 1967: figures; Bruce, 2009: rediagnosis of family).

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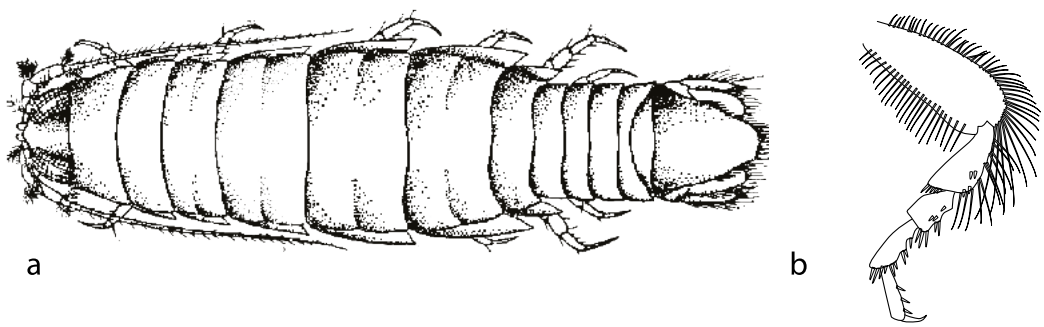


Figure 5.14. Barybrotidae, *Barybrotes indus* Schioedte and Meinert, 1879. a, habitus; b, pereopod 7.

Family Cirolanidae Dana, 1852

Figures 5.15–5.21

The Cirolanidae is the second-largest family of the aquatic Isopoda with 535 species in 64 genera, of which 466 species in 39 genera are marine or estuarine (on 31 December 2025). The family is found in all marine and estuarine waters. Almost 70 species belonging to 25 genera (plus others from predominantly "marine or brackish-water genera") occur only in fresh water, springs, anchialine caves, marine "blue holes" and ground waters, largely in Central America, Europe and lands surrounding the Mediterranean. These genera are not included in this chapter.

Marine cirolanids occur worldwide, with highest diversity within the tropics, and are largely absent from polar waters. The family is dominated by four marine genera, *Cirolana* Leach, 1818, *Eurydice* Leach, 1816 (on sand beaches and subtidal sands), *Metacirolana* Kussakin, 1979 (particularly on coral reefs) and *Natatolana* Bruce, 1981; these large genera comprise 76% of all marine cirolanid species. The family is near exclusively scavenging and predatory in feeding habits (see Bruce 1986; Brusca et al., 1995), with two species known to be commensals of other invertebrates, namely *Cartetolana integra* (Miers, 1884) which associates with crinoids, and *Neocirolana hermitensis* (Boone, 1919) which associates with hermit crabs of the genus *Dardanus* and is probably an egg predator. The scavenging species, which occur in their thousands at times, play a probably important ecological role in marine environments from the intertidal to the upper continental slope. Cirolanids are generally scarce at depths greater than 500 m, and rare beyond 1000 m; 27 species (7%) are known from depths of 1000 m or more, and of these only nine species are known from more than 2000 m depth.

Diagnosis. Eyes widely separated, lateral, sometimes small or absent. Antennular peduncle 3-articled. Antenna with peduncle and flagellum distinct. Mouthparts not forming a buccal cone; mandibular incisor broad, tridentate, wider than 50% width (rarely less) of mandible body; lacinia mobilis indistinct or absent, spine row present; molar, large, bladelike, anterior margin usually toothed. Maxillula lateral endite with 10–13 acute, often keratinised, robust setae. Maxilla with 1 or 2 endites. Maxillipedal endite as long as palp article 1; palp of 5 articles. Pereopods 1–3 ambulatory with robust dactyli or subprehensile; pereopods 4–7 ambulatory or natatory.

Implicit generic attributes. Body not elongate, < 4 times as long as wide. Dorsum vaulted, dorsal surface smooth. Pleon (pleonites 1–5, excluding pleotelson) short, < 20% body length, usually 10–14% body length, with 5 visible segments. Antennular peduncle articles 1–3 colinear; peduncle articles 1 and 2 short, article 3 longest. Antennal peduncle articles 1–3 short, 4 and 5 subequal in length and longest. Mandible incisor not massive; wide, > 0.55 times basal width. Pereopods 1–3 propodus ambulatory, dactylus less than 0.55 length of propodus; dactylus not extending to carpus when folded; inferior margin of merus without connate spines (spines without suture at base). Pleopod 1 rami not (rarely) operculate; endopod 0.50–0.68 as wide as exopod. Pleopods without respiratory branchiae. Pleopods 2–5 peduncle lateral margins without well-developed laminar lobe. Uropod peduncle posterior mesial margin produced. Uropod rami as long as mesial length of peduncle; endopod lateral margin without excision; exopod laminar, rami subequal in length. Pleotelson posterior margin without prominent spines.

Key to the marine and estuarine genera of Cirolanidae

Priority has been given to using characters that can be seen without dissection, so use of mouthparts has been minimised; the key is therefore not subjectively phylogenetic. Maxilliped palp article 5 is either distally rounded (fig. 5.18l, n), or quadrate (fig. 5.18m), which can be used to confirm genus identity, with most genera of Eurydicinae showing a quadrate or subquadrate article 5.

BL = body length. The pleon refers to pleonites 1–5, excluding pleotelson. Five genera cannot be clearly placed within subfamilies and do not appear in the key. They are diagnosed under the heading "Unassigned to subfamily": *Bathylana* Kensley, 1989; *Scutulana* Bruce, 1996; *Seychellana* Kensley and Schotte, 1994; *Sululana* Bruce and Shimomura, 2019; and *Xylolana* Kensley, 1979.

1. Clypeus ventrally flat (fig. 5.18c, d). Pleon short (< 20% BL, usually 10–14%) (fig. 5.15c, d). Pleonite 4 may be laterally enclosed by pleonite 3. Pleonite 5 laterally enclosed by pleonite 4 (fig. 5.16e, h, i) 2

– Clypeus with ventrally- or antero-ventrally projecting blade (best viewed laterally; fig. 5.18f, g, h). Pleon long (10–35% BL, usually 15–35% BL) (fig. 5.15f, g, j). Pleonites 4 and 5 with free lateral margins or with free posterolateral angle (pleonite 5 rarely laterally enclosed by pleonite 4) (fig. 5.16k, l) ..... Eurydicinae ... 3

2. Pereopods 1–3 with ischium and merus superodistal angles strongly produced (fig. 5.19f), without blunt or molariform robust setae. Pereopods 5–7 with numerous slender setae and acute robust setae (fig. 5.19o); dactylus secondary unguis absent or slender (fig. 5.19j). Antennal peduncle articles 3 and 4 subequal in length and shorter than article 5 (fig. 5.17k) ..... Conilerinae … 13

– Pereopods 1–3 with ischium and merus superodistal angles not or weakly produced, inferior margins usually with blunt robust or molariform robust setae (fig. 5.19a). Pereopods 5–7 usually with few slender setae and acute robust setae (fig. 5.19k. l); dactylus secondary unguis usually robust (fig. 5.19h) or absent. Antennal peduncle articles 1–3 short, 4 and 5 subequal in length and longest (fig. 5.17j) ..... Cirolaninae ... 19

Eurydicinae Stebbing, 1905

3. Antennular peduncle articles 2 and 3 set at right angles to article 1 (fig. 5.17l). Uropod peduncle posterior mesial margin not produced (fig. 5.21b). Male pleopod 2 endopod with appendix masculina attached mid-length on mesial margin (fig. 5.20m) ..... *Eurydice*

– Antennular peduncle articles 1–3 colinear (fig. 5.17i, m). Uropod peduncle posterior mesial margin produced (fig. 5.21d) or not. Male pleopod 2 endopod with appendix masculina attached mesially or sub-basally (fig. 5.20j–l) 4

4. Pleon of 2 or 3 visible segments (short, 5–10% BL) (fig. 5.15e) ..... *Colopisthus*

– Pleon of 4 or 5 visible segments (variable 10–35% BL) (e.g., fig. 5.15g, j) 5

5. Pleonite 5 laterally enclosed by pleonite 4 (fig. 5.16o, p) 6

– Pleonite 5 with free lateral margins, or free posterolateral point (fig. 5.16k, l) 8

6. Pleotelson lateral margins sinuate, posterior margins narrowly rounded (fig. 5.16o). Anterior pereopods with connate spines (marginal spines without suture at base) (fig. 5.19q) ..... *Aphantolana*

– Not as above 7

7. Pleon 10–15% BL (fig. 5.15o). Antennular peduncle article 2 without process. Uropodal exopod cylindrical, exceeding endopod length, exopod 1.3–2.2 times as long as endopod (fig. 5.21a). Pleotelson posteriorly narrow, lateral margins concave (fig. 5.15o) ..... *Atarbolana*

– Pleon 15–18% BL (fig. 5.15p). Antennular peduncle article 2 with prominent, posteriorly directed acute process (fig. 5.17n). Uropodal exopod laminar with lateral margin indented (fig. 5.21h), rami subequal in length. Pleotelson lateral margins evenly convex (linguiform) (fig. 5.15p) ..... *Pseudaega*

8. Rostrum large, extending anteriorly to anterior margin of antennular peduncle, wholly separating antennular bases, often anteriorly dilated (fig. 5.16c, d) 9

– Rostrum small or absent, not extending to anterior of margin antennula (fig. 5.15f, j) 11

9. Rostrum anteriorly truncate in dorsal view (fig. 5.16d). Adult male antennular peduncle dilated; antennular and antennal flagella extending beyond pleotelson posterior margin (fig. 5.15m) [pelagic; nektonic] ..... *Pontogelos*

– Not as above 10

10. Pleonites 1 and 2 narrower than pleonites 3–5 (fig. 5.15a). Frontal lamina extended anteriorly, usually visible in dorsal view, not fusing or abutting rostrum. Rostrum acute, not anteriorly dilated (fig. 5.16q). Uropodal endopod lateral margin without excision. Head and pereonites 1 or 2 may have horn-like processes (fig. 5.15a) ..... *Annina*

– Pleonites 1 and 2 subequal in width to pleonites 3–5 (fig. 5.15g). Frontal lamina extended anteriorly, usually visible in dorsal view, usually fusing or abutting rostrum. Rostrum truncate or anteriorly dilated (fig. 5.16c). Uropodal endopod lateral margin with excision. Head and pereonites 1 and 2 without horn-like processes (fig. 5.15g) ..... *Excirolana*

11. Frontal lamina ventral margin linear, blade-like (fig. 5.18k) ..... *Pseudolana*

– Frontal lamina ventrally flat, wide anteriorly, posteriorly with stem (fig. 5.18h) 12

12. Pereopod 1 propodus subchelate (fig. 5.19e, i). Pereopods 2–7 slender, with few robust and slender setae (fig. 5.19n) ..... *Metacirolana*

– Pereopod 1 ambulatory (fig. 5.19b). Pereopods 2–7 stout, with numerous robust and slender setae (fig. 5.19m) ..... *Eurylana*

Conilerinae Kensley and Schotte, 1989

13. Uropodal endopod lateral margin with distinct notch (fig. 5.21g) 14

– Uropodal endopod lateral margin without notch, inflected or convex (fig. 5.21e) 15

14. Frontal lamina short, as long as posterior width, triangular (fig. 5.18j) ..... *Orphelana*

– Frontal lamina elongate, > 3 times as long as posterior width (fig. 5.18i) ..... *Politolana*

15. Body elongate, 4.0–5.6 times as long as wide (fig. 5.15l). Pleopod 1 peduncle quadrate or elongate, 0.9–1.3 as long as wide (fig. 5.20e, f). Pleopod 1 exopod or both rami operculate (fig. 5.17g, h) 16

– Body not elongate, < 4.0 times as long as wide (fig. 5.15k). Pleopod 1 peduncle usually < 0.9 times as long as wide (fig. 5.20g). Pleopod 1 rami not operculate (fig. 5.17e) 17

16. Pleopod 1 peduncle 1.3 times as long as wide (fig. 5.20e); rami subequal, both rami forming operculum (fig. 5.17h) ..... *Conilera*

– Pleopod 1 peduncle quadrate, about as long as wide; exopod large, forming operculum (fig. 5.20f) ..... *Conilorpheus*

17. Frontal lamina broad (2.4–4.0 times posterior width), anteriorly flat, posteriorly with ventrally directed process (horn) (fig. 5.18e). Pleonite 3 laterally large, with carina (fig. 5.16j) ..... *Dolicholana*

– Frontal lamina slender (3.8–7.6 times posterior width) (fig. 5.18i), ventrally flat, ventrally without posteriorly directed process. Pleonite 3 not laterally large, without lateral carina (fig. 5.16m) 18

18. Pereopod 1 dactylus haptorial (as long as propodal palm) (fig. 5.19g) ..... *Sintorolana*

– Pereopod 1 dactylus ambulatory, < 0.7 length of propodal palm (fig. 5.19f) ..... *Natatolana*

Cirolaninae Dana, 1852

19. Body length “huge”, adults 70–>300 mm (fig. 5.15b). Pleopods with respiratory branchiae (fig. 5.20c, o) 20

– Body length “normal”, adults 3–30 mm, rarely to 70 mm. Pleopods without respiratory branchiae (fig. 5.20a, b, d) 21

20. Body length 70–80 mm. Pleopod branchiae on pleopod 1 peduncle and at base of pleopods 1 and 2 exopods (fig. 5.20o). Pleotelson posterior margin without prominent spines ..... *Parabathynomus*

– Body length 70–>300 mm. Pleopod branchiae at base of pleopods 1 and 2 exopods only (fig. 5.20c). Pleotelson posterior margin with prominent spines (fig. 5.15b) ..... *Bathynomus*

21. Mandible large, conspicuous in dorsal view. Frontal lamina dorsally displaced, visible in dorsal view (fig. 5.15h) (monotypic South African endemic) ..... *Gnatholana*

– Not as above. Mandible not large, not visible in dorsal view. Frontal lamina not dorsally displaced 22

22. Pleopod 1 exopod or both rami operculate (fig. 5.17f–h) 23

– Pleopod 1 rami not operculate (fig. 5.17d, e) 24

23. Pleonite 5 as wide or slightly wider than pleotelson anterior margin (fig. 5.15d, l). Pleopod 1 exopod forming operculum (fig. 5.17g) ..... *Oncilorpheus*

– Pleonite 5 distinctly narrower than pleotelson anterior margin (fig. 5.17o). Pleopod 1 exopod and endopod forming operculum (fig. 5.17f) ..... *Calyptolana*

24. Pleonite 3 epimeron broad, expanded, with setose longitudinal carina, extending posteriorly beyond pleonite 5 (fig. 5.16e, n). Anterior margin of head medially indented, without rostrum (fig. 5.16a) 25

– Pleonite 3 epimeron not markedly expanded, not extending or extending posteriorly beyond pleonite 5 (fig. 5.16f, h, i). Anterior margin of head not medially indented, with or without rostrum (fig. 5.16b) 26

25. Pereopods 6 and 7 ischium, merus and carpus flattened, with long acute robust setae (fig. 5.19p). Pleopod 1 peduncle quadrate (fig. 5.20i). Penial process absent, openings flush with sternite 7 ..... *Plakolana*

– Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae (fig. 5.19k). Pleopod 1 peduncle shorter than wide (fig. 5.20a). Penial processes quadrate (fig. 5.17a) ..... *Aatolana*

26. Head fused to pereonite 1. Rostrum and frontal lamina both produced, forming 2 horn-like processes (fig. 5.18b). Pleonite 3 epimeron dorsoventrally expanded (fig. 5.16g) ..... *Ceratolana*

– Head not fused to pereonite 1 (fig. 5.16b). Rostrum small or absent, frontal lamina not strongly produced (fig. 5.18a, c, d, g). Pleonite 3 epimeron not dorsoventrally expanded (fig. 5.16f, h, i) 27

27. Frontal lamina with 2 parts, flat anterior part and ventrally produced posterior part (fig. 5.18a). Pleonite 3 epimeron with ventral margin with ventral blade-like process (fig. 5.16f). Pleopods 2–5 peduncle lateral margin with well-developed laminar lobe (fig. 5.20k) ..... *Booralana*

– Frontal lamina ventral surface all flat (fig. 5.18c, d, g). Pleonite 3 ventrolateral margin without process (fig. 5.16h, i). Pleopod peduncles lateral margin without laminar lobe (fig. 5.20j, l, n) 28

28. Pleopod 1 peduncle quadrate or subquadrate (c. 0.75–1.0 times as long as wide) (fig. 5.20h, j) 29

– Pleopod 1 peduncle short (0.45–0.70 times as long as wide) (fig. 5.20d) 30

29. Pleopod 1 endopod narrow (0.26–0.42 times width of exopod) (fig. 5.20b). Appendix masculina submesially attached (fig. 5.20j). Penial processes distally rounded, flat (fig. 5.17b) ..... *Baharilana*

– Pleopod 1 endopod 0.62–0.68 times as wide as exopod (fig. 5.20h). Appendix masculina basally attached. Penial processes papilliform or absent ..... *Odysseylana*

30. Dorsum strongly vaulted (fig. 5.16r). Mandible massive, prominent in ventral view, incisor biscuspid, heavily keratinised (fig. 5.18o) [associate of crinoids] ..... *Cartetolana*

– Dorsum not strongly vaulted. Mandible not massive (fig. 5.18p–r), left incisor tricuspid (fig. 5.18p), not heavily keratinised 31

31. Dorsum flattened. Head widest anteriorly, anterior margin straight (fig. 5.15i). Pereopod 1 robust, propodus subprehensile, 0.8 times as wide as long, dactylus extending to carpus when folded (fig. 5.19c). Appendix masculina unknown ..... *Hansenolana*

– Dorsum vaulted. Head widest mid-length, anterior margin convex (fig. 5.16b). Pereopod 1 propodus stout, c. 0.55 times as wide as long, dactylus not extending to carpus when folded (fig. 5.19a). Appendix masculina basal (fig. 5.20l) or sub-basal 32

32. Mandible incisor narrow, less than half basal width (fig. 5.18r) (head therefore appearing relatively narrow). Uropodal endopod lateral margin with or without prominent excision on lateral margin (fig. 5.21f) ..... *Neocirolana*

– Mandible incisor more than half basal width (fig. 5.18p) (head not appearing relatively narrow). Uropodal endopod lateral margin without prominent excision (fig. 5.21i) 33

33. Pereopod 1 merus inferior margin without molariform robust setae; dactylus with slender secondary unguis (fig. 5.19d). Frontal lamina posteriorly narrowed (abutting clypeus) (fig. 5.18g). Penial processes as flat articulating lobes ..... *Limicolana*

– Pereopod 1 merus inferior with molariform robust setae (fig. 5.19a); dactylus with stout secondary unguis (fig. 5.19h). Frontal lamina posteriorly wide or slightly narrower than at mid-length (fig. 5.18c,d). Penes usually opening flush with sternite 7 (fig 5.17c) ..... *Cirolana*

Subfamily Conilerinae Kensley and Schotte, 1989

Diagnosis. Clypeus ventrally flat. Pleon short, < 20% BL, usually 10–14%. Pleonite 4 sometimes laterally enclosed by pleonite 3. Pleonite 5 laterally enclosed by pleonite 4. Pereopods 1–3 with ischium and merus superodistal angles strongly produced, without blunt or molariform robust setae. Pereopods 5–7 with numerous slender setae and acute robust setae; dactylus secondary unguis absent or slender. Antennal peduncle articles 3 and 4 subequal in length and shorter than article 5.

Conilera Leach, 1815

Diagnosis. Body elongate, 4.0–6.5 times as long as wide; BL 7–24 mm. Head anterior margin medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, or absent. Pleon < 20% BL, usually 10–14% BL; pleonites 1 and 2 subequal in width to pleonites 3–5; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5; posterolateral margin of pleonite 4 acute, not extending beyond

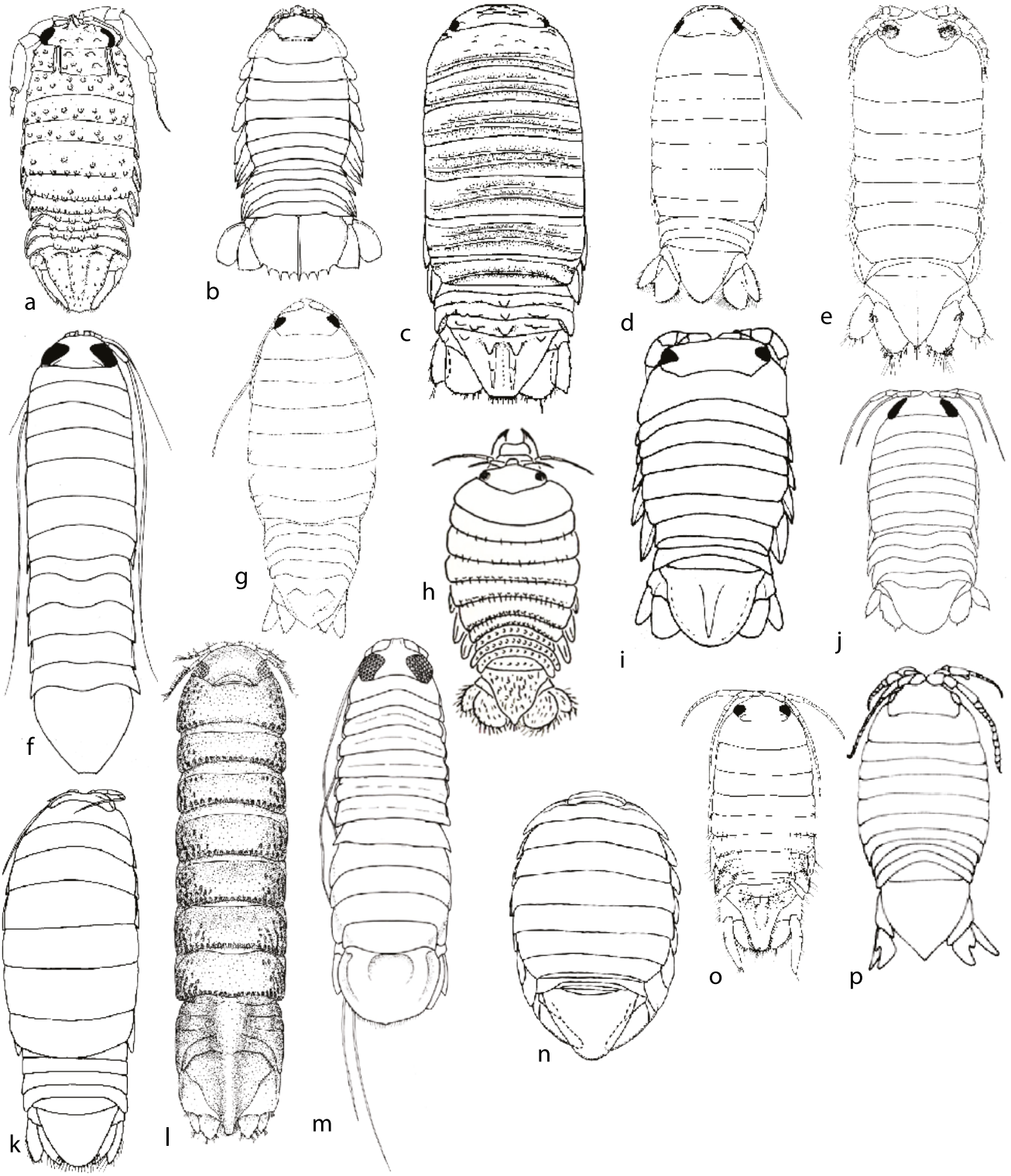


Figure 5.15. Cirolanidae. a, *Annina lacustris* Budde-Lund, 1908; b, *Bathynomus lowryi* Bruce and Bussarawit, 2004; c, *Cirolana cristata* Bruce, 1995; d, *Cirolana kokoru* Bruce, 2004; e, *Colopisthus parvus* Richardson, 1902; f, *Eurydice wongat* Bruce, 1986; g, *Excirolana chiltoni* Richardson, 1909; h, *Gnatholana mandibularis* Barnard, 1920; i, *Hansenolana anisopous* Stebbing, 1900; j, *Metacirolana serrata* (Bruce, 1980); k, *Natatolana rekohu* Bruce, 2003; l, *Oncilorpheus jerrybarnardi* Brusca, Wetzer and France, 1995; m, *Pontogelos asegokeros* Stebbing, 1910; n, *Scutulana pezata* Bruce, 1996; o, *Atarbolana exoconta* Bruce and Javed, 1987; p, *Pseudaega punctata* Thomson, 1884.

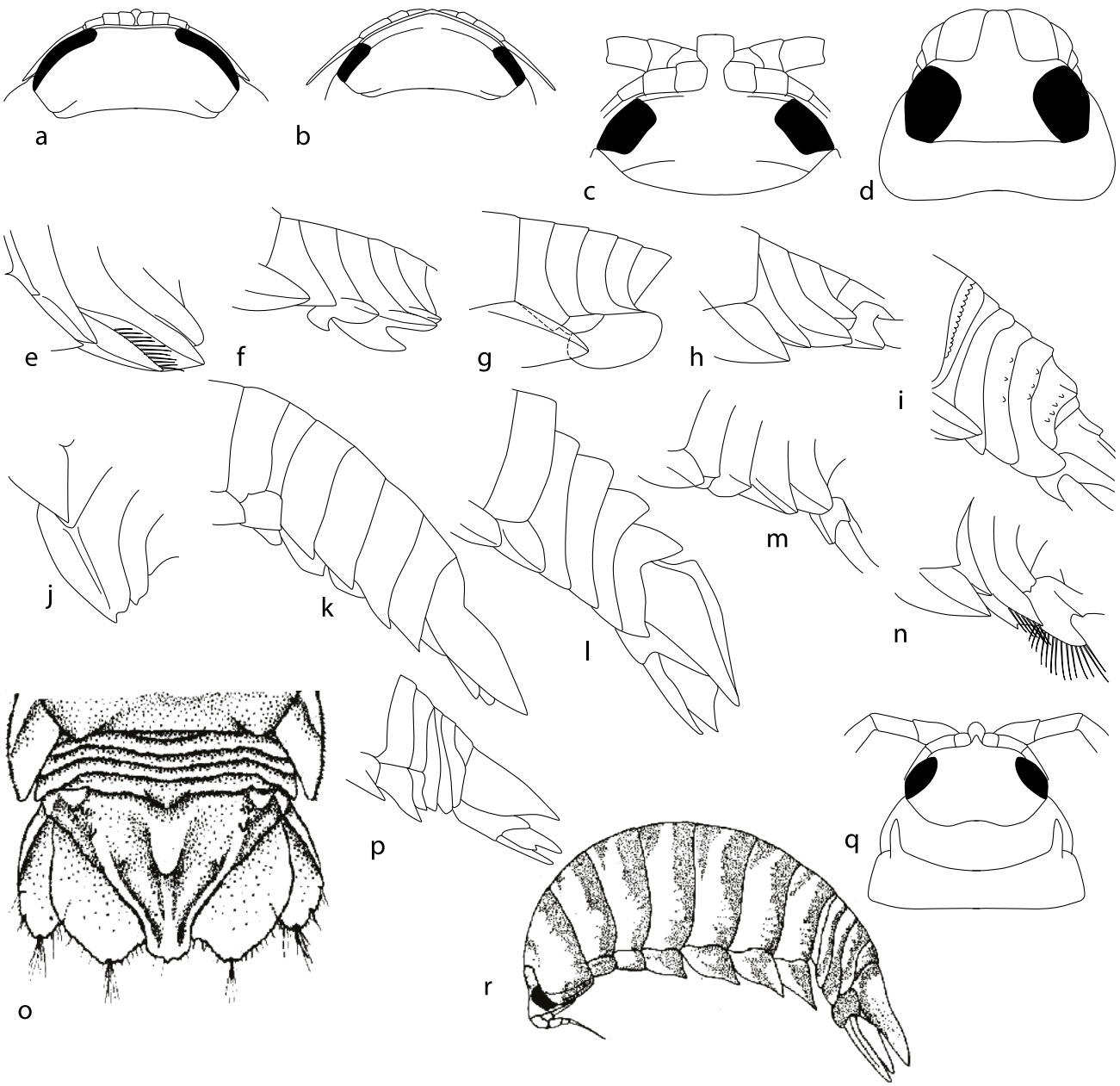


Figure 5.16. Cirolanidae. Head, dorsal view: a, *Aatolana rapax* Bruce, 1993; b, *Cirolana kokoru* Bruce, 2004; c, *Excirolana orientalis* (Dana, 1852); d, *Pontogelos asegokeros* Stebbing, 1910. Pleon lateral view: e, *Aatolana rapax* Bruce, 1993; f, *Booralana bathynella* (Bruce, 1981); g, *Ceratolana papuae* Bowman, 1977; h, *Cirolana kokoru* Bruce, 2004; i, *Cirolana parawongat* Rodcharoen and Bruce, 2021; j, *Dolicholana enigma* Keable, 1999; k, *Eurydice acuticauda* Bruce, 1981; l, *Metacirolana nicosmiti* Bruce and Rodcharoen, 2021; m, *Natatolana rekohu* Bruce, 2003; n, *Plakolana accola* Bruce, 1993; o, *Aphantolana costaricensis* Moore and Brusca, 2003, pleon and pleotelson, dorsal view; p, *Pseudaega punctata* Thomson, 1884, pleon, lateral view; q, *Annina fustis* Bowman and Iliffe, 1991, head, dorsal view; r, *Cartetolana integra* (Miers, 1884), habitus, lateral view.

posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded, or with apical point; lateral margins evenly convex Antennal peduncle articles 3 and 4 subequal in length, 5 longest; flagellum not extending beyond posterior margin of pereonite 1. Frontal lamina extended anteriorly, usually visible in dorsal view, not fused to or abutting rostrum; ventral surface flat; narrowing posteriorly, not stem-like, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus secondary unguis not known; merus inferior margin without molariform

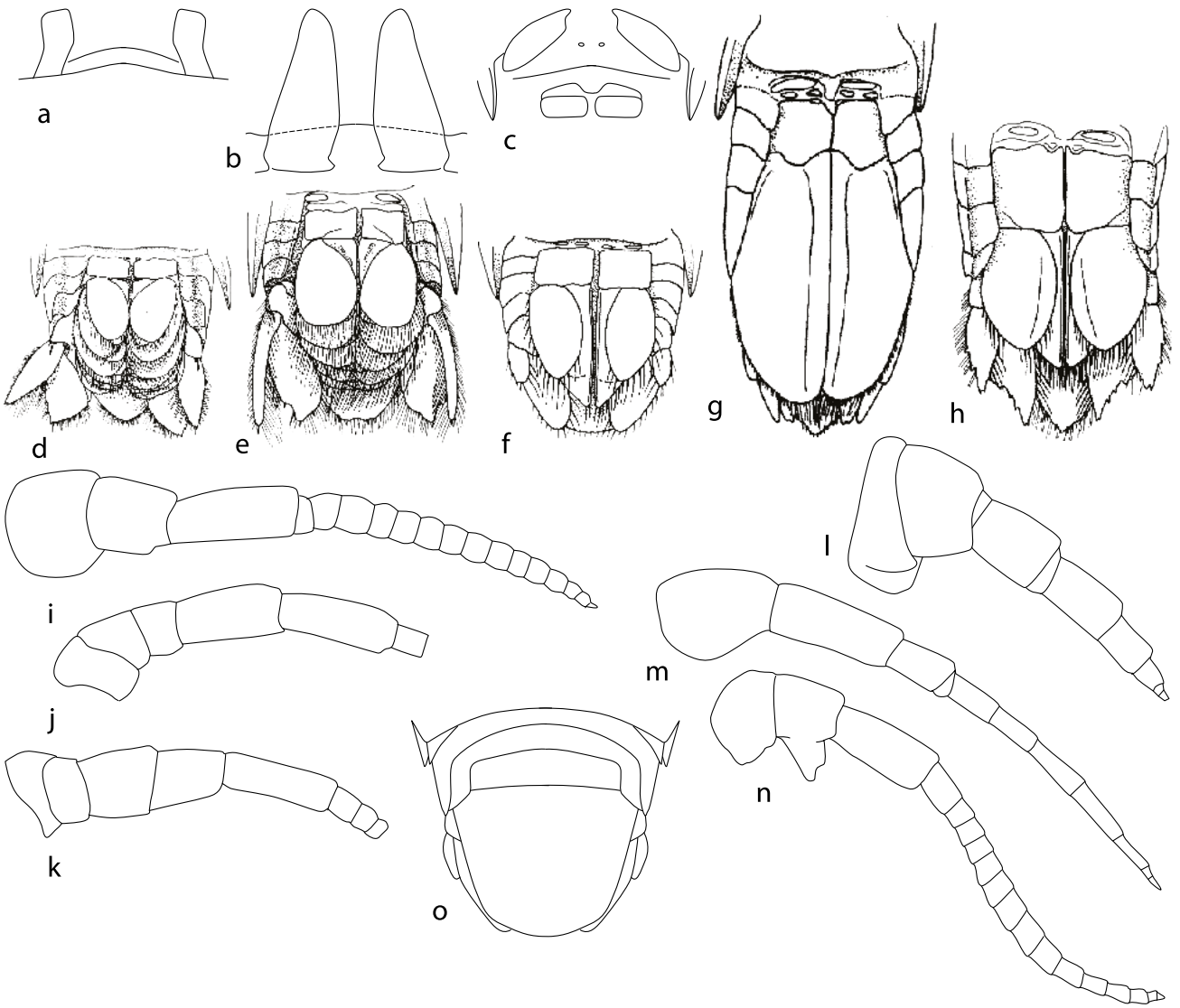


Figure 5.17. Cirolanidae. Penial processes: a, *Aatolana rapax* Bruce, 1993; b, *Baharilana richmondi* Bruce and Svavarsson, 2004; c, *Cirolana kokoru* Bruce, 2004, sternite 7. Pleon, ventral view: d, *Cirolana cranchii* Leach, 1818; e, *Politolana concharum* (Stimpson, 1853); f, *Calyptolana hancocki* Bruce, 1985; g, *Oncilorpheus stebbingi* Paul and Menzies, 1972; h, *Conilera cylindracea* (Montagu, 1805). i, *Cirolana kokoru* Bruce, 2004, antennula; j, *Cirolana kokoru* Bruce, 2004, antenna peduncle; k, *Natatolana rekohu* Bruce, 2003, antennal peduncle; l, *Eurydice kenselyi* Bruce and Soares, 1996, antennula; m, *Metacirolana nicosmiti* Bruce and Rodcharoen, 2021, antennula; n, *Pseudaega punctata* Thomson, 1884, antennula; o, *Calyptolana hancocki* Bruce, 1985, pleon, dorsal.

robust setae. Pereopods 1–3 with ischium and merus superodistal angles strongly produced. Pereopods 2–7 slender, with few robust and slender setae. Pereopods 6 and 7 ischium, merus and carpus with long robust setae and long slender setae. Penes low tubercles. Pleopod 1 peduncle 1.3 times as long as wide; rami operculate, with both rami forming operculum; endopod not narrow, 0.50–0.7 times as wide as exopod. Male pleopod 2 appendix masculina attached basally, sub-basally, or submesially.

Subtidal–slope (1–510 m). North Atlantic, Tropical Eastern Pacific (Americas). 3 species (Brusca et al., 1995).

Conilorpheus Stebbing, 1905

Diagnosis. Body elongate, 6 times as long as wide; dorsal surfaces smooth, with or without nodules; BL 6–10 mm, rarely longer. Head anterior margin with rostrum. Rostrum small, not extending to anterior margin of antennular peduncle, not anteriorly truncate in dorsal view, acute, not anteriorly dilated. Pleon < 20% BL, usually 10–14% BL, with 2 or 3 visible segments; pleonites 3 and 4 not extending beyond posterior margin of pleonite 5; pleonite 5 laterally enclosed by pleonite 4, distinctly narrower than anterior margin of pleotelson. Pleotelson

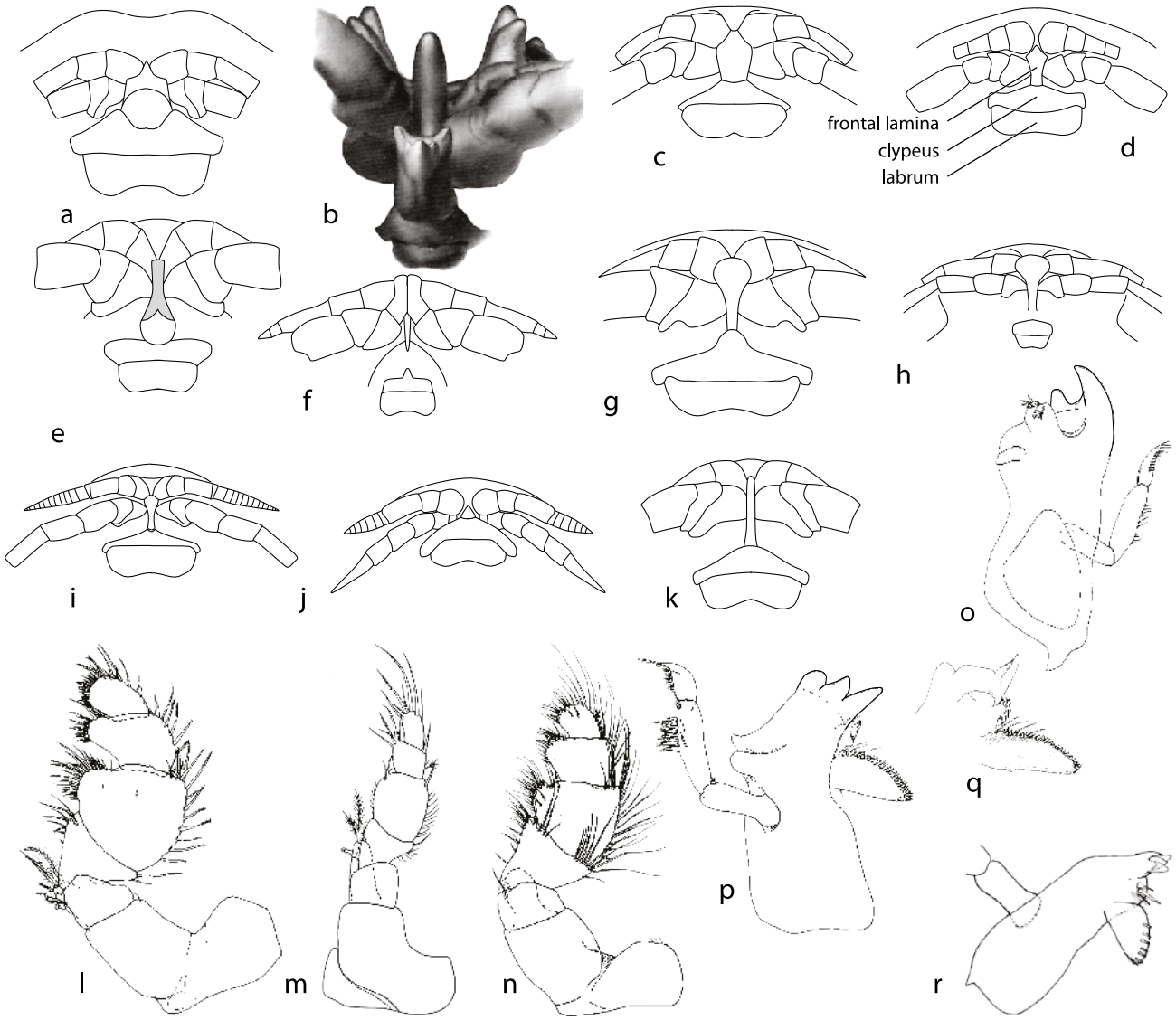


Figure 5.18. Cirolanidae. Frons (comprising rostrum, antennulae, antennae, frontal lamina, clypeus and labrum): a, *Booralana wundurra* Bruce, 1986; b, *Ceratolana papuae* Bowman, 1977; c, *Cirolana kokoru* Bruce, 2004; d, *Cirolana merlion* Sidabalok and Bruce, 2018; e, *Dolicholana elongata* Milne-Edwards, 1840; f, *Eurydice longicornis* (Studer, 1882); g, *Limicolana dinjerra* Bruce, 1986; h, *Metacirolana nicosmiti* Bruce and Rodcharoen, 2021; i, *Natatolana rekohu* Bruce, 2003; j, *Orphelana perplexa* Bruce, 1981; k, *Pseudolana towrae* Bruce, 1983. Maxilliped: l, *Cirolana kokoru* Bruce, 2004; m, *Metacirolana nicosmiti* Bruce and Rodcharoen, 2021; n, *Limicolana dinjerra* Bruce, 1986. Mandible: o, *Cartetolana integra* (Miers, 1884); p, q, *Cirolana kokoru* Bruce, 2004 (right, left); r, *Neocirolana salebra* Bruce, 1994.

linguiform; posterior margin narrowly rounded or truncate; lateral margins evenly convex. Antennal peduncle articles 3 and 4 subequal in length, 5 longest; flagellum not extending beyond posterior margin of pereonite 1. Frontal lamina extended anteriorly usually visible in dorsal view, not fused to or abutting rostrum, ventral surface flat; posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with small blunt secondary unguis; merus inferior margin with molariform robust setae. Pereopods 1–3 merus superodistal angle moderately produced. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus with long robust setae and long slender setae. Pleopod 1 peduncle about as long as wide; rami operculate (not indurate); with exopod forming operculum; endopod narrow, 0.26–0.45 times width of exopod. Uropod exopod notably shorter in length than endopod.

Subtidal, shelf (1–41 m). Western and Central Indo-Pacific (South Africa, Sri Lanka and Thailand). 3 species. The genus is almost certainly not monophyletic and species other than the type species are inadequately described. Diagnosis primarily based on type species from redescription by Bruce and Olesen (2002).

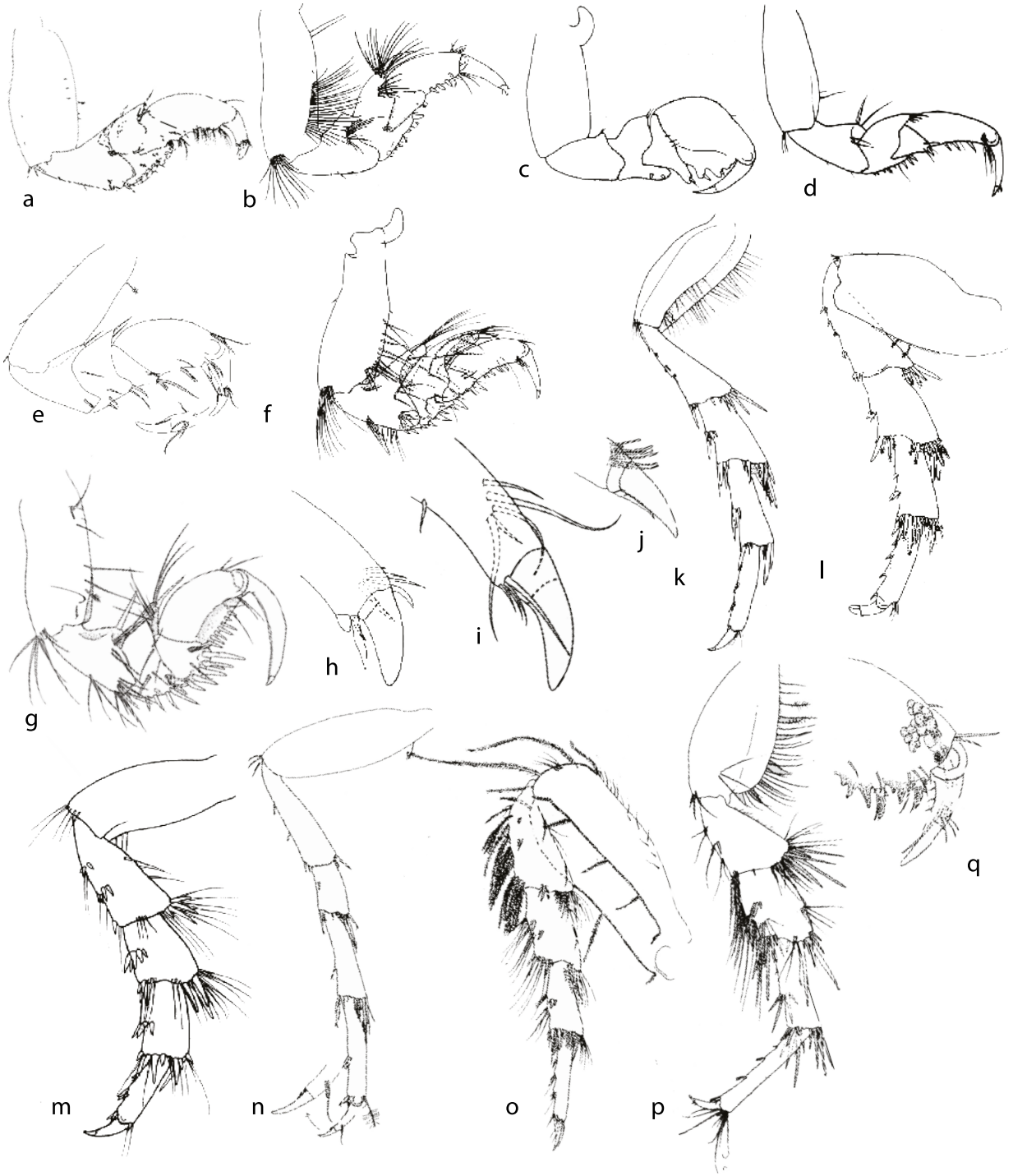


Figure 5.19. Cirolanidae. Pereopod 1: a, *Cirolana kokoru* Bruce, 2004; b, *Eurylana arcuate* (Hale, 1925); c, *Hansenolana anisopous* Stebbing, 1900; d, *Limicolana dinjerra* Bruce, 1986; e, *Metacirolana lombok* Sidabalok and Bruce, 2018; f, *Limicolana dinjerra* Bruce, 1986; g, *Sintorolana atrox* Bruce, 1996. Pereopod 1, dactylar unguis: h, *Cirolana kokoru* Bruce, 2004; i, *Metacirolana nicosmiti* Bruce and Rodcharoen, 2021; j, *Natatolana rekohu* Bruce, 2003. Pereopod 7: k, *Aatolana rapax* Bruce, 1993; l, *Cirolana kokoru* Bruce, 2004; m, *Eurylana arcuate* (Hale, 1925); n, *Metacirolana lombok* Sidabalok and Bruce, 2018; o, *Natatolana rekohu* Bruce, 2003; p, *Plakolana accola* Bruce, 1993; q, *Aphantolana costaricensis* Moore and Brusca, 2003.

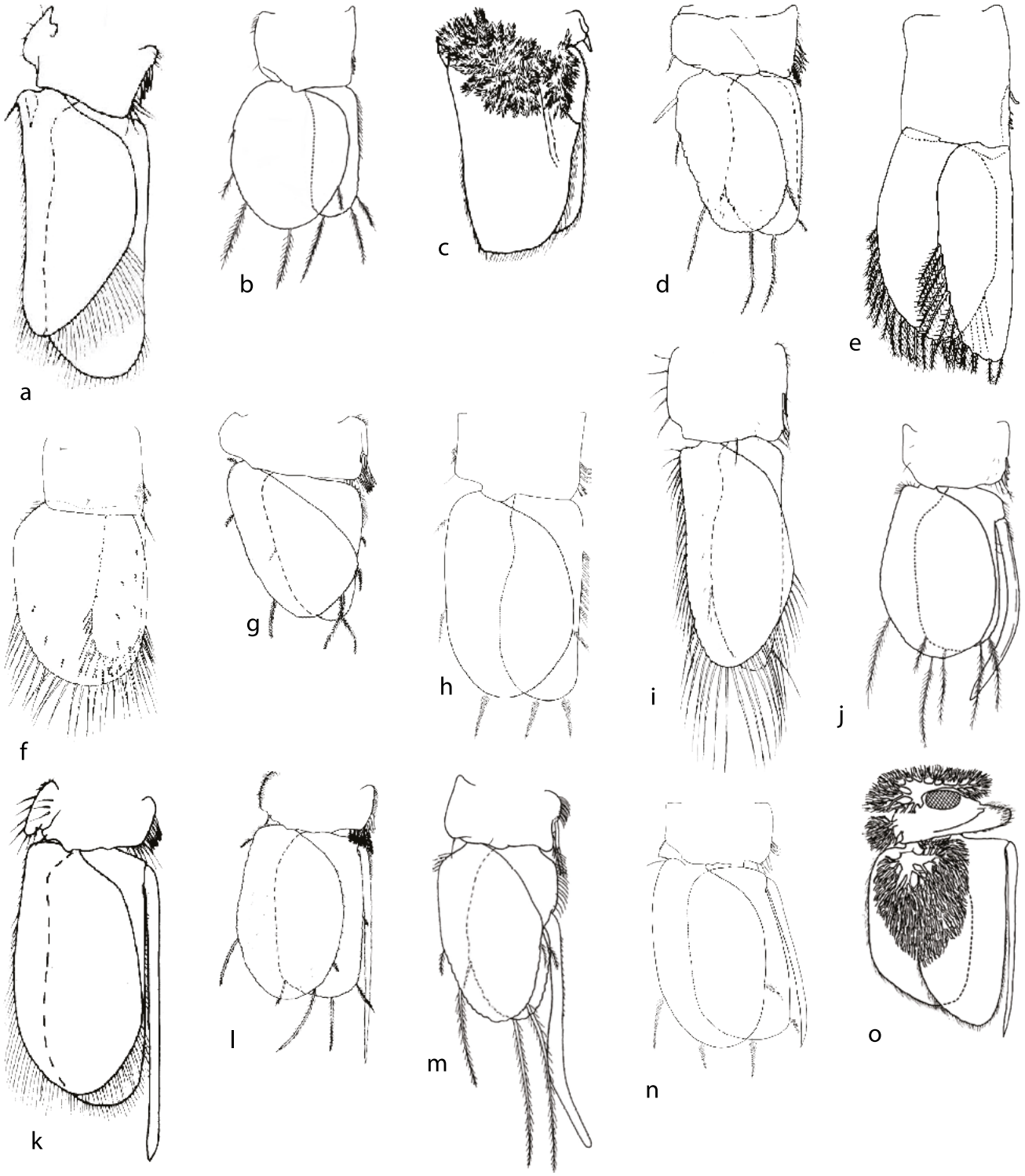


Figure 5.20. Cirolanidae. Pleopod 1: a, *Aatolana rapax* Bruce, 1993; b, *Baharilana richmondi* Bruce and Svavarsson, 2004; c, *Bathynomus immanis* Bruce, 1986; d, *Cirolana kokoru* Bruce, 2004; e, *Conilera bullisi* Brusca et al., 1995; f, *Conilorpheus herdmani* Stebbing, 1905; g, *Natatolana rekohu* Bruce, 2003; h, *Odysseylana temesak* Sidabalok and Bruce, 2015; i, *Plakolana accola* Bruce, 1993. Male pleopod 2: j, *Baharilana richmondi* Bruce and Svavarsson, 2004; k, *Booralana bathynella* (Bruce, 1981); l, *Cirolana kokoru* Bruce, 2004; m, *Eurydice kensleyi* Bruce and Soares, 1996; n, *Odysseylana temasek* Sidabalok and Bruce, 2015; o, *Parabathynomus natalensis* Barnard, 1924.

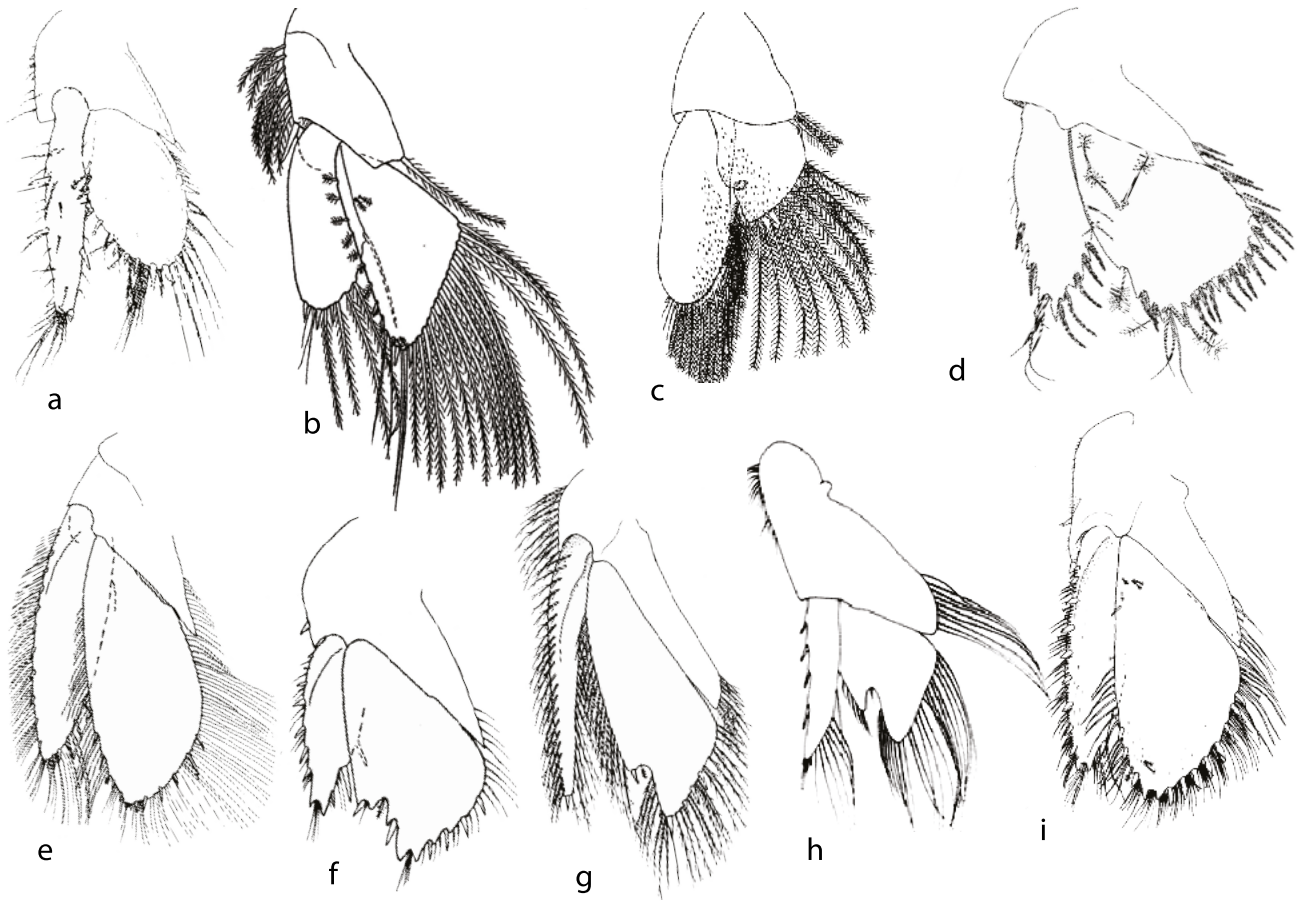


Figure 5.21. Cirolanidae. Uropod: a, *Atarbolana exoconta* Bruce and Javed, 1987; b, *Eurydice kensleyi* Bruce and Soares, 1996; c, *Excirolana braziliensis* Richardson, 1912 (Brusca et al. 1995); d, *Metacirolana nicosmiti* Bruce and Rodcharoen, 2021; e, *Natatolana rekohu* Bruce, 2003; f, *Neocirolana excisa* (Richardson, 1910); g, *Politolana concharum* (Stimpson, 1853); h, *Pseudaega melanica* Jansen, 1978; i, *Cirolana kokoru* Bruce, 2004.

Dolicholana Bruce, 1986

Diagnosis. Body about 3–4 times as long as wide; BL 6–40 mm. Head anterior margin without rostrum, medially indented. Pleon < 20% BL, usually 10–14% BL, with 4 or 5 visible segments; pleonite 3 epimeron broad, acute, dorsoventrally expanded, with longitudinal carina, extending posteriorly or not beyond pleonite 5; posterolateral margin of pleonite 4 acute, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin sometimes overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, < 0.9 times width of anterior margin of pleotelson. Pleotelson posterior margin with apical point or broadly rounded; lateral margins evenly convex. Antennal peduncle articles 3 and 4 subequal in length, 5 longest; flagellum not extending beyond posterior margin of pereonite 5. Frontal lamina extended anteriorly, usually visible in dorsal view, not fused to or abutting rostrum; ventral surface flat or posterior margin with downwardly directed process (horn); posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with or without secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles strongly produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus with long robust setae and long slender setae. Penes usually absent. Pleopod 1 peduncle subquadrate, c. 0.75–1.0 times as long as wide. Pleopods 2–5 peduncle lateral margin with well-developed laminar lobe. Male pleopod 2 appendix masculina attached basally, sub-basally, or submesially.

Subtidal–slope (6–508 m). Tropical Atlantic (Brazil), Indo West-Pacific. 5 species (Bruce 1986; Keable, 1999a; Paiva and Souza-Filho, 2015, 2023a).

Natatolana Bruce, 1981

Diagnosis. Body dorsal surfaces polished in appearance or sparsely punctate; BL 8–40 mm. Head anterior margin with or without rostrum, medially or not medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, not anteriorly truncate in dorsal view. Pleon < 20% BL, usually 10–14% BL, with 4 or 5 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, narrowly rounded or acute; posterolateral margin of pleonite 4 narrowly rounded or acute, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson linguiform, lateral margins evenly convex. Antennal peduncle articles 3 and 4 subequal in length, 5 longest; flagellum usually not extending posteriorly beyond pereonite 3 but may extend beyond posterior of pleotelson. Frontal lamina extended anteriorly, slightly visible or not visible in dorsal view, slender (3.8–7.6 times posterior width), ventrally flat, without posteriorly directed process; posteriorly as wide or wider than at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with slender secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles strongly produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus flattened, with long acute robust setae. Penes absent or flat lobes. Pleopod 1 peduncle short, 0.45–0.70 times as long as wide. Male pleopod 2 appendix masculina attached basally or sub-basally. Uropod endopod lateral margin with or without prominent excision.

Subtidal–abyssal (1–6000 m). Cosmopolitan. 75 species (Keable, 2006; Paiva and Souza-Filho, 2023a).

Orphelana Bruce, 1981

Diagnosis. Body dorsum strongly vaulted; BL 11 mm. Head anterior margin widest anteriorly; anterior margin without rostrum, not medially indented. Pleon 14% BL; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, rounded; posterolateral margin of pleonite 4 rounded, not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, < 0.9 width of anterior margin of pleotelson. Pleotelson posterior margin broadly rounded; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 1. Frontal lamina short (as long as posterior width), triangular, not visible in dorsal view, ventral surface flat. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with slender secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles strongly produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus flattened, with long acute robust setae. Penes absent. Pleopod 1 peduncle quadrate, about as long as wide; rami not operculate; endopod narrow, 0.4 times width of exopod. Male pleopod 2 appendix masculina attached submesially. Uropod endopod lateral margin with prominent excision.

Shelf (15 m). Temperate Australasia (Victoria, Australia). 1 species (Bruce, 1986: rediagnosis).

Politolana Bruce, 1981

Diagnosis. Body elongate, 4.0–6.5 times as long as wide; dorsal surfaces smooth, polished or sparsely punctate; BL 9–46 mm. Head anterior margin markedly widest anteriorly; anterior margin without rostrum, medially indented. Pleon 6–15% BL, with 3–5 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 4; posterolateral margin of pleonite 4 narrowly rounded, not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin varied, narrowly rounded, truncate, medially indented, with or without apical point; lateral margins evenly convex. Antennal peduncle articles 3 and 4 subequal in length, 5 longest; flagellum not extending beyond pereonite 2. Frontal lamina extended anteriorly, slightly or not visible in dorsal view, elongate, > 3 times as long as posterior width; ventral surface flat, narrowest at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with small blunt secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles strongly produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus flattened, with long acute robust setae. Penes flat lobes. Pleopod 1 peduncle subquadrate, c. 0.75–1.0 times as long as wide. Male pleopod 2 appendix masculina attached basally or sub-basally (where described). Uropod endopod lateral margin with prominent excision.

Shelf, slope (9–1301 m). Tropical and temperate Atlantic, Central Indo-Pacific. 15 species (Paiva and Souza-Filho, 2023a; Riseman and Brusca, 2002; Sidabalok and Bruce, 2016).

Sintorolana Bruce, 1996

Diagnosis. Body dorsal surfaces polished in appearance; BL 5 mm. Anterior margin without rostrum, not medially indented. Pleon 16% BL; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 4; pleonite 4 posterolateral margin posteriorly broad, rounded, extending slightly beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded; lateral margins evenly convex. Antennal peduncle articles 3 and 4 subequal in length, 5 longest. Antennal flagellum not extending beyond posterior margin pereonite 2. Frontal lamina extended anteriorly, not visible in dorsal view, slender (3.8–7.6 times posterior width), ventrally flat, narrowest at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1

propodus haptorial (dactylus as long as propodal palm); dactylus with or without secondary unguis; dactylus extending to carpus when folded; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles strongly produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Pleopod 1 peduncle short, 0.45–0.70 times as long as wide. Male pleopod 2 appendix masculina attached basally or sub-basally.

Slope (1639 m). Central Indo-Pacific (New Caledonia). 1 species (Bruce, 1996).

Subfamily Eurydicinae Stebbing, 1905

Diagnosis. Clypeus with ventrally- or antero-ventrally projecting blade. Pleon usually long (usually 15–35% BL). Pleonites 4 and 5 with free lateral margins or with free posterolateral angle (pleonite 5 rarely laterally enclosed by pleonite 4). Pereopods 1–3 with ischium and merus superodistal angles not or weakly produced; dactylus secondary unguis robust or slender (may be absent). Pereopods 5–7 usually with slender setae and acute robust setae. Antennal peduncle of 4 or 5 visible articles.

Annina Budde-Lund, 1908

Diagnosis. Body length 5–10 mm, < 4 times as long as wide. Head anterior margin markedly widest anteriorly; anterior margin with rostrum, not medially indented; pereonites 1 and 2 (and head) may have horn-like processes. Rostrum large, extending anteriorly to anterior margin of antennular peduncle, wholly separating antennular bases, not anteriorly dilated. Pleon usually long, 14–25% BL, with 5 visible segments; pleonites 1 and 2 narrower than pleonites 3–5; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; posterolateral margin of pleonite 4 acute, not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 with free lateral margins, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded; lateral margins distinctly sinuate or evenly convex. Antennular peduncle articles slender. Antennal peduncle of 4 visible articles, 1 and 2 short, 4 as long as 2; flagellum not extending beyond pleotelson posterior margin of pereonite 6. Frontal lamina extended anteriorly usually visible in dorsal view, not fusing to or abutting rostrum; ventral surface flat, elongate, > 3 times as long as posterior width; narrowing posteriorly, stem-like, not abutting clypeus. Clypeus with ventrally or anteroventrally triangular blade. Maxilliped palp article 5 quadrate or subquadrate. Pereopod 1 dactylus with robust secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae and long slender setae. Penes flat lobes. Pleopod 1 peduncle short, usually < 0.9 times as long as wide.

Freshwater, estuarine, marine, intertidal, subtidal. Western and Central Indo-Pacific (mangroves). 6 species (Bowman and Iliffe, 1991; Khalaji-Pirbalouty, 2013; Mitra and Tabassum, 2020; Schotte, 1994).

Aphantolana Moore and Brusca, 2003

Diagnosis. Body dorsum flat or weakly vaulted; dorsal surfaces smooth or sparsely punctate; BL 3–10 mm, rarely longer. Head anterior margin markedly widest anteriorly; anterior margin with rostrum, not medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, not anteriorly truncate in dorsal view. Pleon 10–12% BL; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, narrowly rounded; posterolateral margin of pleonite 4 narrowly rounded, not extending beyond posterior margin of pleonite 5 (or slightly beyond); pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 narrower than 4, with free posterolateral point, distinctly narrower than anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded; lateral margins distinctly sinuate. Antennal flagellum not extending beyond posterior margin of pereonite 2. Frontal lamina extended anteriorly, not or slightly visible in dorsal view, posteriorly narrowed, not abutting clypeus. Clypeus with ventrally or anteroventrally triangular blade. Maxilliped palp article 5 quadrate or subquadrate. Pereopod 1 propodus subchelate (dactylus c. 0.8 length of propodus); dactylus with slender secondary unguis; merus inferior margin with molariform robust setae. Pereopod 1 dactylus with slender secondary unguis. Pereopods 1–3 with ischium and merus superodistal angles not produced; with connate spines. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes flat lobes. Pleopod 1 peduncle short, 0.45–0.70 times as long as wide. Male pleopod 2 appendix masculina attached submesially.

Intertidal, subtidal. Indo West-Pacific, Tropical Eastern Pacific (coral reefs). 4 species (Anil and Jayaraj, 2020; Moore and Brusca, 2003).

Atarbolana Bruce and Javed, 1987

Diagnosis. Body dorsal surfaces punctate, or coarsely pitted; BL 3–8 mm. Head anterior margin widest at mid-length; anterior margin with rostrum, not medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, not anteriorly truncate in dorsal view, not anteriorly dilated. Pleon 10–15% BL, with 4 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5; posterolateral margin of pleonite 4 posteriorly broad, truncate, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, distinctly narrower than anterior

margin of pleotelson. Pleotelson posterior margin narrowly rounded; lateral margins distinctly sinuate or concave. Antennular peduncle articles progressively shorter distally. Antennal peduncle of 4 visible articles, 2 and 3 short. Frontal lamina extended anteriorly, slightly visible in dorsal view; ventral surface flat; narrowing posteriorly, not stem-like, abutting clypeus. Clypeus with ventrally or anteroventrally triangular blade. Antennal flagellum not extending beyond anterior margin of pereonite 4. Maxilliped palp article 5 quadrate or subquadrate. Pereopod 1 dactylus with robust secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 slender, with few robust and slender setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes flat lobes. Pleopod 1 peduncle short, usually < 0.9 times as long as wide. Male pleopod 2 appendix masculina attached mid-length. Uropod peduncle posterior mesial margin weakly produced; rami as long as mesial length of peduncle; exopod cylindrical, 1.3–2.2 times as long as endopod.

Intertidal, subtidal. Western Indo-Pacific. 4 species (Bruce and Javed, 1987; Castelló, 2017; Castelló et al., 2020; Khalaji-Pirbalouty et al., 2015).

Colopisthus Richardson, 1902

Diagnosis. Body dorsum flat or weakly vaulted; dorsal surfaces sparsely punctate; BL 3–10 mm, rarely longer. Head anterior margin markedly widest anteriorly; anterior margin with rostrum, not medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, acute, not anteriorly dilated. Pleon 5–10% BL, with 2 or 3 visible segments; pleonites 1 and 2 narrower than pleonites 3–5; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5; posterolateral margin of pleonite 4 narrowly rounded, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, < 0.9 times width of anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded; lateral margins distinctly sinuate. Antennular peduncle article 1 shortest, articles 2 and 3 subequal. Antennal flagellum not extending beyond posterior margin of pereonite 1. Frontal lamina extended anteriorly, not visible in dorsal view; ventral surface flat, narrowing posteriorly, stem-like, not abutting clypeus. Clypeus with ventrally or anteroventrally triangular blade. Maxilliped palp article 5 quadrate or subquadrate. Pereopod 1 propodus subchelate, dactylus c. 0.8 times length of propodus, with slender secondary unguis; merus inferior margin with molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced; inferior margin of merus with connate spines. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes flat lobes. Pleopod 1 peduncle short, usually < 0.9 times as long as wide. Male pleopod 2 appendix masculina attached submesially.

Intertidal. Tropical Atlantic. 5 species (Moore and Brusca, 2003); also Senegal, West Africa (Monod, 1952).

Eurydice Leach, 1815

Diagnosis. Body 3–4 times as long as wide (female usually proportionally shorter than male); BL 3–8 mm. Head anterior margin widest mid-length; anterior margin with rostrum, medially indented; pereonite 1 without horn-like process. Rostrum small, not extending to anterior margin of antennular peduncle. Pleon long, 18–35% BL; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 with free lateral margins, or with free posterolateral point, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded or truncate; lateral margins evenly convex. Antennular peduncle articles with articles 2 and 3 set at right angles to article 1. Antennal peduncle of 5 visible articles, 1 and 2 short, 4 as long as 2, 5 longest; flagellum long, may extend beyond pleon and pleotelson, but usually shorter. Frontal lamina extended anteriorly, not visible in dorsal view, slender (3.8–7.6 times posterior width), ventrally flat, not strongly anteriorly produced beyond antennula; narrowing posteriorly, stem-like, not abutting clypeus. Clypeus with ventrally or anteroventrally directed triangular blade. Maxilliped palp article 5 distal margin rounded. Pereopod 1 propodus subchelate (dactylus c. 0.8 length of propodus); dactylus with slender secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus flattened, with long acute robust setae. Penes flat lobes. Pleopod 1 peduncle about as long as wide. Male pleopod 2 appendix masculina attached mid-length. Uropod peduncle posterior mesial margin not produced; rami subequal in length, as long as mesial length of peduncle; exopod laminar.

Intertidal; sandy beaches. Cosmopolitan, nocturnal surface plankton to more than 2000 m. 57 species (Bruce 1986; Brusca et al. 1995).

Eurylana Jansen, 1981

Diagnosis. Body length 6–19 mm. Head anterior margin with rostrum, not medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, not anteriorly truncate in dorsal view. Pleon long, 15–18% BL; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5; posterolateral margin of pleonite 4 narrowly rounded; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 with free lateral margins or free posterolateral point, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 4. Frontal lamina extended anteriorly, slightly visible in dorsal view, ventral surface flat; narrowing posteriorly, not stem-like, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with slender secondary unguis; merus inferior margin without molariform robust setae. Pereopods 2 and 3 merus moderately produced. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6

and 7 ischium, merus and carpus not flattened, with short robust setae and long slender setae. Penes flat lobes. Pleopod 1 peduncle subquadrate, c. 0.75–1.0 times as long as wide. Male pleopod 2 appendix masculina attached mid-length.

Estuarine, marine, intertidal, subtidal (0–9 m). Central Indo-Pacific, Temperate South America (Chile), Temperate Australasia. 3 species; one species introduced to California (Bowman et al., 1981; Bruce, 1982; Bruce 1986; Jansen, 1981).

Excirolana Richardson, 1912

Diagnosis. Body length 3–15 mm, rarely longer. Head anterior margin markedly widest anteriorly; anterior margin with rostrum, not medially indented. Rostrum large, extending anteriorly to anterior margin of antennular peduncle, wholly separating antennular bases, sometimes anteriorly dilated or anteriorly truncate in dorsal view. Pleon usually long, 12–26% BL, with 5 visible segments; pleonites 1 and 2 narrower than pleonites 3–5; pleonite 3 epimeron not markedly expanded, , narrowly rounded not extending posteriorly beyond pleonite 5; posterolateral margin of pleonite 4 acute, not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 with free lateral margins or free posterolateral point, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin not narrowly rounded; lateral margins evenly convex. Antennular peduncle articles progressively shorter distally or article 1 shortest, articles 2 and 3 subequal. Antennal peduncle of 4 visible articles, 1 and 2 short; flagellum not extending beyond posterior margin of pereonite 4. Frontal lamina extended anteriorly, usually visible in dorsal view, usually fusing or abutting rostrum; ventral surface flat, or elongate, > 3 times as long as posterior width, narrowing posteriorly, not stem-like, abutting clypeus. Clypeus with ventrally or anteroventrally triangular blade. Maxilliped palp article 5 quadrate or subquadrate. Pereopod 1 dactylus with robust secondary unguis, not extending to carpus when folded; merus inferior margin with or without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae and long slender setae. Penes flat lobes. Pleopod 1 peduncle short, 0.45–0.70 times as long as wide. Pleopods 2–5 peduncle lateral margin with or without well-developed laminar lobe. Male pleopod 2 appendix masculina attached submesially. Uropod endopod lateral margin usually with prominent excision.

Intertidal–shelf (0–16 m). Tropical Atlantic, Indo West-Pacific; sandy beaches. 14 species (Brusca et al., 1995; Jones, 1971). *Pontogeloides* Barnard, 1914 is a synonym.

Metacirolana Kussakin, 1979

Diagnosis. Body dorsal surfaces smooth or sparsely punctate, occasionally with nodules; BL 2–10 mm, rarely shorter or longer. Head anterior margin markedly widest anteriorly, not medially indented, with rostrum. Pereonite 1 may have horn-like processes. Rostrum small, not extending to anterior margin of antennular peduncle, acute, not anteriorly dilated. Pleon usually long, 21–35% BL, with 5 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; posterolateral margin of pleonite 4 acute, not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 with free lateral margins or free posterolateral point, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin rounded, narrowly rounded or truncate; lateral margins evenly convex. Antennular peduncle article 2 longest. Antennal flagellum not extending beyond posterior margin of pereonite 6, usually shorter. Frontal lamina extended anteriorly, slightly or not visible in dorsal view; ventral surface flat, narrowing posteriorly, stem-like, not abutting clypeus. Clypeus with ventrally or anteroventrally triangular blade. Maxilliped palp article 5 quadrate or subquadrate. Pereopod 1 propodus subchelate (dactylus c. 0.8 times length of propodus); dactylus with slender secondary unguis; dactylus may extend to carpus when folded; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 usually with sparse slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes flat lobes. Pleopod 1 peduncle short, 0.45–0.70 times as long as wide. Male pleopod 2 appendix masculina attached basally or sub-basally.

Anchialine caves, intertidal–slope (0–2049 m). Temperate to tropical oceans; speciose in coral reefs. 38 species (Bruce, 1986; Bruce and Rodcharoen, 2021, 2023; Brusca et al., 1995; Paiva and Souza-Filho, 2023b; Sidabalok and Bruce, 2018b).

Pontogelos Stebbing, 1910

Diagnosis. Body length 4–8 mm. Head anterior margin with rostrum, not medially indented. Rostrum large, extending anteriorly to anterior margin of antennular peduncle, wholly separating antennular bases, anteriorly truncate in dorsal view. Pleon long, 35% BL, with 5 visible segments; pleonite 3 epimeron not expanded, not extending posteriorly beyond pleonite 4, narrowly rounded; pleonite 4 not overlapped by pleonite 3; lateral margin free, acute; pleonite 5 with free posterolateral point, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin broadly rounded; lateral margins evenly convex. Antennular peduncle article 3 extremely short (rudimentary in male), peduncle articles progressively shorter distally. Flagella of both antennula and antenna extending beyond pleotelson in male (shorter in female). Frontal lamina extended anteriorly, not visible in dorsal view, narrowing posteriorly, stem-like, not abutting clypeus. Clypeus with anteroventral triangular blade. Maxilliped palp article 5 quadrate. Pereopod 1 dactylus with slender secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 slender, with few robust and slender setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae, without long plumose setae. Penes flat lobes. Pleopod 1 peduncle short, < 0.9 times as long as wide. Male pleopod 2 appendix masculina attached sub-basally. Uropod peduncle posterior mesial margin weakly produced; rami as long as mesial length of peduncle; exopod laminar, exopod notably shorter in length.

Pelagic, nektonic. Indo West-Pacific. 1 species (Bruce, 1995c).

Pseudaega Thomson, 1884

Diagnosis. Body length 3–9 mm. Head anterior margin markedly widest anteriorly; anterior margin with rostrum, not medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, acute, not anteriorly dilated. Pleon 12–17% BL, with 4 or 5 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; posterolateral margin of pleonite 4 narrowly rounded or acute, not extending beyond posterior margin of pleonite 5, pleonite 4 lateral margin pertly overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, distinctly narrower than anterior margin of pleotelson. Pleotelson posterior margin with apical point; lateral margins evenly convex. Antennular peduncle article 2 with prominent, posteriorly directed acute process. Antennal flagellum not extending beyond pereonite 4, usually shorter. Frontal lamina elongate, > 3 times as long as posterior width, usually visible in dorsal view, not fusing or abutting rostrum; ventral surface flat; posteriorly as wide or widest at mid-length, abutting clypeus. Clypeus with ventrally or anteroventrally triangular blade. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with slender secondary unguis (not clear in original figures); merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles moderately produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae and long slender setae. Penes flat lobes. Pleopod 1 peduncle subquadrate, c. 0.75–1.0 times as long as wide. Male pleopod 2 appendix masculina attached mid-length. Uropod endopod lateral margin with prominent excision.

Intertidal–shelf (0–55 m). Temperate Australasia (New Zealand). 5 species (Jansen, 1978).

Pseudolana Bruce, 1979

Diagnosis. Body length 5–10 mm. Head anterior margin markedly widest anteriorly; anterior margin with rostrum, not medially indented. Rostrum acute, not anteriorly dilated. Pleon long, 16–22% BL, with 5 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 4, acute; posterolateral margin of pleonite 4 acute, not extending beyond posterior margin of pleonite 5; pleonite 4 posterolateral margin, free, not overlapped by pleonite 3; pleonite 5 with free lateral margins or free posterolateral point, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin not narrowly rounded; lateral margins evenly convex. Antennular peduncle article 2 longest. Antennal flagellum not extending beyond pereonite 6, usually shorter. Frontal lamina, blade-like, extending anteriorly, not visible in dorsal view; abutting clypeus. Clypeus with ventrally or anteroventrally triangular blade. Maxilliped palp article 5 quadrate or subquadrate. Pereopod 1 dactylus with slender secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles weakly produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes flat lobes. Pleopod 1 peduncle subquadrate, c. 0.75–1.0 times as long as wide. Male pleopod 2 appendix masculina attached mid-length.

Intertidal, subtidal (0–14 m). Central Indo-Pacific (Papua New Guinea, Australia only). 7 species (Bruce, 1986).

Subfamily Cirolaninae Dana, 1852

Diagnosis. Clypeus ventrally flat. Pleon short, < 20% BL, usually 10–14%. Pleonite 4 sometimes laterally enclosed by pleonite 3. Pleonite 5 laterally enclosed by pleonite 4. Pereopods 1–3 with ischium and merus superodistal angles not or weakly produced, inferior margins usually with blunt robust or molariform robust setae; dactylus secondary unguis usually robust or absent. Pereopods 5–7 usually with few slender setae and acute robust setae. Antennal peduncle articles 1–3 short, 4 and 5 subequal in length and longest.

Aatolana Bruce, 1993

Diagnosis. Body length 8–40 mm. Head anterior margin medially indented, without rostrum. Pleon short, < 20% BL; pleonite 3 epimeron broad, acute, dorsoventrally expanded, with setose longitudinal carina, extending posteriorly beyond pleonite 5; posterolateral margin of pleonite 4 narrowly rounded, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin may be overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson linguiform, posterior margin with apical point; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 6. Frontal lamina extended anteriorly, slightly visible in dorsal view; ventral surface flat or posterior margin with downwardly directed process (horn); posteriorly abutting clypeus, as wide or wider at mid-length. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with small blunt secondary unguis; merus inferior margin with molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae and long slender setae. Penes flat lobes. Pleopod 1 peduncle short, usually < 0.9 times as long as wide. Pleopods 2–5 peduncle lateral margin with well-developed laminar lobe. Male pleopod 2 appendix masculina attached basally or sub-basally.

Shelf (16–200 m). Indo West-Pacific. 3 species (Bruce, 1993; Keable, 1998).

Baharilana Bruce and Svavarsson, 2003

Diagnosis. Body length 5–10 mm. Head anterior margin without rostrum, not medially indented. Pleon 7–15% BL, with 4 or 5 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; posterolateral margin of pleonite 4 narrowly rounded or acute, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson linguiform; posterior margin narrowly rounded or truncate; lateral margins distinctly sinuate or evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 2. Frontal lamina extended anteriorly, not visible in dorsal view; ventral surface flat; posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with robust secondary unguis; merus inferior margin with molariform robust setae. Pereopods 2 and 3 merus moderately produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, distally widest, with long robust setae and long slender setae. Penes flat lobes. Pleopod 1 peduncle quadrate, about as long as wide; rami not operculate; endopod narrow, 0.26–0.45 times width of exopod. Male pleopod 2 appendix masculina attached submesially.

Intertidal, subtidal, shelf (0–70 m, one species at 1850 m). Western Indo-Pacific. 5 species (Bruce and Svavarsson, 2003; Khalaji-Pirbalouty and Wägele, 2011; Schotte and Kensley, 2005).

Bathynomus A. Milne Edwards, 1879

Diagnosis. Body dorsal surfaces smooth or punctate; BL 70–300 mm or more. Head anterior margin markedly widest anteriorly; anterior margin with rostrum, not medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, acute, not anteriorly dilated. Pleon long, usually 15–35% BL, with 5 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; posterolateral margin of pleonite 4 acute, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin may be overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, < 0.9 width of anterior margin of pleotelson. Pleotelson posterior margin truncate, with prominent spines; lateral margins evenly convex. Antennular peduncle articles progressively shorter distally. Antennal flagellum not extending beyond posterior margin of pereonite 4, usually shorter. Frontal lamina extended anteriorly, usually visible in dorsal view, usually fused to or abutting rostrum; frontal lamina ventral surface flat, broad (2.4–4.0 times posterior width); posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 triangular. Pereopod 1 dactylus with or without secondary unguis, extending to carpus when folded; merus inferior margin without molariform robust setae. Pereopods 1–3 with merus superodistal margin strongly produced. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes flat lobes. Pleopods with respiratory branchiae at base of pleopods 1 and 2 exopods. Pleopod 1 peduncle short, 0.45–0.70 times as long as wide. Pleopods 2–5 peduncle lateral margin with well-developed laminar lobe. Male pleopod 2 appendix masculina attached submesially.

Shelf–bathyal (100–2500 m, occasionally at 20 m). Cosmopolitan, 35°N to 35°S. 22 extant species. Lowry and Dempsey (2006) characterised two groups of species: “giants”, with a length range of 80–140 mm, and “supergiants”, 150–500 mm (Huang and Bruce, 2024; Huang et al., 2022; Kou et al., 2017; Shipley et al., 2016; Sidabalok et al., 2020).

Booralana Bruce, 1986

Diagnosis. Body dorsal surfaces smooth or sparsely punctate; BL 20–60 mm. Head anterior margin widest at mid-length; anterior margin without rostrum, medially indented. Pleon 12–18% BL; pleonite 3 epimeron ventral margin with ventral blade-like process, narrowly rounded; posterolateral margin of pleonite 4 narrowly rounded; pleonite 4 lateral margin may be overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin truncate, or broadly rounded; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 5. Frontal lamina posterior margin with downwardly directed process (horn); posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with or without secondary unguis; merus inferior margin with molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles strongly produced. Pereopods 2–7 slender, with few robust and slender setae. Penes flat lobes. Pleopod 1 peduncle short, 0.45–0.70 times as long as wide. Pleopods 2–5 peduncle lateral margin with well-developed laminar lobe. Male pleopod 2 appendix masculina attached basally or sub-basally.

Shelf, slope (22–610 m). Tropical western Atlantic, Temperate Australasia. 4 species (Bruce, 1986; Camp and Heard, 1988; Shipley et al., 2024).

Calyptolana Bruce, 1985

Diagnosis. Body dorsum strongly vaulted; BL 3–4 mm. Head anterior margin with rostrum, not medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, not anteriorly truncate in dorsal view. Pleon 8% BL, with 4 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, rounded; posterolateral margin of pleonite 4 rounded, not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, distinctly narrower than anterior margin of pleotelson. Pleotelson posterior margin broadly rounded; lateral margins evenly convex. Antennular peduncle articles 1 and 2 fused. Antennal flagellum not extending beyond posterior margin of pereonite 1. Frontal lamina extended anteriorly, not visible in

dorsal view, ventral surface flat, widest at mid-length, abutting clypeus. Clypeus narrow, less than half basal width; ventral surface flat. Maxilliped palp article 5 subquadrate or rounded. Pereopod 1 dactylus with robust secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 slender, with few robust and slender setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Pleopod 1 peduncle short, usually < 0.9 times as long as wide; both rami forming operculum; endopod 0.50–0.68 times as wide as exopod. Uropod endopod shorter than mesial length of peduncle; exopod laminar, much shorter than endopod.

Subtidal, shelf (1–43 m). Tropical Atlantic (Netherland Antilles and Caribbean Colombia). 1 species (Bruce, 1985; Müller 1993).

Cartetolana Bruce, 1981

Diagnosis. Body dorsum strongly vaulted; BL 9–12 mm. Head anterior margin without rostrum, not medially indented. Pleon 13% BL; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, narrowly rounded; not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin laterally overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded; lateral margins evenly convex. Antennular peduncle articles 1 and 2 short, fused, article 3 longest. Antennal flagellum not extending beyond posterior margin of pereonite 2. Frontal lamina extended anteriorly, not visible in dorsal view, ventral surface flat; posteriorly as wide as mid-length, abutting clypeus. Clypeus ventral surface flat. Mandible incisor massive, not visible in dorsal view. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with small blunt secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 pereopods 2 and 3 merus moderately produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus flattened, with long acute short robust setae. Pleopod 1 peduncle short, 0.43 times as long as wide. Male pleopod 2 appendix masculina unknown.

Subtidal, shelf (1–23 m); commensal with Crinoidea. Central Indo-Pacific. 1 species (Bruce, 1986).

Ceratolana Bowman, 1977

Diagnosis. Body dorsal surfaces sparsely punctate, with nodules; BL 22–34 mm. Head anterior margin with rostrum, medially indented; posterior margin fused to pereonite 1 (not clear according to Bruce, 1995b). Rostrum large, extending anteriorly to anterior margin of antennular peduncle, wholly separating antennular bases, not anteriorly truncate in dorsal view, acute. Pleon 11% BL; pleonites 1 and 2 about as wide as pleonites 3–5; pleonite 3 epimeron ventral margin with ventral blade-like process, rounded; posterolateral margin of pleonite 4 acute, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, < 0.9 times width of anterior margin of pleotelson. Pleotelson posterior margin broadly rounded; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 5. Frontal lamina extended anteriorly, visible in dorsal view, not fusing or abutting rostrum; ventral surface flat; posteriorly as wide or wider at mid-length, abutting clypeus; anterior part a horn-like process. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with small blunt secondary unguis, not extending to carpus when folded; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 slender, with few robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes low tubercles. Pleopod 1 peduncle short, 0.36 times as long as wide. Male pleopod 2 appendix masculina attached submesially.

Intertidal; in mangroves. Central Indo-Pacific (Malaysia, southeastern Papua New Guinea). 1 species (Bowman, 1977; Bruce, 1995b).

Cirolana Leach, 1818

Diagnosis. Body sparsely punctate or nodular; BL 3–30 mm. Head anterior margin widest at mid-length; anterior margin with or without rostrum, not medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, not anteriorly truncate in dorsal view, acute, not anteriorly dilated. Pleon < 20% BL, usually 10–14% BL, with 4 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, rounded, narrowly rounded or acute; posterolateral margin of pleonite 4 rounded, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin sometimes overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson linguiform; posterior margin narrowly rounded or truncate; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 5. Frontal lamina extended anteriorly, slightly or not visible in dorsal view, ventral surface flat, broad (2.4–4.0 times posterior width); posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with robust secondary unguis; merus inferior margin with molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 usually with slender acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes absent, or low tubercles, which may be medially united. Pleopod 1 peduncle short, 0.45–0.70 times as long as wide. Male pleopod 2 appendix masculina attached basally or sub-basally.

Freshwater, caves, estuarine, marine, intertidal–shelf. All oceans from 72°S (Ross Sea) to 53°N (Ireland). 146 species, with several distinct groups that could be defined as genera in the future. Thirteen species occur below 100 m depth, and three species below 1,000 m. Bruce (1981, 1986) and Brusca et al. (1995) gave genus reviews and diagnoses. Recent significant species accounts were by Bruce (1995a: Papua New Guinea), Schotte and Kensley (2005: Indian Ocean), Sidabalok and Bruce (2017, 2018a: Indonesia), Rodcharoen et al. (2016, 2017: Thailand) and Rodcharoen and Bruce (2021: Thailand).

Gnatholana Barnard, 1920

Diagnosis. Body dorsal surfaces sparsely punctate; BL 5.5 mm. Pleon 23% BL, with 4 visible segments; narrowly rounded; posterolateral margin of pleonite 4 narrowly rounded, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, distinctly narrower than anterior margin of pleotelson. Pleotelson posterior margin with apical point; lateral margins distinctly sinuate. Antennal flagellum not extending beyond posterior margin of pereonite 2. Frontal lamina extended anteriorly, usually visible in dorsal view, not fusing or abutting rostrum, dorsally displaced by mandible. Clypeus ventral surface flat. Mandible incisor massive, visible in dorsal view, narrow, distally acute, less than half basal width.

Shelf (155 m). Western Indo-Pacific (South Africa). 1 species (Barnard, 1920). *Gnatholana mandibularis* Barnard, 1920 needs redescription.

Hansenolana Stebbing, 1900

Diagnosis. Body dorsum flat or weakly vaulted; dorsal surfaces smooth or sparsely punctate; BL 6–10 mm. Head anterior margin markedly widest anteriorly, transversely straight, not medially indented. Rostrum small, acute, not extending to anterior margin of antennular peduncle. Pleon 12% BL, with 4 visible segments; pleonites 1 and 2 narrower than pleonites 3–5; pleonite 4 clearly extending beyond posterior margin of pleonite 5, pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, distinctly narrower than anterior margin of pleotelson. Pleotelson posterior margin broadly rounded; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 1. Frontal lamina extended anteriorly not visible in dorsal view, ventral surface flat; narrowing posteriorly, not stem-like, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 quadrate or subquadrate. Pereopod 1 propodus subchelate (dactylus c. 0.8 length of propodus); dactylus with small slender secondary unguis (blunt on pereopod 2); dactylus extending to carpus when folded; merus inferior margin with molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 slender, with few robust and slender setae. Pleopod 1 peduncle short, 0.45 as long as wide; rami not operculate; endopod narrow, 0.45 width of exopod. Uropod peduncle posterior mesial margin weakly produced; rami as long as mesial length of peduncle, subequal; exopod laminar.

Intertidal. Central Indo-Pacific. 1 species (Bruce, 1986).

Limicolana Bruce, 1986

Diagnosis. Body dorsal surfaces polished in appearance; BL 13–15 mm. Anterior margin with rostrum, medially indented. Rostrum acute, not anteriorly dilated. Pleon 17% BL; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 4, acute; posterolateral margin of pleonite 4 acute, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin with apical point; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 5. Frontal lamina extended anteriorly, slightly visible in dorsal view; ventral surface flat; narrowing posteriorly, not stem-like, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 propodus subchelate (dactylus c. 0.8 length of propodus); dactylus without secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae and long slender setae. Penes flat lobes. Pleopod 1 peduncle short, 0.45–0.70 times as long as wide. Pleopods 2–5 peduncle lateral margin with well-developed laminar lobe. Male pleopod 2 appendix masculina attached submesially.

Intertidal; mangroves. Central Indo-Pacific (northern Australia). 1 species (Bruce, 1986).

Neocirolana Hale, 1925

Diagnosis. Body dorsal surfaces smooth, or punctate; BL 3–10 mm. Head widest anteriorly or widest at mid-length; anterior margin with rostrum, not medially indented. Rostrum small, acute, not extending to anterior margin of antennular peduncle, not anteriorly dilated. Pleon < 20% BL, usually 10–14% BL, with 4 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; posterolateral margin of pleonite 4 narrowly rounded, not extending beyond posterior margin of pleonite 5, lateral margin may be overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded, or truncate; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 5 (usually shorter). Frontal lamina extended anteriorly, not visible in dorsal view, ventral surface flat; posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Mandible incisor not massive; narrow, less than half basal width. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with robust secondary unguis; merus inferior margin with or without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes absent. Pleopod 1 peduncle short, usually < 0.9 times as long as wide. Male pleopod 2 appendix masculina attached basally or sub-basally. Uropod endopod lateral margin with or without prominent excision.

Subtidal, shelf (1–49 m). Tropical Atlantic, Indo West-Pacific. 11 species (Bruce 1986; Bruce and Hughes, 2020).

Odysseylana Malyutina, 1995

Diagnosis. Body length 5–11 mm. Head anterior margin without rostrum, not medially indented. Pleon < 20% BL, usually 10–14% BL; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; posterolateral margin of pleonite 4 rounded, clearly extending beyond posterior

margin of pleonite 5; pleonite 4 lateral margin sometimes overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson linguiform; posterior margin narrowly rounded or truncate; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 2. Frontal lamina extended anteriorly, not visible in dorsal view; ventral surface flat; posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with small blunt secondary unguis; dactylus extending to carpus when folded; merus inferior margin with molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles moderately produced. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae and long slender setae. Penes absent, or low tubercles. Pleopod 1 peduncle quadrate, about as long as wide. Male pleopod 2 appendix masculina attached basally or sub-basally.

Subtidal–slope (3–300 m). Central Indo-Pacific. 4 species (Sidabalok and Bruce, 2015).

Oncilorpheus Paul and Menzies, 1971

Diagnosis. Body elongate, 4.0–6.5 times as long as wide; dorsal surfaces smooth or coarsely pitted; BL 8–15 mm. Head anterior margin markedly widest anteriorly; anterior margin with or without rostrum, medially indented or not. Rostrum small, not extending to anterior margin of antennular peduncle. Pleon 11% BL, with 5 visible or medially fused segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 4; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, slightly wider than anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded; lateral margins distinctly sinuate, or evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 1. Frontal lamina not visible in dorsal view; ventral surface flat; posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with small blunt secondary unguis; merus inferior margin with molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae and long slender setae. Penes flat lobes. Pleopod 1 peduncle subquadrate, c. 0.75–1.0 times as long as wide; rami operculate; with exopod forming operculum; endopod narrow, 0.26–0.45 times width of exopod. Male pleopod 2 appendix masculina attached basally or sub-basally. Uropod peduncle posterior mesial margin weakly produced; rami shorter than mesial length of peduncle, subequal in length; exopod laminar.

Shelf (28–73 m). Tropical Atlantic, Tropical Eastern Pacific (Central America). 2 species (Brusca et al., 2015). *Oncilorpheus* has some distinctive uniting and probably apomorphic characters, but the genus is highly unusual in that one species *O. jerrybarnardi* Brusca, Wetzer and France, 1995 has all pleonites medially fused, whereas the other has five unfused pleonites.

Parabathynomus Barnard, 1924

Diagnosis. Body length 70–80 mm. Head anterior margin widest posteriorly, margin without rostrum, not medially indented. Pleon 17% BL, with 5 visible segments; pleonite 3 epimeron not markedly expanded, extending to posterior of pleonite 5, narrowly rounded; posterolateral margin of pleonite 4 narrowly rounded, not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin truncate; lateral margins not distinctly sinuate. Antennal flagellum not extending beyond posterior margin of pereonite 4. Frontal lamina extended anteriorly, not visible in dorsal view; ventral surface flat; posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 triangular. Pereopod 1 dactylus not extending to carpus when folded; merus inferior margin without molariform robust setae. Pereopods 1–3 with merus superodistal margin strongly produced. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes flat lobes. Pleopods with respiratory branchiae on pleopod 1 peduncle and at base of pleopods 1 and 2 exopods. Pleopod 1 peduncle short, 0.5 times as long as wide. Pleopods 2–5 peduncle lateral margin with well-developed laminar lobe. Male pleopod 2 appendix masculina attached basally.

Slope (230–766 m). Temperate Southern Africa (E coast). 1 species (Kensley, 1978).

Plakolana Bruce, 1993

Diagnosis. Body length 6–15 mm. Head anterior margin widest at mid-length; anterior margin without rostrum. Pleon 11–13% BL, with 4 or 5 visible segments; pleonite 3 epimeron broad, dorsoventrally expanded, with longitudinal carina, extending posteriorly beyond pleonite 5; posterolateral margin of pleonite 4 posteriorly broad, truncate, extending slightly beyond posterior margin of pleonite 5; pleonite 4 lateral margin overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly narrower than anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded; lateral margins evenly convex, converging to apical point. Antennal flagellum not extending beyond posterior margin of pereonite 5. Frontal lamina extended anteriorly, not visible in dorsal view; ventral surface flat, slender (3.8–7.6 times posterior width), posteriorly as wide as at mid-length, abutting clypeus. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with or without secondary unguis; merus inferior margin with molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus flattened, with long acute robust setae. Penes flat lobes. Pleopod 1 peduncle about as long as wide. Male pleopod 2 appendix masculina attached basally or sub-basally.

Subtidal–slope (8–450 m). Central Indo-Pacific. 6 species (Bruce, 1993; Keable, 1997; 1999b).

Unassigned to subfamily

Bathylana Kensley, 1989

Diagnosis. Body length 3–4 mm. Head anterior margin without rostrum, not medially indented. Pleon long, 20% BL, with 5 visible segments; pleonites 1 and 2 narrower than pleonites 3–5; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; posterolateral margin of pleonite 4 acute, not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4 (with free posterolateral points), as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin broadly rounded; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 3. Frontal lamina extended anteriorly, not visible in dorsal view; ventral surface flat; narrowing posteriorly, stem-like, not abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 subquadrate. Pereopod 1 propodus subchelate (dactylus c. 0.8 times length of propodus); dactylus with slender secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 slender, with few robust and slender setae. Penes short lobes. Pleopod 1 peduncle short, 0.5 times as long as wide. Male pleopod 2 appendix masculina attached submesially. Uropod peduncle posterior mesial margin weakly produced; rami as long as mesial length of peduncle, subequal in length; exopod laminar.

Slope (1000–1450 m). Temperate Southern Africa (Saint Paul and Amsterdam Islands). 1 species (Kensley, 1989). The pereopods, pleopods, maxilliped and frontal lamina all accord with *Metacirolana*; most relatable characters point to Eurydicinae; the frontal lamina appears posteriorly stemmed and not abutting the clypeus, but the clypeus lacks a ventral blade-like projection.

Scutulana Bruce, 1996

Diagnosis. Body short, BL < 4 mm, less than twice as long as wide, dorsum flat. Head anterior margin not medially indented, with small rostrum not extending to anterior margin of antennular peduncle. Pleon 9% BL; pleonites 1 and 2 wider than pleonites 3–5; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, pleonites 3–5 narrow, pleonite 5 narrowest; pleonites 4 and 5 laterally enclosed by pleonite 3, distinctly narrower than anterior margin of pleotelson. Pleotelson posterior margin broadly rounded; lateral margins evenly convex. Antennular peduncle article 1 shortest, articles 2 and 3 subequal. Antennal flagellum not extending beyond posterior margin of pereonite 2. Frontal lamina extended anteriorly, not visible in dorsal view; ventral surface flat; narrowing posteriorly, stem-like, not abutting clypeus. Clypeus ventral surface flat. Mandible incisor not massive, narrow, less than half basal width. Maxilliped palp article 5 quadrate. Pereopod 1 slender, dactylus with prominent slender secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 slender, with few robust and slender setae. Pereopods 6 and 7 ischium, merus and carpus with both (but few) long robust and long slender setae. Pleopod 1 peduncle subquadrate, c. 0.7 times as long as wide; rami not operculate; endopod narrow, 0.40–0.45 times width of exopod. Uropod exopod notably shorter than endopod.

Slope (440 m). Central Indo-Pacific (New Caledonia). 1 species (Bruce, 1996). Pereopods are of the Cirolaninae form; the pleon is short, with 5 pleonites, but pleonites 3–5 are narrow and overlapped by pleonite 2, with pleonites 4 and 5 subequal in width and laterally enclosed by pleonite 3; the frontal lamina is posteriorly stemmed, but the clypeus does not laterally enclose the labrum; the pereopods have a stout secondary unguis.

Seychellana Kensley and Schotte, 1994

Diagnosis. Body length 6.0–6.6 mm. Head anterior margin without rostrum, not medially indented. Pleon long, 18% BL, with 5 visible segments; pleonite 3 epimeron broad, dorsoventrally expanded, extending posteriorly beyond pleonite 5; pleonite 4 posteriorly rounded; not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin overlapped by pleonite 3; pleonite 5 with free lateral margins (but laterally overlapped by pleonite 3), as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin broadly rounded; lateral margins evenly convex. Antennular peduncle articles with articles 2 and 3 weakly offset to article 1. Antennal peduncle articles 3 and 4 subequal in length, 5 longest. Antennal flagellum not extending beyond pereonite 5. Frontal lamina extended anteriorly, visible in dorsal view, not fusing or abutting rostrum; > 3 times as long as posterior width; narrowing mid-length, stem-like, not abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 quadrate. Pereopod 1 propodus subchelate; dactylus c. 0.8 length of propodus, without secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1 merus superodistal angle moderately produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus weakly flattened, with long acute robust setae; pereopod 6 markedly shorter than pereopod 7. Penes low tubercles. Pleopod 1 peduncle short, 0.40 times as long as wide. Male pleopod 2 appendix masculina attached sub-basally. Uropod rami inflected or convex.

Shelf (30 m). Western Indo-Pacific (Seychelles). 1 species (Kensley and Schotte, 1994). While superficially similar to *Eurydice*, many differences indicate it is not close to that genus, nor to others of the Eurydicinae. The antennal peduncle and uropod are of the Conilerinae form, as is the basal appendix masculina; the pleon is long and pleonite 5 has free lateral margins; pereopod 1 and other pereopods are *Plakolana*-like; while pereopod 1 merus has the superodistal margin produced, but pereopod 2 does not. Pleopods are generally similar to Cirolaninae with a basally attached appendix masculina. Penial processes are absent, but low tubercles are present. The strongest characters pointing to Eurydicinae are the frontal lamina being posteriorly stemmed, the shape and narrowness of the clypeus, the long pleon, and pleonite 5 with free lateral margins.

Sululana Bruce and Shimomura, 2019

Diagnosis. Body dorsal surfaces polished smooth; BL < 3 mm. Head anterior margin medially indented, with small rostrum not extending to anterior margin of antennular peduncle. Pleon 11% BL; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; posterolateral margin of pleonite 4 acute, pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 with free lateral margins, wider than anterior margin of pleotelson. Pleotelson posterior margin broadly rounded; lateral margins evenly convex. Antennular peduncle article 2 longest. Antennal peduncle articles 1–3 short, 4 longer, article 5 longest; flagellum not extending beyond posterior margin of pereonite 1. Frontal lamina extended anteriorly, not visible in dorsal view, ventral surface flat. Clypeus ventral surface flat, anteriorly narrowed, not projecting ventrally. Mandible incisor not massive, wide, > 0.55 times basal width; left mandible bicuspid. Maxilliped palp article 5 subquadrate. Pereopod 1 propodus haptorial (dactylus as long as propodal palm); dactylus without secondary unguis; dactylus extending to carpus when folded; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 slender, with few robust and slender setae. Pereopods 6 and 7 ischium, merus and carpus with long robust setae and long slender setae (very few setae). Pleopod 1 peduncle sub-quadrate, about 0,7 as long as wide; rami operculate; with exopod forming operculum; endopod narrow, 0.22 times width of exopod; uropodal rami as long as mesial length of peduncle; exopod laminar, exopod notably shorter in length.

Slope (1012–1016 m). Central Indo-Pacific (Sulu Sea). 1 species (Bruce and Shimomura, 2016). *Sululana* seem closer to *Metacirolana* than to other genera on the basis of antennular peduncle article 2 being longest and the characters of the pleon, maxilliped and pereopods, but has an operculate pleopod 1 (among other characters) that exclude the only species from that genus.

Xylolana Kensley, 1987

Diagnosis. Body about 4 times as long as wide; BL < 4 mm. Head anterior margin with large, anteriorly dilated rostrum extending anteriorly to anterior margin of antennular peduncle, wholly separating antennular bases; anteriorly truncate in dorsal view; rostrum and frontal lamina together produced, forming horn-like process (abutting but not fused). Pleon 9% BL; pleonites 1 and 2 narrower than pleonites 3–5 (pleonite 1 narrowest); pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5; pleonite 4 posterolateral margin posteriorly broad, truncate (expanded), clearly extending beyond posterior margin of pleonite 5, lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, distinctly narrower than anterior margin of pleotelson. Pleotelson posterior margin truncate; lateral margins straight. Antennal peduncle articles progressively increasing in length; flagellum not extending beyond posterior margin of pereonite 1. Frontal lamina not visible. Clypeus ventral surface flat, anteriorly conical anteriorly produced and acute. Mandible incisor not massive, wide, about half width. Left mandible bicuspid. Maxilliped palp article 5 subquadrate. Pereopod 1 dactylus with robust secondary unguis; merus inferior margin with molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 robust, with few robust and slender setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae and few long slender setae. Penes flat lobes. Pleopod 1 peduncle subquadrate, c. 0.75 times as long as wide. Male pleopod 2 appendix masculina attached subdistally. Uropod peduncle posterior mesial margin moderately produced; rami as long as mesial length of peduncle, subequal in length; exopod laminar.

Intertidal; mangroves. Tropical Atlantic (Belize). 1 species (Kensley, 1987). This genus does not belong in the Eurydicinae, as placed by Kensley and Schotte (1989), and is here regarded as *incertae sedis*. Pleonite 5 is fully enclosed by pleonite 4, and the pleon is "short". The clypeus does have an anteriorly produced apex, but not a ventrally projecting blade, and the appendix masculina is subdistal in position; the pereopods have stout robust setae and molariform setae on the pereopod 1 merus and the dactylus has a secondary unguis; these and the pleon characters indicate Cirolaninae is more appropriate. The present interpretation is that the labrum is relatively wide, and the clypeus is ventrally flat with an anterior projection (similar to some Cirolaninae) that abuts the rostrum; it seems that the frontal lamina is lost or hidden from view.

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Corallanidae Hansen, 1890

Figure 5.22

Corallanidae is a small family of six genera and 84 species (including three *incertae sedis* species), primarily occurring in tropical and subtropical shallow waters (Delaney, 1989). Some species are symbionts of fishes feeding on fish mucus and fish blood, while others are associated wholly or occasionally with sponges. The biology of many species is not known, though it is probable that some species of *Lanocira* Hansen 1890 feed on polychaetes. At least one species of *Argathona* Stebbing, 1905 is known to attach to fish gills, and others occupy the nasal passages of fish. The genus *Tachaea* Schioedte and Meinert, 1879 is primarily freshwater (one marine species) and is a micropredator of freshwater shrimp (e.g. Mariappan et al., 2003). *Excorallana* Stebbing, 1904 is exclusively New World in distribution (Santos Silva and Souza-Filho, 2017; Vigneshwaran et al., 2021). Species of the family are occasionally pests of aquaculture fishes (e.g. Kua and Bruce, 2010). The mandibular incisor in this family is narrow, giving a typically "narrow-headed appearance", but the buccal cone is not as distinct as in the Aegidae and Cymothoidae, and the pereopod dactyli, while sometimes distally curved, are not prehensile. In comparison to the Cirolanidae, corallanids are generally more dorsally setose and have somewhat larger eyes, in *Excorallana* the eyes of some species being medially united (Bruce et al., 1982).

The species-level taxonomy is difficult, with rather many unrecognizable species and several species incorrectly placed in genera (Anil et al., 2022; Bruce et al., 2022). The genera are most reliably identified by the mouthpart characters, but the key below uses some characters that are more easy to observe. Several of the species of Corallanidae described from Japan by Nunomura (1988, 1994, 2006a) were incorrectly identified at genus level.

Diagnosis. Eyes well developed; dorsum often ornamented with setae, spines, tubercles or carinae; head may have well-developed anteriorly produced rostrum (*Argathona*, *Lanocira*); sexual dimorphism in ornamentation common. Antennula peduncle 2- or 3-articulate, basal article sometimes expanded (*Corallana*, *Tachaea*). Antenna peduncle articles 1–3 short, 4–5 elongate. Frontal lamina and clypeus always flat. Mandibular always narrow, less than 0.4 basal width, incisor variously truncate, bidentate, tridentate or falcate; lacinia mobilis absent, molar process reduced occasionally absent. Maxillula lateral lobe with 1–2 large falcate apical spines, with 0–5 smaller subapical (accessory) spines in some genera; mesial lobe with simple, sparsely setose. Maxilla uniramous, minute, 1–3-articulate; apex morphology various, devoid of robust setae, sparsely setose. Maxilliped without endite; palp slender, 5-articulate, with occasional partial fusion of articles, without apical acute or hooked robust setae; various maxilliped articles elongate in different genera.

Additional characters. Many species are often dorsally setose, usually on the pleotelson, pleon and posterior margin of the pereonites, sometimes over the entire dorsum. Several species have a strongly developed rostrum, nodules or process on the head, pereonite 1, posterior pereonites and sometimes the pleon. The frons is always narrow, with a narrow mandibular incisor.

Key to genera of Corallanidae

1. Pleotelson lateral margin with (fig. 5.22b), rarely without (fig. 5.22c), incision. Eyes large, separated by less than half head width to medially contiguous (fig. 5.22b, c). Maxilliped elongate, palp article 3 elongate, about twice as long as wide (fig. 5.22u) ..... *Excorallana*

– Pleotelson lateral margin without incision. Eyes small ("cirolanid-sized") to moderate in size, separated by more than 0.45 head width (fig. 5.22a). Maxilliped palp article 3 not elongate, less than twice as long as wide (fig. 5.22s) 2

2. Maxilliped slender, basis elongate, 2–4 times as long as wide; palp articles subquadrate (fig. 5.22t). Frontal lamina small, variously shaped but not elongate, or absent (fig. 5.22e, f) ..... *Corallana*

– Maxilliped not slender, palp articles 2–5 short (fig. 5.22s, v), articles 2–5 partly or wholly fused. Frontal lamina variously shaped, elongate (fig. 5.22d, g) 3

3. Mandibular trunk wide (fig. 5.22h); incisor narrow, bi- or tridentate; molar process present (fig. 5.22i). Maxillula lateral lobe with single large terminal robust seta and several subapical smaller robust setae on mesial margin. Maxilla a single rounded or subtruncate article (fig. 5.22o) ..... *Argathona*

– Mandibular trunk and incisor narrow, bi-dentate or unicuspid; molar process absent (fig. 5.22j). Maxillula lateral lobe with large terminal robust setae or with 1 or 2 stout curved terminal robust setae 4

4. Mandible mesial margin serrate (fig. 5.22j). Maxillula lateral lobe with single large terminal strongly hooked robust seta (fig. 5.22l). Maxilla 2- or 3-articled, terminal article sublinear, with prominent terminal setae (fig. 5.22p) ..... *Lanocira*

– Mandible without serrations. Maxillula lateral lobe with 1 or 2 large stout, curved robust setae. Maxilla short, rounded lobe (fig. 5.22n, q) 5

5. Mandibular incisor unicuspid, acute or narrowly rounded. Maxilliped palp margins quadrate (fig. 5.22w). Maxillula lateral lobe with 1 large stout, curved robust seta (fig. 5.22m). Pereopod 1 dactylus simple (fig. 5.22y). Body dorsal surfaces not setose (mainly freshwater on decapod crustaceans) ..... *Tachaea*

– Mandibular incisor truncate or weakly bi-dentate. Maxilliped palp lateral margins convex, (fig. 5.22r). Maxillula lateral lobe with 2 large stout, curved robust setae, with accessory setae in between. Pereopod 1 dactylus with well-developed spines (fig. 5.22x). Body dorsal surfaces often setose ..... *Alcirona*

Alcirona Hansen, 1890

Diagnosis. Eyes normal in size, less than half head width. Pleotelson lateral margin without excision. Antennula article 1 not anteriorly produced. Mandibular incisor bicuspid or truncate; molar process present. Maxillula lateral lobe with 2 stout curved robust setae, with accessory setae between. Maxilla small short rounded lobe. Maxillipedal palp short, articles with lateral margins convex, not fused; article 3 less than twice as long as wide; article 5 longer than article 4. Pereopod 1 dactylus ambulatory, shorter than propodus; inferior margin with comb-like row of spines. Uropodal rami subequal in length.

Intertidal, shelf (to 106 m). Cosmopolitan in tropical and temperate shallow waters. 9 species (Koening, 1979; Nunomura, 2006b).

Argathona Stebbing, 1905

Diagnosis. Eyes normal in size, less than half head width. Pleotelson lateral margin without excision. Antennula article 1 not anteriorly produced. Mandibular incisor tridentate or bicuspid; molar process present. Maxillula lateral lobe with single stout curved robust seta and 1–4 mesial accessory setae. Maxilla small subtruncate lobe. Maxillipedal palp short, articles with lateral and mesial margins straight; articles not fused; article 3 less than twice as long as wide; article 5 longer than article 4. Pereopod 1 dactylus ambulatory, shorter than propodus; inferior margin even, without row of spines. Uropodal rami subequal in length.

Intertidal–slope (to 267 m; one species at 760 m) (Bruce et al. 2022; Longstaff et al., 2025). Indo-West Pacific. 20 species; several species strongly associated with fish as commensals or micropredators (Bruce et al., 2022).

Corallana Dana, 1853

Diagnosis. Eyes normal in size, less than half head width. Pleotelson lateral margin without excision. Antennula article 1 not anteriorly produced. Mandibular incisor tridentate, bicuspid or elongate, falcate; molar process present. Maxillula lateral lobe with single stout curved robust seta, without accessory setae. Maxilla small, elongate (longer than basal width) rounded lobe. Maxillipedal palp elongate, articles quadrate, not fused; article 3 less than twice as long as wide; article 5 shorter than article 4. Pereopod 1 dactylus ambulatory, shorter than propodus; inferior margin even, without row of spines. Uropodal exopod of adult male longer than endopod.

Intertidal–shelf (marine and estuarine, to 106 m). Indo-West Pacific (SE Africa to Philippines). 16 species (Delaney, 1989; Müller, 1991).

Excorallana Stebbing, 1904

Diagnosis. Eyes large, occupying half or more than half head width. Pleotelson lateral margin with or without excision. Antennula article 1 expanded. Mandibular incisor elongate, falcate; molar process present or absent. Maxillula lateral lobe

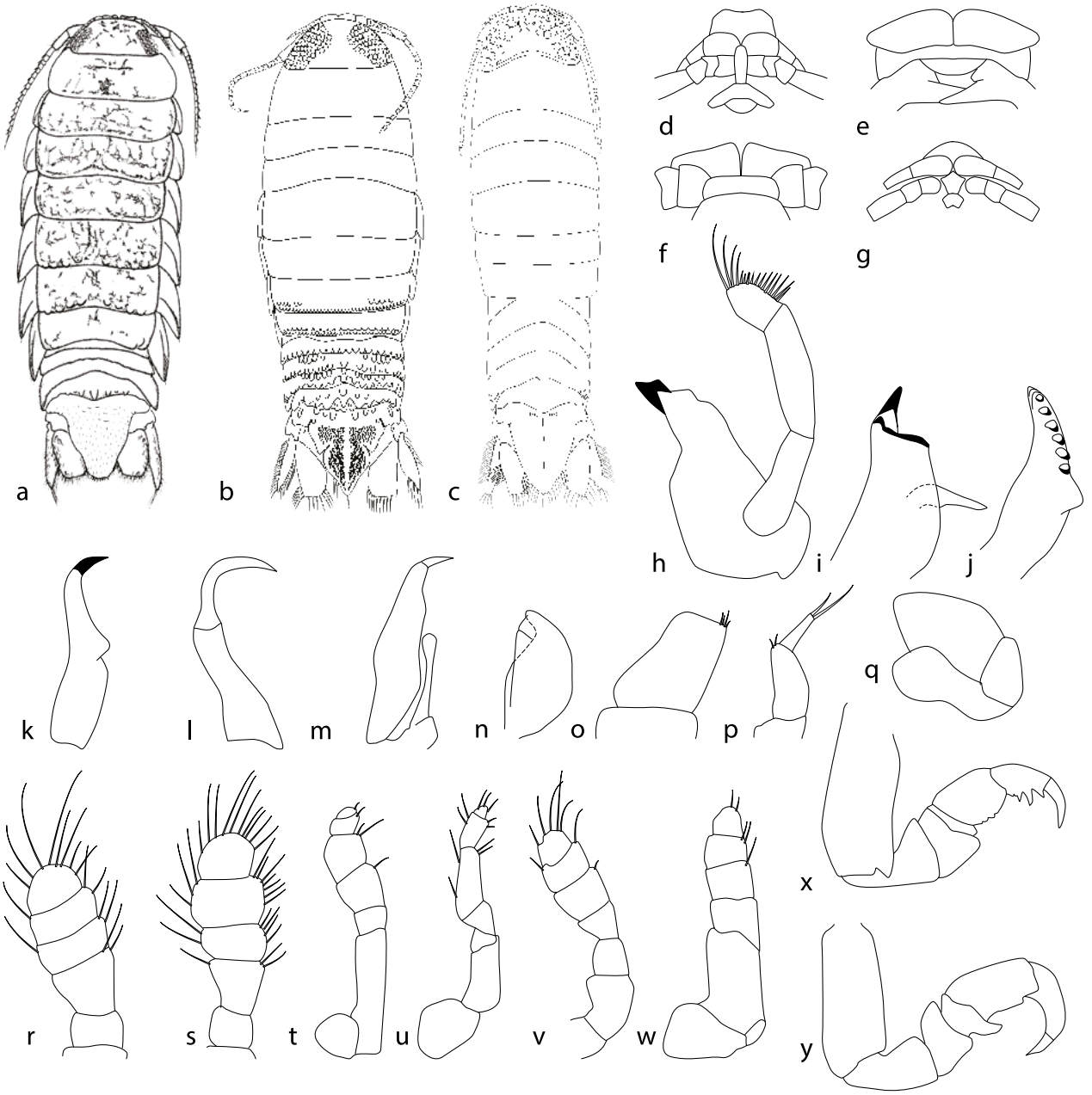


Figure 5.22. Corallanidae. a, *Corallana societensis* Müller, 1991; b, *Excorallana oculata* (Hansen, 1890); c, *Excorallana warmingii* (Hansen, 1890). Frons: d, *Argathona*; e, f, *Corallana*; g, *Lanocira*. Mandibles: h, i, *Argathona*; j, *Lanocira*. Maxillula: k, *Corallana*; l, *Lanocira*; m, *Tachaea*. Maxilla: n, *Alcirona*; o, *Argathona*; p, *Lanocira*; q, *Tachaea*. Maxilliped: r, *Alcirona*; s, *Argathona*; t, *Corallana*; u, *Excorallana*; v, *Lanocira*; w, *Tachaea*. Pereopod 1: x, *Alcirona*; y, *Tachaea*.

with single stout curved robust seta and 1–4 mesial accessory setae, or with large strongly hooked robust seta. Maxilla with 2 small, short, rounded lobes. Maxilliped palp elongate, articles quadrate, not fused; article 3 twice as long as wide; article 5 shorter than article 4. Pereopod 1 dactylus ambulatory, shorter than propodus; inferior margin even, without spines. Uropodal rami subequal in length.

Intertidal–shelf (to 183 m). Tropical Atlantic, Tropical Eastern Pacific (Americas). 23 species (Delaney, 1984; Stone and Heard, 1989: key to 8 species without lateral incision on pleotelson; biology; Santos Silva and Souza-Filho, 2017: descriptions and key to 12 species from Brazil). All records from the Indo-West Pacific are misidentifications.

Lanocira Hansen, 1890

Diagnosis. Eyes normal in size, less than half head width. Pleotelson lateral margin without excision. Antennula article 1 not anteriorly produced. Mandibular incisor bicuspid; molar process present. Maxillula lateral lobe with large strongly hooked robust seta. Maxilla 2- or 3-articled, terminal article linear. Maxilliped palp short, articles with lateral margins convex, not fused; article 3 less than twice as long as wide; article 5 longer or shorter than article 4. Pereopod 1 dactylus subprehensile, subequal in length to dactylus, strongly recurved; inferior margin even, without spines. Uropodal rami subequal in length.

Intertidal–shelf (to 120 m). Indo-West Pacific, Tropical Western Atlantic; primarily on or around coral reefs. 9 species (Bruce and Sidabalok, 2011).

Tachaea Schioedte and Meinert, 1879

Diagnosis. Eyes normal in size, less than half head width. Pleotelson lateral margin without excision. Antennula article 1 anteriorly produced. Mandibular incisor truncate; molar process absent. Maxillula lateral lobe with large strongly hooked robust seta. Maxilla small short rounded lobe. Maxilliped palp short, articles with lateral and mesial margins straight; articles 2–5 variably fused; article 3 less than twice as long as wide; article 5 longer than article 4. Pereopod 1 dactylus subprehensile, subequal in length to dactylus, strongly recurved; inferior margin even, without spines. Uropodal exopod of adult male longer than endopod.

Primarily freshwater (3 estuarine species). Temperate Northern Pacific, Western and Central Indo-Pacific (India, SE Asia, East Asia, tropical Australia); micropredator of shrimps. 8 species (Vigneshwaran et al., 2021).

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Cymothoidae Leach, 1814

Figures 5.23–5.30

Cymothoidae are one of the largest families of aquatic Isopoda with 47 genera holding 394 accepted species names (including *species inquirenda* and *nomina dubia*), of which 38 genera and about 350 species are marine or estuarine (Boyko et al., 2026, at 31 Dec 2025). Cymothoids are all obligate and exclusively fish parasites, occupying four sites of attachment on the body of their

host, namely: externally or "scale attaching"; buccal or mouth attaching ("tongue replacement" cymothoids of Brusca and Gilligan, 1983); gill or opercular cavity attaching; and flesh burrowing (see Smit et al., 2014: fig. 2). Attachment site and host taxon is reflected in the body shape of cymothoid genera and species, and historically body shape and attachment site also influenced the interpretation of phylogenetic relationships between of genera (e.g. Brusca, 1981), although it had become apparent by the 1990s that position of attachment did not reflect phylogeny (Bruce, 1990; Smit et al., 2014). Most recently, molecular analyses have strongly and consistently demonstrated that body shape and attachment site are independent of phylogeny with, for example, the generally similar-looking and tongue-attaching genera *Ceratothoa* Dana, 1852 and *Cymothoa* Fabricius, 1873 consistently being basally separated (e.g. Fujita et al., 2023; Hata et al., 2017; Martin et al., 2024).

The family primarily occurs in marine waters and to a far lesser degree in estuaries or euryhaline environments. It is only in South America that there is a diverse freshwater cymothoid fauna composed of ten endemic genera and 33 species (Thatcher, 1991, 1993a, 1993b). Marine cymothoids occur from cool temperate waters to tropical waters worldwide, with highest diversity within the tropics, and are entirely absent from polar waters. The family is strongly depth limited, being largely confined to the continental shelf, with fewer than ten species recorded from a depth greater than 500 m (Smit et al., 2014). In common with many taxa, the large species from commercially fished hosts were historically described first; at present, little is known about those species that use small tropical and coral reef fishes as hosts. The family is dominated by seven large (with more than 20 species) marine genera: *Anilocra* Leach, 1818, *Ceratothoa*, *Cymothoa*, *Elthusa* Schioedte and Meinert, 1884, *Mothocya* Costa *in* Hope, 1851, *Nerocila* Leach, 1818 and *Renocila* Miers, 1880, together comprising 66% of all marine cymothoid species.

The Cymothoidae is one of the earliest described families of the Isopoda. The family concept was framed in a global series of comprehensive monographs by Schioedte and Meinert (1881, 1883, 1884), which clearly established the family as obligate parasites of fishes, and the unity of the family has remained. Subsequently, there were few further global revisions, but several regional revisions of significance were published, notably by Hale (1926, 1940) on Australian cymothoids. Trilles (1971–2014) published extensively on the taxonomy of many taxa, accompanied by comprehensive synonymies and literature citations; most notably his *Prodromus* (Trilles, 1994) is a highly useful resource for all known genera and species to that date. Brusca (1981) revised the Cymothoidae of the tropical eastern Pacific. Contemporaneously, Williams and Williams began their ongoing revisions of Caribbean and Japanese isopods (Williams and Bunkley-Williams publishing between 1978 and 2000), while Bruce (1987–1990) revised the Australian externally attaching and gill attaching genera. In the twenty-first century there have been significant regional contributions on the cymothoids of South Africa (Hadfield, with Smit and Bruce, 2010–2021), Australia (Martin et al., 2013–2016), and India (Aneesh and co-authors, 2013–2025). Smit et al. (2014) gave a more detailed review of the history of discovery in the Cymothoidae.

Diagnosis (of adult female). Fish parasites. Body dorsum weakly to strongly vaulted. Pleon (pleonites 1–5 without pleotelson) with 5 unfused somites. Eyes widely separated, lateral, often with indistinct ommatidia, sometimes small or absent. Antennula and antenna not differentiated into peduncle and flagellum. Mouthparts forming a buccal cone; mandibular incisor narrow, usually unidentate; lacinia mobilis and spine row absent; molar process absent or represented by small flat lobe. Maxillula lateral endite with 3–5 terminal flat robust setae. Maxilla with 1 subapical endite; both lobes usually with 1–3 recurved ("hooked") robust setae. Maxilliped without endite; palp of 2 articles, article 2 or 3 with apical recurved robust setae. Pereopods 1–7 with prehensile dactyli. Pleopods without plumose marginal setae.

Implicit generic attributes. Pereonite 1 anterior margin not incised. Pleonites without sublateral gaps. Coxae 5–7 not strongly produced ventrally. Pleonites not strongly produced ventrally. Pleonites 1 and 2 ventrolateral margins not produced. Pleonites 3–5 or 4 and 5 more than half width (c. 0.7) of pereon. Pleotelson lateral margins symmetrical. Antennae both slender. Antennula with more than 5 articles; article 3 not anteriorly lobed. Pereopod 1 propodus without robust setae.

In the diagnoses below the size of the eye is given as "small" or "large" defined by whether it is less than or more than 40% of the head width.

Practical key to marine genera of Cymothoidae

This key applies only to ovigerous adult female cymothoids, those that have oostegites. Males cannot be determined using this key. Cymothoid genera can, fairly consistently, be grouped into four modes of attachment to the fish host: externally attaching; gill attaching; buccal attaching (mostly on the tongue, but also the roof or side of the mouth); and flesh burrowing. A few genera have species that attach to both the mouth and gills. One such is *Catoessa*, which therefore appears twice in the key. One species of *Nerocila* has been recorded from the host gills; it too appears twice in the key.

The key must be used with some cautionary provisos. One is that cymothoid species are truly variable in many aspects of their morphology, and within the large genera one or more species may not show all the genus characters. Identifications should therefore be made on the overall balance of characters. Secondly, any generic identification should be compared to the most recent detailed generic description. Thirdly, new genera of Cymothoidae are still being discovered and revealed through revisions, with four genera established since 2019 (*Bambalocra*, *Brucethoa*, *Gibbothoa*, *Glyptothoa* and *Sandythoa*). Species therefore may be encountered that do not "key out" to any genus.

Host data are not given because cymothoid genera are not specific to particular fish taxa, although a few (such as *Mothocya*, which prefers species of Belonifomes as host) show a family-level preference. In contrast, host identity is critical in aiding species-level identification. Similarly, defined depth range is largely unknown for most genera because for the most part it has not been recorded.

Exclusions. Two monotypic genera are insufficiently characterised and not included in the key: *Lathreana* Schioedte and Meinert, 1881, *Riothra* Schioedte and Meinert, 1884. *Aegathoa* Dana, 1853 is a "form genus" based in immature specimens and is also excluded. The otherwise South American freshwater genus *Telotha* Schioedte and Meinert, 1884 includes *Telotha indica* Nierstrasz, 1915, reported from a marine location in Indonesia, but not adequately described and could equally belong to *Ichthyoxenos* Herklots, 1870 or other similar genus.

1. Attaching within buccal cavity (i.e. mouth), gill chamber or burrowing in flesh 2
– Attaching to host body external surfaces (above eye, external gill operculum, fins, caudal peduncle etc.) 4
2. Burrowing in host body tissues (fig. 5.25f) ..... *Ourozeuktes*
– Not burrowing in host body; attached within buccal cavity or gills 3
3. Attached to host gills 11
– Attached to buccal cavity, on tongue, roof or sides of mouth 28

Externally attaching genera

4. Head posterior margin trisinuate (figs 5.23e, f, 5.27c). Coxae 5–7 as long as or longer than respective pereonite (fig. 5.23f, g, 5.27h) (except *Nerocila lomatia* Bruce, 1987) 5
– Head posterior margin not or weakly trisinuate (figs 5.23a, b, 5.27a). Coxae 5–7 manifestly shorter than respective pereonite (fig. 5.23b, 5.27g, i) 8
5. Pleonites 1 and 2 ventrolateral margins produced (fig. 5.27d) ..... *Nerocila*
– Pleonites 1 and 2 ventrolateral margins not produced (fig. 5.27b) 6
6. Body dorsal surface strongly vaulted. Coxae 5–7 ventrally directed; pleonites strongly produced ventrally (fig. 5.23g) ..... *Plotor*
– Body dorsal surface weakly vaulted. Coxae 5–7 posteriorly directed; pleonites not strongly produced ventrally 7
7. Uropod rami long, extending well beyond posterior of pleotelson. Coxae conspicuous in dorsal view (fig. 5.27h) ..... *Amblycephalon*
– Uropod rami short, not extending beyond posterior of pleotelson. Coxae inconspicuous in dorsal view (fig.5.27i) ..... *Creniola*
8. Head without distinct rostrum, or rostrum not projecting between antennula bases (fig. 5.29c). Antennula broader than and as long as, or longer than antenna (fig. 5.29h). Posterolateral margins of pereonites 5–7 moderately to strongly produced (fig. 5.27g) ..... *Renocila*
– Rostrum folded under, projecting between antennula bases (fig. 5.29a). Antennula more slender than and shorter than antenna. Posterolateral margins of pereonites 6 and 7 produced (*Bambalocra*) or not produced (fig. 5.23a, c) 9
9. Coxae ventral in position, not or barely visible in dorsal view. Posterolateral margins of pereonites 6 and 7 posteriorly produced, rounded (fig. 5.23c). Pleopods 3–5 endopods with weak lobes; pleopods hardly visible in dorsal view (fig. 5.30l) ..... *Bambalocra*
– Coxae lateral in position, largely not visible in dorsal view (fig. 5.23a, b), posterolateral margins of pereonites 5–7 not produced (fig. 5.23b). Pleopod 5 only with prominent folded fleshy lobes; pleopods clearly visible in dorsal view (fig. 5.30k) 10
10. Mandible palp article 3 shorter than article 2 (fig. 5.30a). Antennula articles 4–8 short (fig. 5.27a). Pleonites 3–5 or 4 and 5 more than half width (c. 0.7) of pereon (fig. 5.23a). Maxilla with 2 short, hooked robust setae each on mesial and lateral lobe, mesial lobe partly fused to lateral (fig. 5.30b) ..... *Anilocra*
– Mandible palp article 3 longer than article 2 (fig. 5.30d). Antennula articles 4–8 elongate (fig. 5.27e). Pleonites 3–5 or 4 and 5 less than half width (c. 0.45) of pereon (fig. 5.27f). Maxilla with 2 large nodular robust setae each on mesial and lateral lobe, mesial lobe distinct (fig. 5.30c) ..... *Pleopodias*

Gill attaching

11. Pleonites 1 and 2 with ventrolateral processes (fig. 5.27d) ..... *Nerocila* (one species)

– Pleonites 1 and 2 without ventrally directed processes (fig. 5.24b, f) 12

12. Body strongly bilaterally distorted, asymmetrical; pereon or pleon may be hunched in lateral view (figs 5.23i, 5.24c) 13

– Body not distorted, bilaterally symmetrical or weakly asymmetrical; body not hunched in lateral view (figs 5.23h, 5.24a, e, g) 17

13. Pleon hunched in lateral view; body weakly twisted. (fig. 5.24j). Antennula with 4 articles (fig. 5.29i) ..... *Kuna*

– Pleon not hunched; body asymmetrical or circular in outline (fig. 5.24b, i). Antennula with more than 5 articles 14

14. Pereon not hunched in lateral view. Coxae greatly enlarged on one side (fig. 5.23j) ..... *Cterissa*

– Pereon hunched in lateral view. Coxae subequal on both sides or, if larger on one side, not conspicuous in dorsal view (figs 5.23i, 5.24c) 15

15. Body weakly asymmetric, near circular in outline; lateral margins of all pereonites not notably expanded (fig. 5.24i). ..... *Ryukyua*

– Body strongly asymmetric; lateral margins of some pereonites notably expanded on one side (figs 5.23i, 5.24c) 16

16. Lateral margin of pereonites 3–5 strongly expanded on one side (fig. 5.23i). Head without dorsally visible rostral point. Brood pouch not strongly protruding (fig. 5.24b) ..... *Agarna*

– Lateral margin of pereonites 4–7 strongly expanded on one side (fig. 5.24c). Head with minute dorsally visible rostral point. Brood pouch strongly protruding (fig. 5.24h) ..... *Gibbothoa*

17. Head with rostral point (may be ventrally directed) (fig. 5.28e) 18

– Head without rostral point, anterior margin variously narrowly rounded to subtruncate (fig. 5.28a, d) 22

18. Brood pouch extending strongly ventrally (fig. 5.24h) 19

– Brood pouch extending weakly ventrally (fig. 5.24b). 20

19. Pleopods not visible in dorsal view. All coxae visible dorsally. Pleon 1.0–1.2 times as wide as widest pereonite (fig. 5.24d) ..... *Glyptothoa*

– Pleopods visible in dorsal view. Coxae of pereonites 6 and 7 not visible in dorsal view. Pleon 0.9 times as wide as widest pereonite (fig. 5.23h) ..... *Brucethoa*

20. Body dorsum not or weakly vaulted. Short gaps between pleonites; pleonite 1 narrow, not laterally extended (figs 5.24k, 5.28g) ..... *Sandythoa*

– Body dorsum vaulted. No gaps between pleonites; pleonite 1 weakly to moderately laterally extended 21

21. Body ovate (fig. 5.24e). Pleonite 1 not markedly narrower than pleonite 2, partly laterally overlapped by pereonite 7 (fig. 5.24e). Pereopod ischium to carpus flattened, widest distally, dactylus short (fig. 5.30g) ..... *Ichthyoxenos*

– Body not strongly ovate. Pleonite 1 narrower than pleonite 2; pleon not immersed in pereon. Pereopod ischium to carpus not widest distally, dactylus long ..... *Idusa*

22. Head posterior margin trilobed (fig. 5.28c). Pleonites 1–5 progressively narrower (fig. 5.28h). Pleopod peduncles with lamellar or fleshy lateral lobe; rami with fleshy lobes (fig. 5.30o, p) 23

– Head posterior margin not trilobed. Pleonites 1–5 not progressively narrower; pleopod peduncles and rami without lateral, fleshy lobes 24

23. Head posterior margin strongly trilobed (fig. 5.28c). Pleonites 1–3 lateral margins bilobed (fig. 5.28i). Pleopodal peduncles with branchiae (fig. 5.30p) ..... *Livoneca*

– Head posterior margin weakly trilobed. Pleonites 1–3 lateral margins not bilobed. Pleopodal peduncle without branchiae ..... *Norileca*

24. Head laterally enclosed by pereonite 1 anterolateral margins. Pereonites 2 and 3 coxae inflated, much larger than remaining coxae (fig. 5.28b) ..... *Joryma*

– Head and coxae not as above 25

25. Pereopods with many fine robust setae. Pereopods 4–6 merus inferior margin with distinct blade (fig. 5.30h) ..... *Pseudirona*

– Pereopods not setose. Pereopods 4–6 merus without distinct blade 26

26. Small gap between pleonites (fig. 26i). Body bilaterally symmetrical; dorsum vaulted. All coxae small. Head not deeply immersed in pereonite 1. Pleon rotationally twisted with narrow pleonite 1 (fig. 5.23d) ..... *Catoessa*

– No gap between pleonites. Body weakly to moderately asymmetrical; dorsum not or weakly vaulted. Posterior coxae often large. Head immersed in pereonite 1. Pleon not rotationally twisted, pleonite 1 variable in width (fig. 5.24a, b, g) 27

27. Uropods short, not reaching posterior of pleotelson (fig. 5.28f). Pleon greater than 0.75 maximum width of pereon (fig. 5.28f). Antennula slender, shorter than antenna (fig. 5.29f) ..... *Elthusa*

– Uropods usually longer, reaching or extending posterior to pleotelson; pleon half as wide to as wide as pereon (fig. 5.28j). Antennula thicker and longer than antenna (fig. 5.29g) ..... *Mothocya*

Buccal attaching

28. Head posterior margin trisinuate (fig. 5.26h). Pereon and pleon strongly colinear (fig. 5.25d). Brood pouch with posterior pocket; oostegites of coxae 6 forming most of marsupium (fig. 5.30j) ..... *Smenispa*

– Head posterior margin concave or straight (fig. 5.26a, d). Pereon and pleon weakly colinear (fig. 5.25a, b). Brood pouch without posterior pockets; oostegites arising from coxae 1–6, all forming marsupium (fig. 5.30i) 29

29. Pleotelson posterior margin subtriangular. Body widest at pereonite 6 (figs 5.25c, 5.26k) ..... *Olencira*

– Pleotelson posterior margin rounded or subtruncate. Body usually widest at pereonite 4 or 5 (fig. 5.25a, b, d) 30

30. Antennula longer than antenna (fig. 5.29d). Pereopod 5–7 basis without well-developed carina (fig. 5.30e). Pleon and pleotelson axially twisted ("rotated") against plane of pereon (fig. 5.26i) ..... *Catoessa*

– Antennula shorter than antenna (fig. 5.29b, e). Pereopods 5–7 basis with well-developed carina (fig. 5.30f). Pleon and pleotelson not axially twisted against pereon 31

31. Antennae thick and expanded. Antennula bases contiguous (fig. 5.29e). Head not or weakly immersed in pereonite 1 (fig. 5.26a) 32

– Antennae slender. Antennula bases separated (fig. 5.29b). Head deeply immersed in pereonite 1 (fig. 5.26c, d) 34

32. Rostrum dorsally not projecting between antennae (fig. 5.26e) ..... *Emetha*

– Rostrum dorsally projecting between antennae (fig. 5.26a, f) 33

33. Pereonite 1 anterolateral margins projecting forward, without slight sublateral incision, anteromesial margin concave (fig. 5.26a) ..... *Ceratothoa*

– Pereonite 1 anterolateral margins projecting laterally, with slight sublateral incision, anteromesial margin straight or concave (fig. 5.26f) ..... *Glossobius*

34. Body weakly vaulted. Anterior margin of head with distinct rostrum. Anterolateral margins of pereonite 1 extending anteriorly beyond eyes, with prominent lobes (fig. 5.26g) ..... *Lobothorax*

– Body strongly vaulted. Anterior margin of head without distinct rostrum. Anterolateral margins of pereonite 1 minute or reaching anterior margin of head, without prominent lobes (fig. 5.26b, c, d) 35

35. Head quadrate. Pleonites subequally wide (fig. 5.25e) ..... *Tetragonocephalon*

– Head not quadrate (fig. 5.26c), anterior margin narrow to moderately broad (fig. 5.26d). Pleonite 1 or 1–3 narrower than remaining pleonites (fig. 5.26j) 36

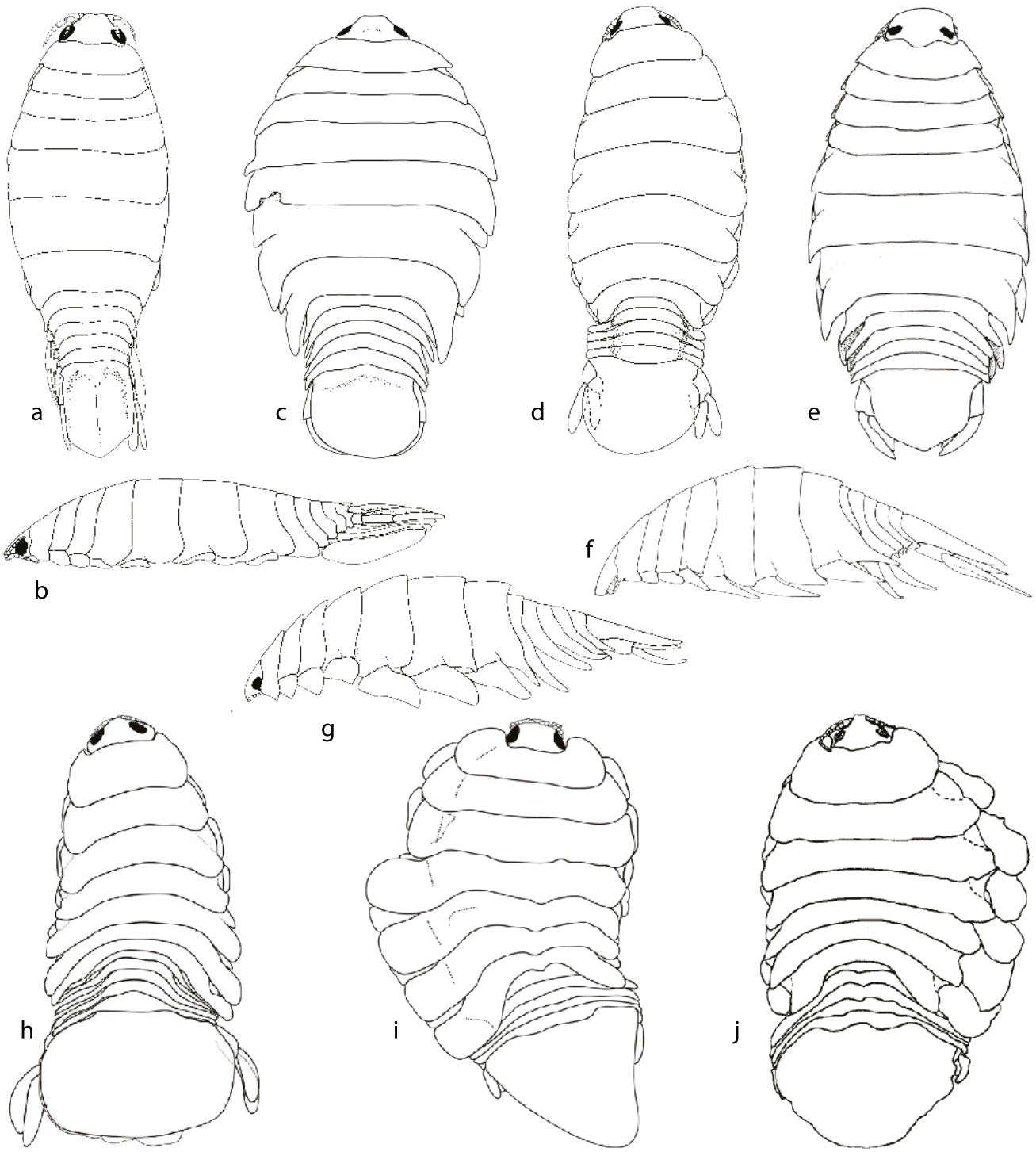


Figure 5.23. Cymothoidae. Externally attaching genera, habitus dorsal and lateral: a, *Anilocra nemipteri* Bruce, 1987a; b, *Anilocra nemipteri* Bruce, 1987a; c, *Bambalocra intwala* Bruce, Welicky, Hadfield and Smit, 2019; d, *Catoessa ambassae* Bruce, 1990; e, *Nerocila orbignyi* (Guérin-Méneville, 1832); f, *Nerocila orbignyi* (Guérin-Méneville, 1832); g, *Plotor indus* Schioedte and Meinert, 1881. Gill-attaching genera, habitus: h, *Brucethoa bharata* Aneesh, Hadfield, Smit, and Biju Kumar, 2020; i, *Agarna cumulus* (Haller, 1880); j, *Cterissa sakaii* Bunkley-Williams and Williams, 1986.

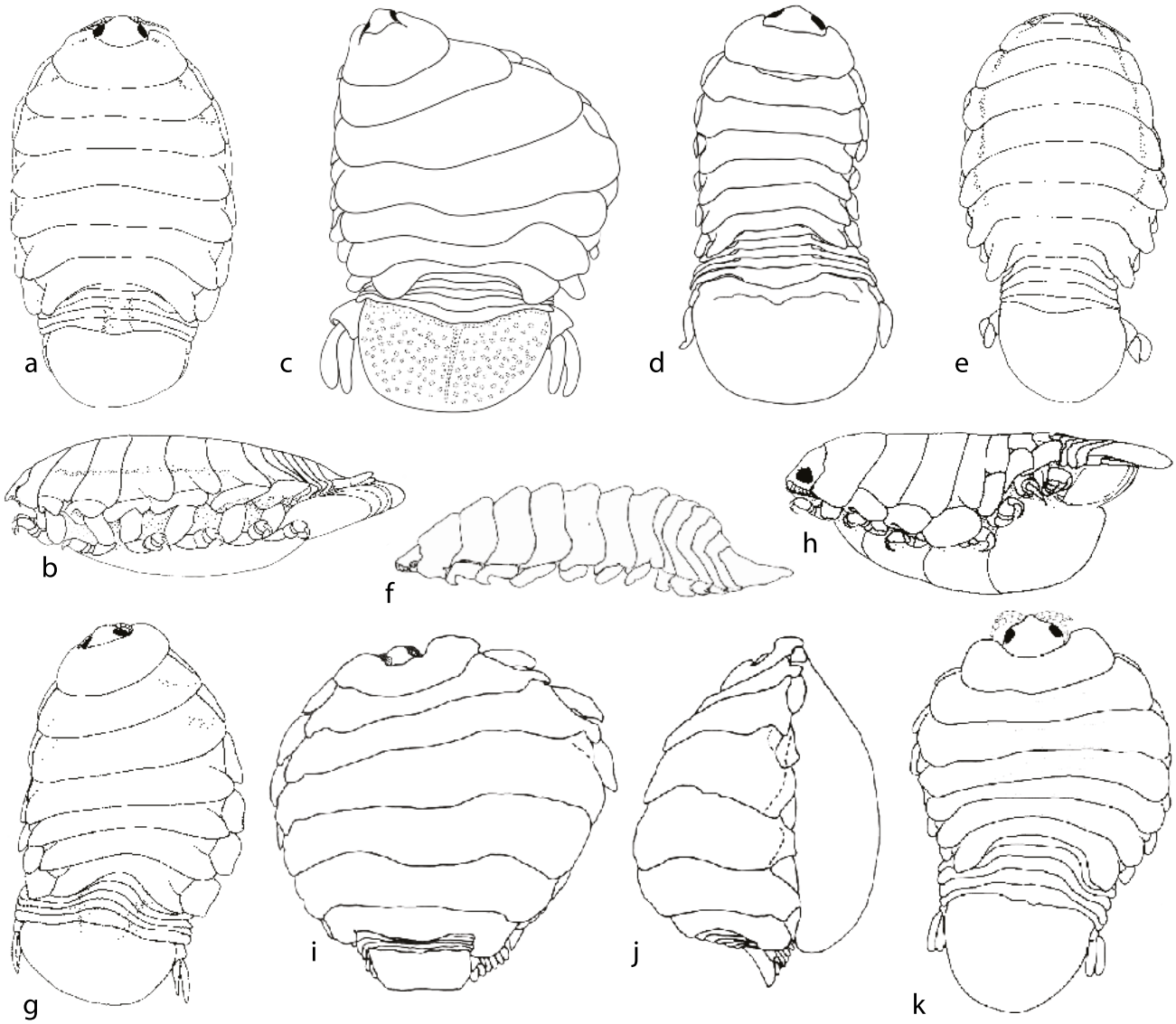


Figure 5.24. Cymothoidae. Gill-attaching genera, habitus dorsal and lateral (continued): a, *Elthusa raynaudii* (Milne Edwards, 1840); b, *Elthusa sigani* Bruce, 1990; c, *Gibbothoa malayi* Aneesh, Hadfield, Smit, and Biju Kumar, in press; d, *Glyptothoa sagara* Helna, Aneesh, Biju Kumar and Ohtsuka, 2023; e, *Ichthyoxenos minabensis* (Shiino, 1951); f, *Kuna insularis* Williams and Williams, 1985; g, *Mothocya melanosticta* (Schioedte and Meinert, 1881); h, *Mothocya melanosticta* (Schioedte and Meinert, 1881); i, *Ryukyua globosa* Williams and Williams, 1994; j, *Ryukyua globosa* Williams and Williams, 1994; k, *Sandythoa tiranga* Aneesh, Bruce, Helna and Biju Kumar, 2024.

36. Anterior margin of head subacute (fig. 5.26b). Body ovate, less than 1.5 times as long as greatest width. Pleopods 3–5 without fleshy folds (fig. 5.30n) ..... *Cinusa*

– Anterior margin of head broadly subtruncate. Body subparallel or weakly ovate, more than 1.5 times as long as greatest width (fig. 5.26d, j). Pleopods 3–5 with fleshy folds (fig. 5.30m) ..... *Cymothoa*

Agarna Schioedte and Meinert, 1884

Diagnosis. Attached to host gills. Body strongly asymmetrical or distorted; lateral margins strongly hunched on one side; dorsum strongly vaulted. Rostrum distinct, rounded, ventrally directed. Head partially immersed in pereonite 1, posterior margin straight, lateral margin convex. Eye small. Coxae unequal on both sides of body; coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 as long as pereonite, strongly ventrally directed, posteriorly narrowly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin rounded and appearing to encompass

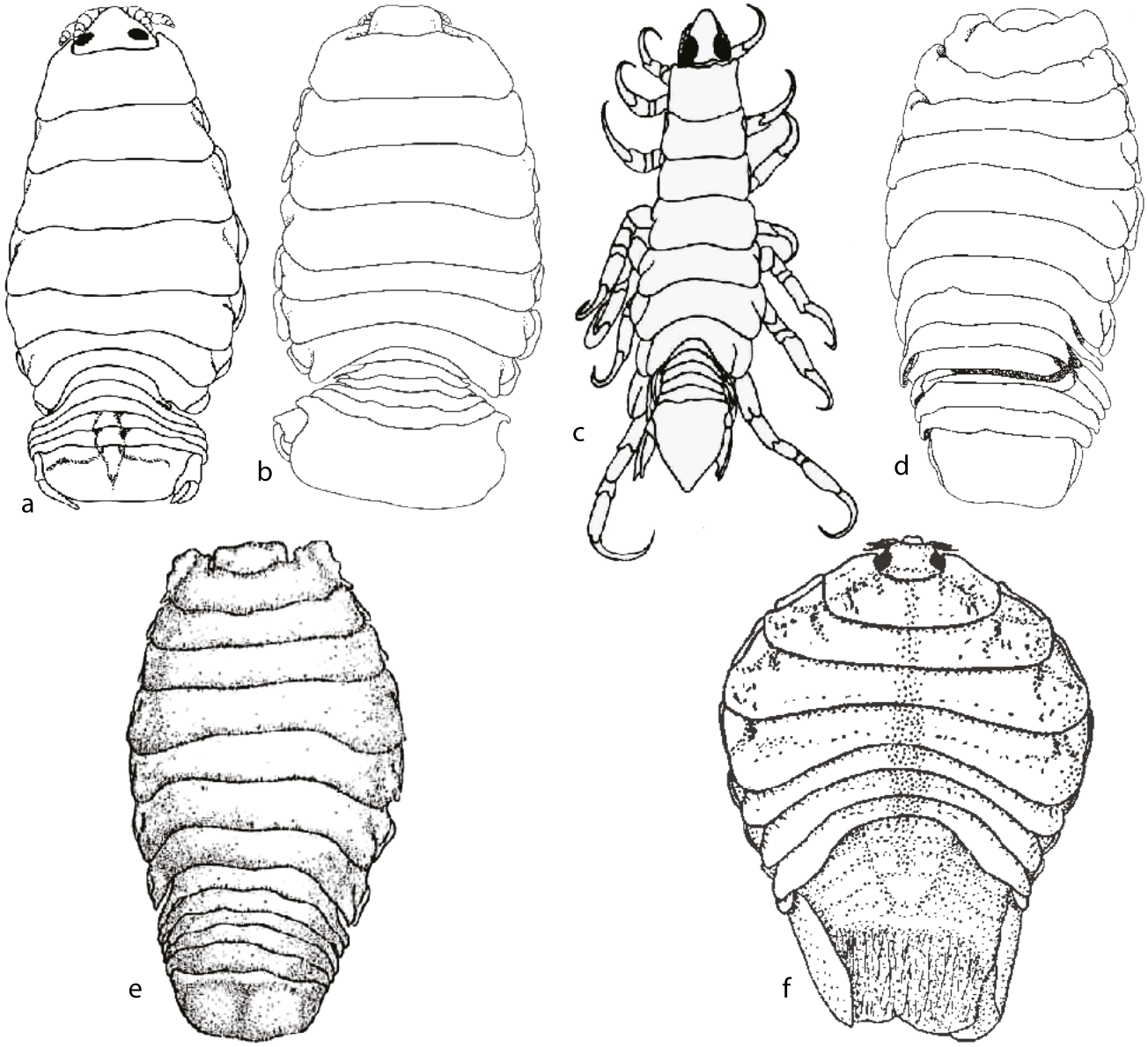


Figure 5.25. Cymothoidae. Buccal-attaching genera, habitus: a, *Ceratothoa banksii* (Leach, 1818); b, *Cymothoa eremita* (Brünnich, 1783); c, *Olencira praegustator* (La Trobe, 1802); d, *Smenispa irregularis* (Bleeker, 1857); e, *Tetragonocephalon lutianus* Avdeev, 1975; f, *Ourozeuktes bopyroides* (Lesueur, 1814).

head (partly encompassing). Pereonites 1–4 of hunched side laterally much expanded from pereopodal bases; posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon about as wide as pereon. Pleonite1 partially visible, laterally concealed by pereonite 7; as wide as other pleonites. Pleotelson lateral margins asymmetrical; narrower than pereonite 7 (slightly). Antennula longer than antenna; narrowly separated; articles 1–4 short; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped without oostegite lobe. Pereopods 5–7 basis superior margin with carina, inferior margin without carina. Brood pouch ventrally strongly protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal. Indo-West Pacific. 4 species (Aneesh et al., 2026).

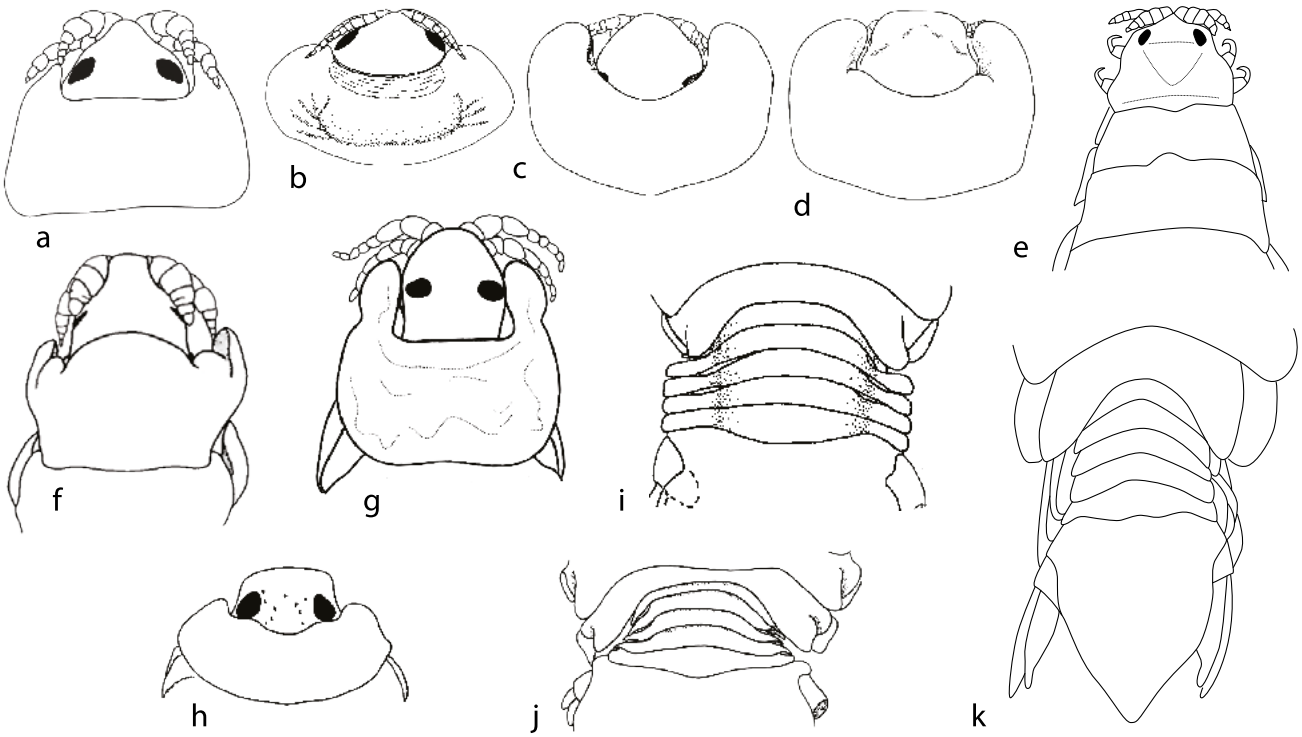


Figure 5.26. Cymothoidae. Buccal-attaching genera, head and pleon: a, *Ceratothoa imbricata* (Fabricius, 1775), head and rostrum; b, *Cinusa tetrodontis* Schioedte and Meinert, 1884, head dorsal; c, *Cymothoa carangi* Avdeev, 1979; d, *Cymothoa eremita* (Brünnich, 1783); e, *Emetha audouini* Schioedte and Meinert 1883, anterior dorsal; f, *Glossobius impressus* (Say, 1818), head and pereonite 1; g, *Lobothorax nicosmiti* Aneesh, Bruce, Biju Kumar, Bincy and Sreenath, 2021, anterior dorsal; h, *Smenispa irregularis* (Bleeker, 1857), head; i, *Catoessa ambassae* Bruce, 1990, pereonite 7, pleon; j, *Cymothoa eremita* (Brünnich, 1783), pereonite 7, pleon; k, *Olencira praegustator* (La Trobe, 1802), pereonite 7, pleon, pleotelson.

Anilocra Leach, 1818

Diagnosis. Attached to host external body surfaces. Body symmetrical; lateral margins subparallel, or ovate; dorsum strongly vaulted. Rostrum distinct, usually ounded or truncate, ventrally and posteriorly folded, projecting between antennulae bases. Head not immersed in pereonite 1, posterior margin straight or convex, lateral margin convex. Eye large. Coxae 2 and 3 similar to other coxae; coxae 2–4 shorter than respective pereonite (coxae 2 and 3 shorter than 4); coxae 5–7 shorter than pereonite, not strongly ventrally directed posteriorly, posteriorly narrowly rounded, partially visible in dorsal view (barely for coxae 6 and 7). Pereonite 1 anterolateral margin not produced, flat. Posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 not extending laterally past pleonite 1. Pleon narrower than pereon. Pleonite 1 visible, wider than other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter than antenna, bases narrowly separated: article 3 anterodistal margins produced or not; articles 4–8 short: terminal article short, nearly reaching or reaching head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe partially fused, with 2 short, hooked robust setae each on mesial and lateral lobe. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis superior margin with carina, inferior margin without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopod 5 only with prominent fleshy ridges; peduncles without lateral lamellar lobes. Uropodal rami long, extending beyond pleotelson posterior margin.

Estuarine, subtidal, shelf (to 550 m). All oceans, except cold and polar waters. 60 species (Bruce, 1987a; Uyeno and Tosuji, 2023; Welicky and Smit, 2019).

Amblycephalon Pillai, 1954

Diagnosis. Attached to host external body surfaces. Body symmetrical; lateral margins subparallel; dorsum not vaulted. Head without rostrum, anterior margin broadly projecting, not immersed in pereonite 1, posterior margin weakly trisinuate, lateral margin straight. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 longer than pereonite, not strongly ventrally directed posteriorly, posteriorly narrowly rounded, conspicuous in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Posterolateral margins of pereonites 6 and 7 weakly produced; pereonite 7 not extending laterally past pleonite 1. Pleon narrower than pereon. Pleonite 1 visible, as wide as other pleonites. Pleotelson narrower than pereonite 7. Antennula broader than and longer than antenna; bases widely separated; articles 1–4 short; terminal article short, nearly reaching or

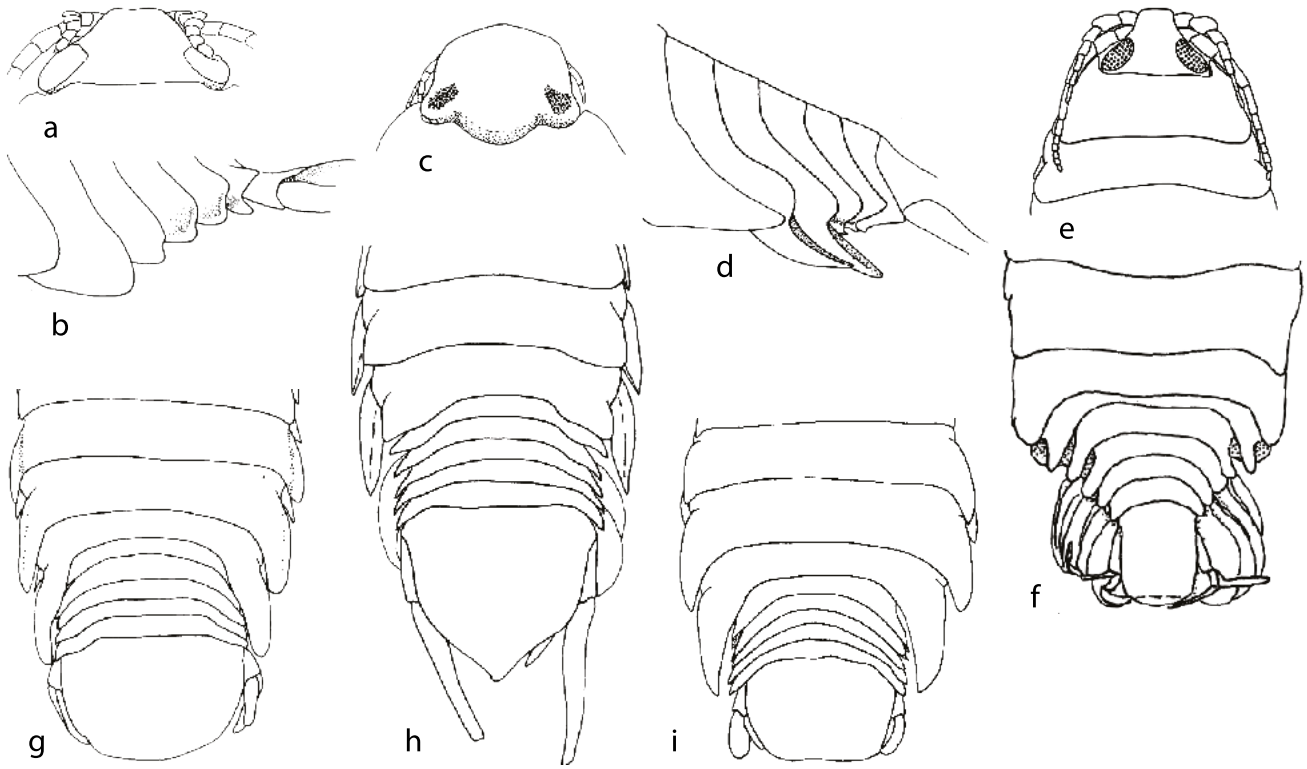


Figure 5.27. Cymothoidae. Externally attaching genera, head and pleon: a, *Anilocra nemipteri* Bruce, 1987, head; b, *Anilocra nemipteri* Bruce, 1987; pleon lateral; c, *Nerocila orbignyi* (Guérin-Méneville, 1832), head dorsal; d, *Nerocila orbignyi* (Guérin-Méneville, 1832), pleon lateral; e, *Pleopodias elongatus* Richardson, 1910, head, pereonites 1, 2, antennae, dorsal; f, *Pleopodias* sp., pereonites, 6, 7, pleon, pleotelson, dorsal; g, *Renocila ovata* Miers, 1880, pereonites 5–7, pleon, pleotelson, dorsal; h, *Amblycephalon schadleri* (Nierstrasz, 1915), pereonites 5–7, pleon, pleotelson, dorsal; i, *Creniola laticauda* (Schioedte and Meinert, 1881), pereonites 5–7, pleon, pleotelson, dorsal.

reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp articles 2 and 3 subequal. Pereopods 5–7 basis margins without carina. Brood pouch not ventrally protruding. Uropodal rami long, extending beyond or well beyond pleotelson posterior margin.

Subtidal. Western Indo-Pacific. 2 species. The genus is in need of redescription (Bruce, 1987c; Pillai, 1966).

Bambalocra Bruce, Welicky, Hadfield and Smit, 2019

Diagnosis. Attached to host external body surfaces. Body symmetrical; lateral margins ovate; dorsum weakly vaulted. Rostrum distinct, truncate, ventrally and posteriorly folded, projecting between antennulae bases. Head not immersed in pereonite 1, posterior margin concave, lateral margin convex. Eye small. Coxae 2 and 3 smaller than other coxae; coxae 2–4 shorter than respective pereonite; coxae 5–7 as long as pereonite, not strongly ventrally directed posteriorly, posteriorly prominent and acute, all coxae ventral positioned, not dorsally visible. Pereonite 1 anterolateral margin not produced, flat. Posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 visible, wider than other pleonites; ventrolateral margins of pleonites 1 and 2 not produced. Pleotelson narrower than pereonite 7. Antennula shorter than antenna; bases narrowly separated; articles 4–8 short; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped with 2 oostegite lobes. Pereopods 5–7 basis margins without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods 3–5 with weak fleshy ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal. Temperate Southern Africa (only from northern Indian Ocean coast of South Africa). 1 species (Bruce et al., 2019).

Brucethoa Aneesh, Hadfield, Smit and Kumar, 2020

Diagnosis. Attached to host gills. Body weakly asymmetrical; lateral margins subparallel (widening posteriorly); dorsum weakly vaulted. Head with distinct rostrum, triangular, ventrally and posteriorly folded, projecting between antennulae bases, not immersed in pereonite 1, posterior margin straight, lateral

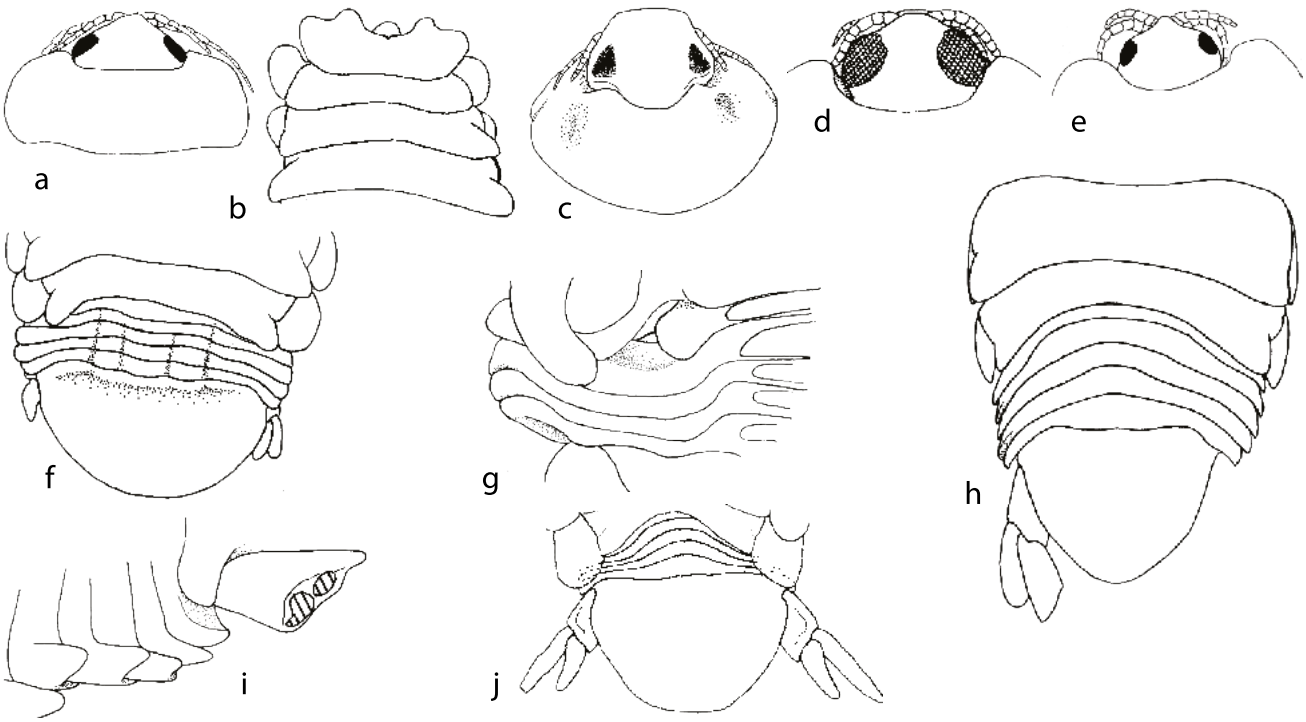


Figure 5.28. Cymothoidae. Gill-attaching genera, head and pleon: a, *Ichthyoxenos minabensis* Shiino, 1951, head, pereonite 1; b, *Joryma sawayah* Bowman and Tareen, 1983, head, anterior pereonites; c, *Livoneca redmanii* Leach, 1818, head, pereonite 1; d, *Mothocya parvostis* Bruce, 1986, head; e, *Sandythoa tiranga* Aneesh, Bruce, Helna and Biju Kumar, 2024, head; f, *Elthusa raynaudii* (Milne Edwards, 1840), pereonite 7, pleon, pleotelson, uropods, dorsal; g, *Elthusa turgidula* (Hale, 1926), pleonites ventral; h, *Livoneca redmanii* Leach, 1818, pereonites 6, 7, pleon, pleotelson, uropod, dorsal; i, *Livoneca redmanii* Leach, 1818, pleonites ventrolateral; j, *Mothocya halei* Bruce, 1986, pereonite 7, pleon, pleotelson, uropod, dorsal.

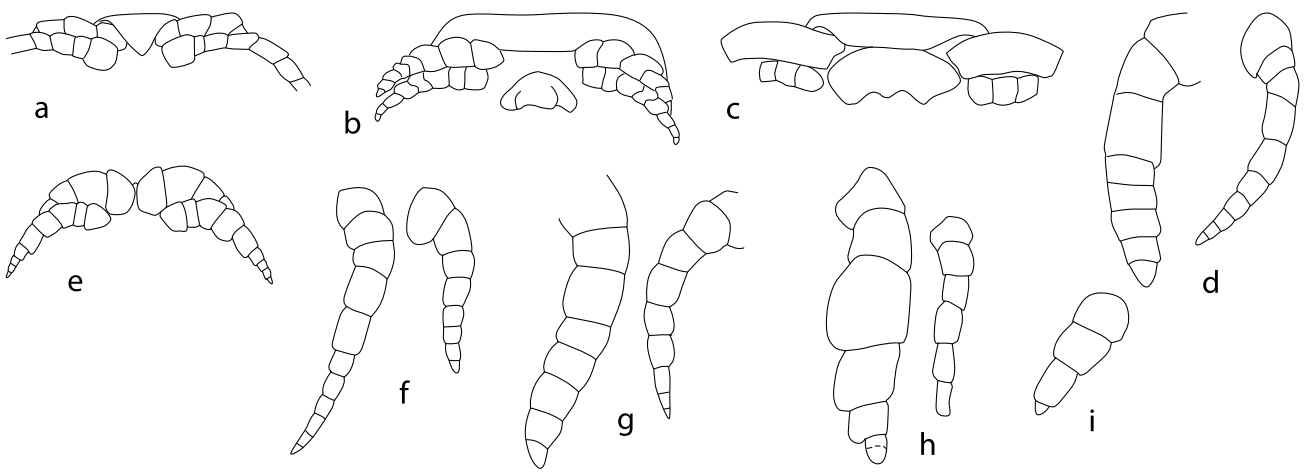


Figure 5.29. Cymothoidae. Frons and antennae: a, *Anilocra nemipteri* Bruce, 1987, frons; b, *Cymothoa eremita* (Brünnich, 1783), antennae ventral; c, *Renocila ovata* Miers, 1880, head ventral; d, *Catoessa ambassae* Bruce, 1990, antenna, antennula; e, *Ceratothoa nipaluna* Bruce, Smit and Hadfield, 2025, antennulae, antennae; f, *Elthusa raynaudii* Milne Edwards, 1840), antenna, antennula; g, *Mothocya colettei* Bruce, 1986, antenna, antennula; h, *Renocila ovata*, Miers, 1880, antenna, antennula; i, *Kuna insularis* (Williams and Williams, 1985), antennula.

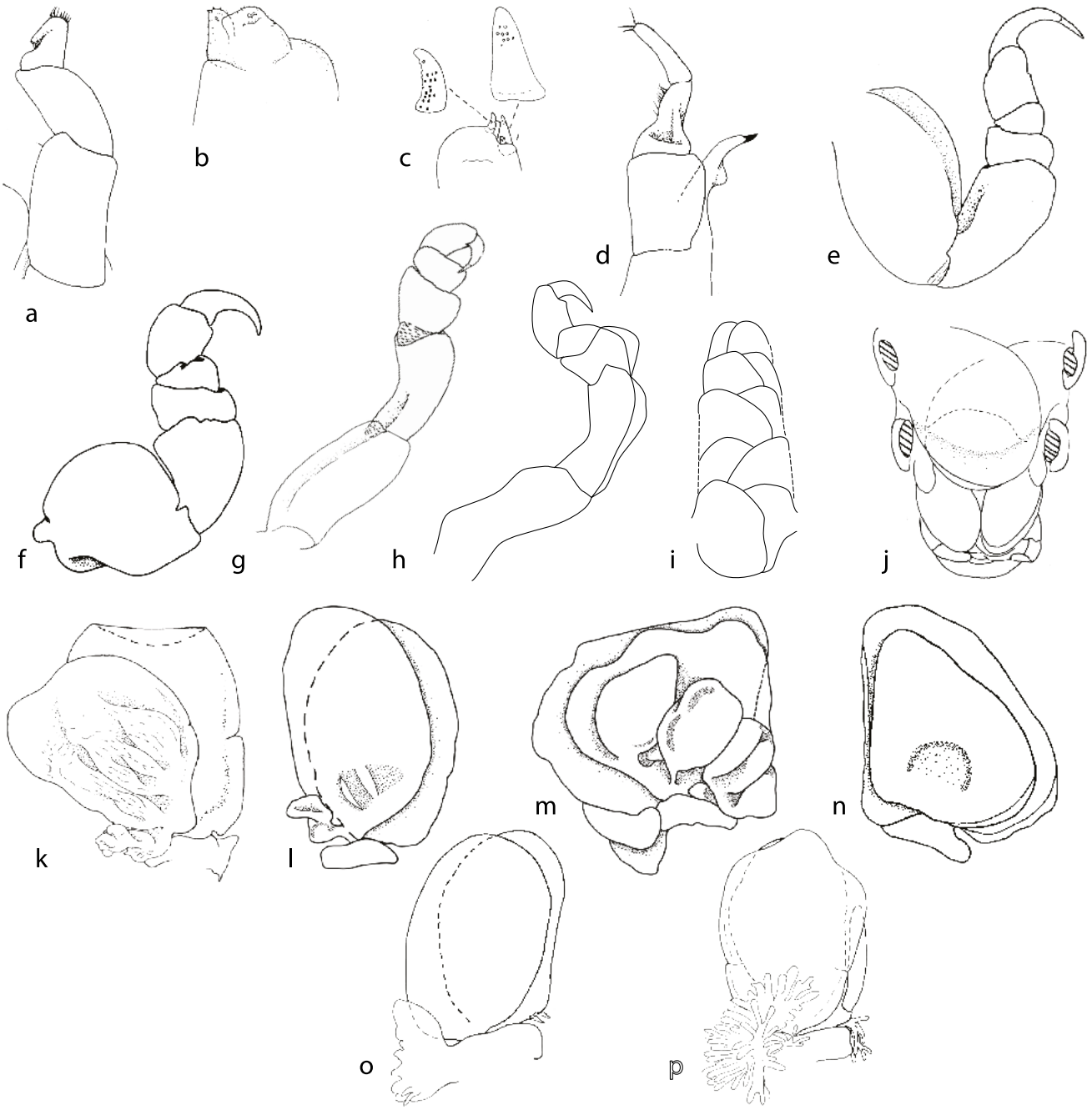


Figure 5.30. Cymothoidae. Appendages and brood pouch: a, *Anilocra nemipteri* Bruce, 1987, mandibular palp; b, *Anilocra nemipteri* Bruce, 1987, maxilla apex; c, *Pleopodias* sp., maxilla apex; d, *Pleopodias* sp., mandibular palp; e, *Catoessa ambassae* Bruce, 1990; pereopod 7; f, *Ceratothoa imbricata* (Fabricius, 1775), pereopod 7; g, *Ichthyoxenos minabensis* Shiino, 1951, pereopod 7; h, *Pseudirona laeopsi* Pillai, 1964, pereopod 7; i, *Ceratothoa banksii* (Leach, 1818), brood pouch; j, *Smenispa irregularis* (Bleeker, 1857), posterior pocket. Pleopods: k, *Anilocra nemipteri* Bruce, 1987, pleopod 5; l, *Bambalocra intwala* Bruce, Welicky, Hadfield and Smit, 2019, pleopod 4; m, *Cymothoa rhina* Schioedte and Meinert, 1884, pleopod 5, dorsal; n, *Cinusa tetrodontis* Schioedte and Meinert, 1884, pleopod 5 dorsal; o, *Livoneca redmanii* Leach, 1818, pleopod 1; p, *Livoneca redmanii* Leach, 1818, pleopod 2, dorsal/posterior.

margin convex. Eye large. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 as long as pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin anteriorly acute. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 moderately to strongly produced, posteriorly rounded; pereonite 7 extending past pleonite 1. Pleon as wide as pereon; pleonites with sublateral gaps. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson wider than pereonite 7. Antennula shorter than antenna; bases narrowly separated; articles 1–4 short; terminal article long, extending beyond head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis margins without carina. Brood pouch ventrally strongly protruding. Pleopods readily visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami extending slightly beyond pleotelson posterior margin.

Slope (300–600 m). Western Indo-Pacific (India). 1 species (Aneesh et al., 2020).

Catoessa Schioedte and Meinert, 1884

Diagnosis. Attached to host gills or buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins ovate; dorsum strongly vaulted. Rostrum truncate, not ventrally and posteriorly folded. Head not immersed in pereonite 1, posterior margin straight, lateral margin concave. Eye large or small. Coxae 2 and 3 similar to other coxae; coxae 2–4 shorter than or as long as respective pereonite; coxae 5–7 shorter than pereonite, posteriorly narrowly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes convex and progressively increasing; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon; rotationally twisted; pleonites with sublateral gaps. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson as wide as or wider than pereonite 7. Antennula subequal to antenna; bases widely separated; articles 1–3 long; terminal article long, extending beyond head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped without oostegite lobe. Pereopods 5–7 basis superior margin with carina, inferior margin without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami not or extending slightly beyond pleotelson posterior margin.

Subtidal. Indo-West Pacific. 4 species (Bowman and Tareen, 1983; Bruce, 1990; Trilles et al., 2012).

Cinusa Schioedte and Meinert, 1884

Diagnosis. Attached to host buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins ovate; dorsum strongly vaulted. Rostrum indistinct, triangular, not posteriorly folded. Head not immersed in pereonite 1, posterior margin concave, lateral margin concave. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, posteriorly narrowly rounded, conspicuous in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes deeply convex and progressively increasing in size; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson as wide as pereonite 7. Antennula broader than and as long as or longer than antenna; bases narrowly separated; articles 1–3 long; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe partially fused. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis superior margin with large blade-like carina, inferior margin with weak carina. Brood pouch ventrally strongly protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal, shelf. Temperate Northern W Pacific; Temperate Southern Africa (South Africa, Japan); from puffer fish. 2 species (Hadfield et al., 2010; Nagasawa, 2021).

Ceratothoa Dana, 1852

Diagnosis. Attached to host buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins subparallel or ovate; dorsum strongly vaulted. Rostrum distinct, triangular, not ventrally and posteriorly folded. Head not or partially immersed in pereonite 1, posterior margin straight, lateral margin straight or concave. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin produced or anteriorly acute or rounded and appearing to encompass head or lobed. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon as wide as or narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson narrower than or as wide as pereonite 7. Antennae thick and expanded. Antennula broader than and as long as, longer or shorter than antenna; bases in contact; articles 1–3 long; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe partially fused. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis superior margin with large blade-like carina, inferior margin without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges, with weak unthickened ridge; peduncles without lateral lamellar lobes. Uropodal rami extending slightly beyond pleotelson posterior margin.

Estuarine, subtidal, shelf (shallow to about 100 m). All oceans except polar seas. 27 species (Hadfield et al., 2014, 2016; Martin et al., 2015b).

Creniola Bruce, 1987

Diagnosis. Attached to host external body surfaces. Body symmetrical or weakly asymmetrical; lateral margins ovate; dorsum weakly vaulted. Head without rostrum, anterior margin truncate, not ventrally and posteriorly folded, not immersed in pereonite 1, posterior margin trisinuate, lateral margin concave. Eye small, partially visible. Coxae 2 and 3 smaller than other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, strongly ventrally directed, posteriorly prominent and acute, not visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 moderately to strongly produced, posteriorly rounded; pereonite 7 extending past pleonite 1. Pleon almost as wide as or narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7, or visible, as wide as other pleonites; 1 and 2 ventrolateral margin not produced. Pleotelson narrower than pereonite 7. Antennula shorter than antenna; bases widely separated; articles 4–8 short; terminal article long, extending beyond head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 longer than article 2. Maxilla mesial lobe partially fused. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis margins without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods 3–5 with weak fleshy ridges; peduncles with lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal, shelf (shallow to 133 m). Central and Eastern Indo-Pacific, Temperate Australasia. 3 species (Bruce, 1987c).

Cterissa Schioedte and Meinert, 1884

Diagnosis. Attached to host gills. Body twisted to one side; lateral margins ovate or somewhat asymmetric; dorsum not vaulted. Rostrum distinct; triangular or truncate, ventrally and posteriorly folded, projecting between antennulae bases. Head immersed in pereonite 1, posterior margin straight, lateral margin convex. Eye small. Coxae unequal on both sides of body; coxae 2 and 3 similar to other coxae; coxae 2–4 longer than respective pereonite; coxae 5–7 longer than pereonite, posteriorly broadly rounded, conspicuous in dorsal view. Pereonite 1 anterolateral margin rounded and appearing to encompass head. Pereonites 1–4 of hunched side not expanded from pereopodal bases; posterolateral lobes deeply convex and progressively increasing in size; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson wider than pereonite 7. Antennula shorter than antenna; bases widely separated; articles short; terminal article nearly reaching or reaching head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilliped with 2 oostegite lobes. Pereopods 5–7 basis superior margin with carina, inferior margin without carina. Brood pouch ventrally not or weakly protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal, shelf. Indo-West Pacific. 4 species (Bunkley-Williams and Williams, 1986). The genus needs revision.

Cymothoa Fabricius, 1793

Diagnosis. Attached to host buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins subparallel; dorsum strongly vaulted. Rostrum indistinct, anterior margin truncate, rounded or concave, ventrally folded, weakly projecting between antennulae bases. Head three quarters immersed in pereonite 1, posterior margin straight, lateral margin concave. Eye absent. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, posteriorly narrowly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin anteriorly acute or rounded, appearing to encompass head. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson as wide as or narrower than pereonite 7. Antennula shorter than antenna; bases widely separated; articles 1–4 short; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct or partially fused. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis superior margin with large blade-like carina, inferior margin without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods 3–5 with well developed fleshy ridges; peduncles with lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Estuarine, subtidal, shelf. World oceans except polar waters. 42 species (Hadfield et al., 2013; Martin et al., 2016).

Elthusa Schioedte and Meinert, 1884

Diagnosis. Attached to host gills. Body symmetrical or weakly asymmetrical; lateral margins ovate; dorsum weakly vaulted. Rostrum distinct, truncate, ventrally and posteriorly folded, projecting between antennulae bases or not ventrally and posteriorly folded. Head three quarters immersed in pereonite 1, posterior margin straight, lateral margin concave. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 as long as pereonite, not strongly ventrally directed posteriorly, posteriorly broadly rounded, conspicuous in dorsal view. Pereonite 1 anterolateral margin anteriorly acute or rounded. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7

extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; as wide as or narrower than other pleonites (usually slightly narrower). Pleotelson as wide as or narrower than pereonite 7. Antennula shorter than antenna; bases narrowly separated; articles 1–3 long; terminal article short, nearly reaching or reaching head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis superior margin with or usually without carina, inferior margin without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal, shelf and slope (shallow to about 1000 m). Worldwide, except polar waters. 34 species. The most recent revision of the genus is that of Aneesh et al. (2020). Since then, several species have been removed to other genera (*Brucethoa*, *Glyptothoa* and *Sandythoa*) and direct comparison to the diagnoses of those recently described genera is advised (Aneesh et al., 2020).

Emetha Schioedte and Meinert, 1883

Diagnosis. Attached to host buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins ovate; dorsum strongly vaulted. Rostrum distinct, triangular, not ventrally and posteriorly folded; dorsally not projecting between antennae. Head partially immersed in pereonite 1, posterior margin straight, lateral margin straight. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin produced. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson narrower than pereonite 7. Antennae thick, expanded. Antennula shorter than antenna; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp articles 2 and 3 subequal. Pereopods 5–7 basis superior margin with large blade-like carina, inferior margin without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view, peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal. Temperate North Atlantic. 2 species. The genus potentially differs from *Ceratothoa* by a single character; no modern revision or redescription exists and many generic characters are unknown (Trilles, 1994).

Gibbothoa Aneesh, Hadfield, Bruce, Helna, Smit and Biju Kumar, 2026

Diagnosis. Attached to host gills. Body strongly asymmetrical or distorted; lateral margins strongly hunched on one side; dorsum strongly vaulted. Rostrum indistinct, weakly ventrally folded. Head partially immersed in pereonite 1, posterior margin concave (arc to posterior), lateral margin convex. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, posteriorly narrowly rounded, conspicuous in dorsal view. Pereonite 1 anterior margin deeply incised, anterolateral margin produced or anteriorly acute. Pereonites 1–4 of hunched side laterally much expanded from pereopodal bases; posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 moderately to strongly produced, or not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson narrower than pereonite 7. Antennula much shorter than antenna; bases narrowly separated; articles short; terminal article nearly reaching or reaching head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped without oostegite lobe. Pereopods 5–7 basis margins without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopod 5 only with prominent fleshy ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Shelf. Central Indo-Pacific (India). 1 species (Aneesh et al., 2026).

Glossobius Schioedte and Meinert, 1883

Diagnosis. Attached to host buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins subparallel; dorsum strongly vaulted. Rostrum distinct, triangular or truncate, not ventrally or posteriorly folded. Head not immersed in pereonite 1, posterior margin straight, lateral margin straight. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 shorter than or as long as respective pereonite; coxae 5–7 shorter than pereonite, not strongly ventrally directed posteriorly, posteriorly broadly rounded, conspicuous in dorsal view. Pereonite 1 anterolateral margin not produced; flat or laterally lobed. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending or not extending laterally past pleonite 1. Pleon as wide as or narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7 or visible, narrower than other pleonites. Pleotelson as wide as or wider than pereonite 7. Antennae thick and expanded. Antennula shorter than antenna; bases in contact; articles 1–3 long; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped with 2 oostegite lobes. Pereopods 5–7 basis superior margin with large blade-like carina, inferior margin without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods 3–5 with weak fleshy ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Shelf. Pelagic. Tropical Atlantic, Temperate Northern W Pacific, Tropical Eastern Pacific, Indo-West Pacific (world

oceans; primarily on pelagic hosts). 8 species (Bruce and Bowman, 1989; Martin et al., 2015a).

Glyptothoa Helna, Aneesh, Kumar and Ohtsuka, 2023

Diagnosis. Attached to host gills. Body symmetrical or weakly asymmetrical; lateral margins ovate; dorsum weakly vaulted. Rostrum distinct; small, acute, anteriorly projecting between antennulae. Head three quarters immersed in pereonite 1, posterior margin straight, lateral margin straight. Eye large. Coxae 2 and 3 larger than other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 as long as pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin produced. Pereonites 1–4 of hunched side not expanded from pereopodal bases; posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon wider than pereon; pleonites with sublateral gaps. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson as wide as pereonite 7. Antennula shorter than antenna; bases narrowly separated; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped with 2 oostegite lobes. Pereopods 5–7 basis margins without carina. Brood pouch ventrally strongly protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal, shelf and slope (shallow to 650 m). Temperate Northern W Pacific, Indo-West Pacific. Northwestern Pacific. 4 species (Helna et al., 2023).

Ichthyoxenos Herklots, 1870

Diagnosis. Attached to host gills or buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins ovate; dorsum strongly vaulted. Rostrum indistinct, triangular or rounded, ventrally and posteriorly folded, weakly projecting between antennulae bases. Head not immersed in pereonite 1, posterior margin straight, lateral margin convex. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, strongly ventrally directed, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; as wide as or slightly narrower than other pleonites. Pleotelson as wide as or narrower than pereonite 7. Antennula shorter than antenna; bases narrowly separated; articles short; terminal article long, extending beyond head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped with 2 oostegite lobes. Pereopods 5–7 basis margins without carina. Brood pouch ventrally strongly protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal, shelf and slope (shallow to at least 366 m). Temperate Northern W Pacific, Indo-West Pacific. Marine species reported primarily from the Pacific Ocean; freshwater species from continental Africa and Asia. 27 species (4 marine). The genus includes freshwater flesh-burrowing species and marine buccal-attaching species, and is likely not monophyletic (Boyko and Bruce, 2026). This diagnosis applies only to the marine species (Bruce, 1990; Mitra and Chowdhury, 2024). The name has sometimes been misspelled as *Ichthyoxenus*.

Idusa Schioedte and Meinert, 1884

Diagnosis. Attached to host gills or buccal cavity. Body symmetrical, weakly asymmetrical or twisted to one side; lateral margins ovate; dorsum strongly vaulted. Rostrum triangular. Head partially immersed in pereonite 1, posterior margin straight, lateral margin convex. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 shorter than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 of hunched side not expanded from pereopodal bases; posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter than antenna; bases narrowly separated. Pereopods 5–7 basis margins without carina. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal. Temperate North Atlantic, Tropical Eastern Pacific, Mediterranean. 3 species. Generic position of the one East Pacific species is doubtful. No detailed generic or species descriptions exists so many characters are unknown (Bruce, 1990).

Joryma Bowman and Tareen, 1983

Diagnosis. Attached to host gills (inner surface of operculum). Body twisted to one side; lateral margins somewhat asymmetric; dorsum weakly or strongly vaulted. Rostrum indistinct, rounded, weakly ventrally folded. Head three quarters immersed in pereonite 1, posterior margin convex, lateral margin convex. Eye small. Coxae 2 and 3 larger than other coxae; coxae 2–4 longer than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly narrowly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin lobed. Pereonites 1–4 of hunched side not expanded from pereopodal bases; posterolateral lobes deeply convex and progressively increasing in size; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon as wide as pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; as wide as other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter than antenna; bases widely separated; articles short; terminal article nearly

reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp stout, articles wholly or partly fused. Maxilla mesial lobe partially fused. Maxilliped without oostegite lobe. Pereopods 5–7 basis margins without carina. Brood pouch ventrally strongly protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles with lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal. Indo-West Pacific. 6 species (Aneesh et al., 2019).

Kuna Bunkley-Williams and Williams, 1986

Diagnosis. Attached to host gills. Body symmetrical or weakly asymmetrical; lateral margins subparallel; dorsum strongly vaulted. Rostrum indistinct, rounded, ventrally and posteriorly folded, projecting between antennulae bases. Head not immersed in pereonite 1, posterior margin straight, lateral margin convex. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 as long as pereonite, not strongly ventrally directed posteriorly, posteriorly narrowly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 not extending laterally past pleonite 1. Pleon about as wide as pereon. Pleonites 1–5 strongly produced ventrally; pleonite 1 visible, as wide as other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter than antenna; widely separated; fewer than 5 short articles; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe partially fused. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis superior margin without carina. Brood pouch not known. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal. Temperate Northern W Pacific. 1 species (Williams and Bunkley-Williams, 1986; Williams and Williams, 1985).

Livoneca Leach, 1818

Diagnosis. Attached to host gills. Body symmetrical, weakly asymmetrical or twisted to one side; lateral margins ovate; dorsum weakly vaulted. Head without rostrum, anterior margin truncate. Head not immersed in pereonite 1, posterior margin trisinuate, lateral margin straight. Eye small. Coxae 2 and 3 smaller than other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 as long as pereonite or longer than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 not extending laterally past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; as wide as other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter than antenna; widely separated; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe partially fused. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis superior margin with carina, inferior margin without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods 3–5 with well developed fleshy ridges; pleopods 2–5 peduncle with well developed branchiae; peduncles with lateral lamellar lobes. Uropodal rami extending slightly beyond pleotelson posterior margin.

Estuarine and subtidal. Temperate North Atlantic, Tropical western Atlantic. 3 species. The genus is New World Atlantic in distribution, with one introduced species now widely reported from Egypt and the Suez Canal region (Bruce, 1990; Mahmoud et al., 2023).

Lobothorax Bleeker, 1857

Diagnosis. Attached to host buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins subparallel; dorsum strongly vaulted. Rostrum distinct, triangular, not ventrally and posteriorly folded. Head three quarters immersed in pereonite 1, posterior margin straight, lateral margin straight. Eye small. Coxae 2 and 3 smaller than other coxae; coxae 2–4 shorter than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterior margin with prominent anterolateral lobes, anterolateral margin lobed. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 not extending laterally past pleonite 1. Pleon subequal to pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; as wide as other pleonites. Pleotelson wider than pereonite 7. Antennula longer than antenna; bases widely separated; articles 1–3 long; terminal article long, extending beyond head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp articles 2 and 3 subequal. Maxilla mesial lobe distinct. Maxilliped without oostegite lobe. Pereopods 5–7 basis superior margin with carina, inferior margin with weak carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods 4 and 5 with very weak fleshy ridges; peduncles with lateral lamellar lobes. Uropodal rami extending slightly beyond pleotelson posterior margin.

Subtidal, shelf. Temperate Northern W Pacific; Central Indo-Pacific. 4 species (Aneesh et al., 2021).

Mothocya Costa *in* Hope, 1851

Diagnosis. Attached to host gills (occasionally buccal cavity). Body symmetrical, weakly asymmetrical or twisted to one side; lateral margins ovate; dorsum not vaulted. Rostrum indistinct, narrowly rounded or truncate, ventrally and posteriorly folded. Head three quarters immersed in pereonite 1, posterior margin straight, lateral margin convex. Eye large. Coxae more-or-less equal on both sides of body (slightly larger on convex side in some species); coxae 2 and 3 smaller than other coxae; coxae 2–4 longer than respective pereonite; coxae 5–7 longer than or as long as pereonite, posteriorly broadly rounded, conspicuous in

dorsal view. Pereonite 1 anterolateral margin rounded, sometimes partly encompassing head. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon about as wide as pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson as wide as or wider than pereonite 7. Antennula broader than, as long as or longer than antenna; bases widely separated; articles short; terminal article nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped without oostegite lobe. Pereopods 5–7 basis margins without carina. Brood pouch strongly ventrally protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without or with weak lateral lamellar lobes. Uropodal rami long, extending beyond pleotelson posterior margin.

Estuarine and subtidal (to at least 908 m). Worldwide except polar waters. 30 species. The genus primarily uses Beloniformes as hosts (Bruce, 1986; Hadfield et al., 2015; van der Wal et al., 2021).

Nerocila Leach, 1818

Diagnosis. Attached to host external body surfaces. Body symmetrical or weakly asymmetrical; lateral margins subparallel or ovate; dorsum not vaulted. Head without rostrum; anterior margin weakly rounded or truncate. Head not immersed in pereonite 1, posterior margin trisinuate, lateral margin convex. Eye large or small. Coxae 2 and 3 smaller than other coxae; coxae 2–4 as long as or longer than respective pereonite; coxae 5–7 longer than or as long as pereonite, not strongly ventrally directed posteriorly, posteriorly prominent and acute or narrowly rounded or broadly rounded, conspicuous in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 variably produced, sometimes acute; pereonite 7 extending laterally past pleonite 1, or not. Pleon narrower than pereon. Pleonite 1 visible, as wide as or wider than other pleonites (usually slightly wider); pleonites 1 and 2 ventrolateral margin strongly produced. Pleotelson narrower than pereonite 7. Antennula ranging from shorter to longer than antenna; bases widely separated; articles 1–3 long; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp articles 2 and 3 subequal or 2 slightly longer. Maxilla mesial lobe usually distinct. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis margins without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods 3–5 with weak fleshy ridges, or endopod 5 only with prominent fleshy ridges; peduncles with lateral lamellar lobes. Uropodal rami long, extending beyond pleotelson posterior margin.

Estuarine, subtidal, shelf. World-wide except polar and subpolar seas. 41 species. While readily recognised by the conspicuous ventrolateral processes on pleonites 1 and 2, other characters, such as the extent to which the posterolateral margins of pereonites 6 and 7 and the coxae are posteriorly produced, vary considerably (Aneesh, Helna et al., 2017; Aneesh, Valarmathi et al., 2017; Bruce, 1987c).

Norileca Bruce, 1990

Diagnosis. Attached to host gills. Body twisted to one side; lateral margins ovate (weakly ovate on one side); dorsum weakly vaulted. Head with distinct rostrum in ventral view; rostrum truncate, ventrally and posteriorly folded, projecting between antennulae bases. Head not immersed in pereonite 1, posterior margin concave, lateral margin straight. Eye large. Coxae 2 and 3 smaller than other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, posteriorly narrowly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 not extending laterally past pleonite 1 or extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 visible, as wide as or wider than other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter than or as long as antenna; bases widely separated; articles 1–3 long; terminal article long, extending beyond head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped without oostegite lobe. Pereopod 1 propodus with robust setae present or absent; pereopods 5–7 basis superior margin without carina or with carina, inferior margin with weak carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopod 5 only with prominent fleshy ridges; peduncles with lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal. Indo-West Pacific. 4 species (Bruce, 1990; Nashad et al., 2022; van der Wal et al., 2017).

Olencira Leach, 1818

Diagnosis. Attached to host gills or buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins subparallel; dorsum strongly vaulted. Head without rostrum. Head not immersed in pereonite 1, posterior margin straight, lateral margin straight. Eye large. Coxae 2 and 3 larger than other coxae; coxae 2–4 shorter than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; as wide as other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter and stouter than antenna; bases in contact; articles 1–3 long; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 longer than article 2. Maxilla mesial lobe distinct. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis margins without carina. Brood pouch ventrally strongly protruding. Pleopods barely

visible in dorsal view; endopods 3–5 with well developed fleshy ridges; peduncles with lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal, shelf. Temperate North Atlantic, Tropical Atlantic (Atlantic coast of North America and northern Caribbean). 1 species (Trilles, 2007).

Ourozeuktes Milne Edwards, 1840

Diagnosis. Burrowing into flesh of host. Body symmetrical or weakly asymmetrical; lateral margins strongly ovate; dorsum weakly vaulted. Head without rostrum. Head partially immersed in pereonite 1, posterior margin concave, lateral margin convex. Eye small. Coxae 2 and 3 similar to or smaller than other coxae; coxae 2–4 longer than respective pereonite; coxae 5–7 as long as pereonite, strongly ventrally directed, posteriorly narrowly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin produced. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon; pleonites fused, without lateral gaps. Pleonites 1 and 2 ventrolateral margin not produced. Pleotelson narrower than pereonite 7. Antennula broad, shorter than antenna; bases widely separated; articles 1–3 long; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe partially fused. Maxilliped with 2 oostegite lobes. Pereopods 5–7 basis superior margin without carina, inferior margin with large blade-like carina (also on ischium). Pleopods barely visible in dorsal view, peduncles with lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal. Temperate Australasia (Australian endemic hosted especially by leatherjackets, family Monacanthidae). 1 species (Hale, 1926). The only species *O. bopyroides* (Lesueur, 1814) needs redescription.

Pleopodias Richardson, 1910

Diagnosis. Attached to host external body surfaces. Body symmetrical; lateral margins subparallel or weakly ovate; dorsum strongly vaulted. Head with distinct rostrum; rostrum truncate in dorsal view, triangular or truncate, ventrally and posteriorly folded, projecting between antennulae bases. Head not immersed in pereonite 1, posterior margin straight, lateral margin straight. Eye large. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, posteriorly narrowly rounded, not visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 not extending laterally past pleonite 1. Pleon narrower than pereon. Pleonites 3–5 or 4 and 5 less than half width (c. 0.45) of pereon. Pleonite 1 visible, not laterally produced; pleonites 1 and 2 lateral margin ventrally produced. Pleotelson posteriorly narrowing strongly; narrower than pereonite 7. Antennula shorter than antenna; bases narrowly separated; articles 1–3 long; article 3 anterodistal margins produced; terminal article long, extending beyond head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct; with 2 large nodular robust setae each on mesial and lateral lobe. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis margins without carina. Brood pouch not ventrally protruding. Pleopods readily visible in dorsal view; endopod 5 only with prominent fleshy ridges (weak lobes); peduncles without lateral lamellar lobes. Uropodal rami long, extending slightly or well beyond pleotelson posterior margin.

Subtidal, shelf and slope (to 380 m). Temperate Northern W Pacific, Indo-West Pacific, Temperate Southern Africa. 4 species (Bruce, 1987a; Hadfield and Smit, 2017).

Plotor Schioedte and Meinert, 1881

Diagnosis. Host attachment not known, but here assumed as external. Body symmetrical; lateral margins ovate; dorsum strongly vaulted. Head without rostrum. Head not immersed in pereonite 1, posterior margin trisinuate, lateral margin convex. Eye small. Coxae 2 and 3 smaller than other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 longer than pereonite, strongly ventrally directed, posteriorly broadly rounded, conspicuous in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 not extending laterally past pleonite 1. Pleon narrower than pereon. Pleonites 1–5 strongly produced ventrally; pleonite 1 visible, wider than other pleonites; pleonites 1 and 2 ventrolateral margin not produced. Pleotelson narrower than pereonite 7. Uropodal rami extending slightly beyond pleotelson posterior margin.

Subtidal. Indo-West Pacific (distribution quoted as “Indian Ocean”; likely coastal Papua or West Papua, Indonesia). 1 species. The genus and species are effectively undescribed (Bruce, 1987c).

Renocila Miers, 1880

Diagnosis. Attached to host external body surfaces. Body symmetrical or weakly asymmetrical; lateral margins subparallel or convex; dorsum weakly vaulted. Head with or without ventral rostrum; anterior margin folded. Head not immersed in pereonite 1, posterior margin straight, lateral margin straight. Eye small. Coxae 2 and 3 larger than other coxae; coxae 2–4 as long as respective pereonite, or longer than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly prominent, acute or rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 produced; pereonite 7 extending laterally past pleonite 1 or not. Pleon narrower than pereon. Pleonite 1 visible or partially visible, laterally concealed by pereonite 7; as wide as or wider than other pleonites. Pleotelson narrower than pereonite 7. Antennula broader than and as long as antenna; bases widely separated; article 5 long, extending beyond head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp article 3 shorter than or subequal to article 2. Maxilla mesial

lobe distinct, or partially fused. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis superior margin without carina, inferior margin without or with weak carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopod 5 only with prominent fleshy ridges; peduncles without lateral lamellar lobes. Uropodal rami extending slightly beyond or not extending beyond pleotelson posterior margin.

Subtidal, shelf. Tropical Atlantic and Indo-West Pacific (shallow-water tropical coastal habitats). 20 species. Many characters vary suggesting that the genus is probably not monophyletic (Aneesh et al., 2022; Bruce, 1987b).

Ryukyua Williams and Bunkley-Williams, 1994

Diagnosis. Attached to host gills. Body symmetrical or weakly asymmetrical; lateral margins ovate (strongly); dorsum strongly vaulted. Head without distinct rostrum; anterior margin rounded, folded, ventrally projecting between antennulae bases. Head partially immersed in pereonite 1, posterior margin straight, lateral margin convex. Eye large. Coxae 2 and 3 similar to other coxae; coxae 2–4 longer than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin lobed. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 produced, posteriorly rounded; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; as wide as other pleonites. Pleotelson narrower than pereonite 7. Antennula longer than antenna; bases widely separated; articles 1–3 long; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe partially fused. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis superior margin with carina, inferior margin with weak carina. Brood pouch ventrally strongly protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles with lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal. Indo-West Pacific (India, southern Japan). 2 species (Williams and Bunkley-Williams, 1994).

Pseudirona Pillai, 1964

Diagnosis. Attached to host gills. Body symmetrical or weakly asymmetrical; lateral margins ovate. Head without distinct rostrum. Head partially immersed in pereonite 1, posterior margin weakly convex, lateral margin convex. Eye large. Coxae 2 and 3 similar to other coxae; coxae 2–4 shorter than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly narrowly rounded, conspicuous in dorsal view. Pereonite 1 anterolateral margin anteriorly acute. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon as wide as pereon. Pleonite 1 not visible, completely concealed by pereonite 7; narrower than other pleonites. Pleotelson wider than pereonite 7. Antennula longer than antenna; articles 1–3 long; terminal article long, extending beyond head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped with 2 oostegite lobes. Pereopod 1 propodus with robust setae; pereopods 5–7 basis superior margin without carina; pereopods 4–7 ischium and merus with conspicuous blade-like carina, inferior margin without carina. Pleopods barely visible in dorsal view. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal (274 m). Western Indo-Pacific (Trivandrum, Kerala Coast, India). 1 species. The setose pereopods and carinate ischium and merus on the posterior pereopods are distinctive. The only species *P. laeopsi* Pillai, 1964 needs redescription (Pillai, 1964; Ravichandran et al., 2019).

Sandythoa Aneesh, Bruce, Helna and Biju Kumar, 2024

Diagnosis. Attached to host gills. Body symmetrical or weakly asymmetrical; lateral margins ovate; dorsum weakly vaulted. Head with rostral point; rostrum rounded or acute, not ventrally and posteriorly folded. Head partially immersed in pereonite 1, posterior margin concave, lateral margin convex. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 shorter than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin produced. Pereonites 1–4 posterolateral lobes convex and consistent, or deeply convex and progressively increasing in size; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon; pleonites with sublateral gaps. Pleonite 1 partially visible, laterally concealed by pereonite 7; much narrower than other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter than antenna; bases narrowly separated; articles short; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp articles 2 and 3 subequal. Maxilla mesial lobe distinct. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis margins without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal, shelf and slope (shallow to 401 m). Indo-West Pacific. 5 species (Aneesh et al., 2024).

Smenispa Özdikmen, 2009

Diagnosis. Attached to host buccal cavity. Body symmetrical or weakly asymmetrical; dorsum strongly vaulted. Head without rostrum; partially immersed in pereonite 1, posterior margin concave, lateral margin convex. Eye small or partially visible. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin produced or rounded, appearing to encompass head. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending laterally past pleonite 1 or not. Pleon narrower than pereon. Pleonite 1

visible, as wide as other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter than antenna; bases widely separated; articles 1–3 long; terminal article short, nearly reaching or reaching head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp articles 2 and 3 subequal. Maxilla mesial lobe partially fused. Maxilliped not described. Pereopods 5–7 basis superior margin with carina, inferior margin without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopod 5 only with prominent fleshy ridges or endopods 3–5 with well developed fleshy ridges; peduncles with lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal, shelf. Tropical Eastern Pacific; Eastern Indo-Pacific (east Pacific off coast of North America, Central America and northern South America). 2 species (Bruce, 1990; Martin et al., 2014). The genus was previously known as *Enispa* Schioedte and Meinert, 1884.

Tetragonocephalon Avdeev, 1975

Diagnosis. Attached to host buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins subparallel. Head without rostrum. Head three quarters immersed in pereonite 1, posterior margin concave (arc to posterior), lateral margin straight. Eye absent. Coxae 2 and 3 larger than other coxae; coxae 2–4 as long as or longer than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin produced. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 not extending laterally past pleonite 1. Pleon narrower than pereon. Pleonite 1 visible, as wide as other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter than antenna; articles short; terminal article long, extending beyond head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Pereopods 5–7 basis superior margin without carina, inferior margin with weak carina. Pleopods barely visible in dorsal view, peduncles with lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal or shelf (depth unknown). Indo-West Pacific (known only from type locality). 1 species (Avdeev, 1975).

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Gnathiidae Leach, 1814

Figures 5.31–5.33

Gnathiids are most unusual isopods, polymorphic in the extreme. Males are immediately recognisable by their large mandibles directed forwards from the cephalosome (figs 5.31a, 5.32). The first pereopods are usually modified as "pylopods", operculate and protecting the other mouthparts (Cohen and Poore, 1994). The pereon bears only 5 pairs of walking legs, pereopod 7 being absent in adults. Males settle after their final instar in crevices in the sediment, mud, submerged wood, sponges, coral rubble or cavities in the reef, do not feed, and may gather a harem of females in their "home" (Klitgaard, 1997; Smit et al., 2003; Tanaka, 2007; Wägele, 1988). Females have more reduced jaws and a thorax swollen with ovary or eggs, sometimes more than a hundred (fig. 5.31b). The juveniles, or praniza larvae (fig. 5.31c), pass through three instars in the only species studied (Juilfs and Wägele, 1987; Wägele, 1988), each feeding on blood as ectoparasites of fishes (Smit and Davies, 2004). The role of the praniza stage (to describe a juvenile with a gut full of blood) and the zuphea (the unfed stage) as ectoparasites of fishes is well studied. The larvae use their sharp mouthparts to penetrate skin and suck blood. They are important ectoparasites, especially on coral reefs (Grutter, 1996, 1999; Smit, 2000; Smit and Davies, 2004; Smit et al., 2003; Tanaka, 2006).

The taxonomy of Gnathiidae was the subject of a monograph by Monod (1926) and was revised more extensively by Cohen and Poore (1994). These authors justified new genera on a cladistic analysis using morphological characters. Since then, Kensley et al. (2009), Smit and coauthors and Svavarsson and Bruce (2019) have added many species. A key to genera similar to the one below can be found in Ota et al. (2025).

Diagnosis. Males with enlarged head, anteriorly directed mandibles, pereonite 1 short, fused into cephalosome; pereonite 7 shorter than pereonites 2–6; females with pereon swollen with ovary or embryos. Eyes contiguous or almost contiguous anterodorsally and extending from anterior margin to posterior margin of head (*Tenerognathia* only), or widely separated, lateral, sometimes small or absent. Mandibles in males enlarged, projecting anteriorly and together forceps-like. Maxillula usually absent. Pereopod 1 modified as pylopod ventrally overlying mouthparts, pereopod 7 absent as adults. Ectoparasitic as juveniles, usually on fishes.

Implicit generic attributes. Eyes present. Paraocular ornamentation on cephalosome absent. Mandibular incisor absent. Maxillula absent. Maxilliped 5-articled, external margins of articles 2–5 bearing plumose setae. Pereonite 1 not produced laterally, immersed in cephalosome. Pereonite 3 without large anteriorly directed projection. Pleon not folded under pereon.

Key to genera of Gnathiidae (adult males only)

1. Pylopod large, distinct (fig. 5.33e–j, m–p, r). Maxillipedal palp 4-articled (fig. 5.33b–d) 2

– Pylopod thin, elongate (difficult to see even under dissecting microscope) (fig. 5.33l, r). Maxilliped absent or reduced (fig. 5.33k, q) 11

2. Pylopod of 5–6 visible articles; basis distinct (fig. 5.33f, g, j, n, o) 3

– Pylopod of 1–3 visible articles; basis fused to pereonite (fig. 5.33e, d, h, i, m) 7

3. Frontal border with processes, transverse; with pronounced paraocular ornamentation (fig. 5.32b) ..... *Euneognathia*

– Frontal border without processes, rounded or produced, or minute process; lacking paraocular ornamentation 4

4. Pylopod pereopod-like, not operculate (fig. 5.33g). Pereonite 1 greatly produced dorsoposteriorly (fig. 5.32n) ..... *Bythognathia*

– Pylopod operculate. Pereonite 1 not greatly produced 5

5. Pylopod 6-articled, ischium longer than wide, merus free, short, more distal articles ovoid (fig. 5.33o). Mandibular blade dentate (fig. 5.32l). Total length <5 mm ..... *Paragnathia*

– Pylopod 5- or 6-articled, merus fused with distal articles forming triangular operculum (fig. 5.33f, n). Mandibular blade smooth or absent (fig. 5.32g, k). Total length >5 mm 6

6. Mandible without blade. Buccal cavity wall extension visible at the end of pronounced rostrum (fig. 5.32g) ..... *Bathygnathia*

– Mandibular blade smooth. Frontal border rounded, without buccal cavity wall protrusion (fig. 5.32k) ..... *Monodgnathia*

7. Cephalosome spherical, eyes occupying entire side (fig. 5.32m) ..... *Tenerognathia*

– Cephalosome box-like; eyes occupying fraction of side 8

8. Pylopod of a single operculate plate (fig. 5.33e). Maxillula present (fig. 5.33a) ..... *Afrignathia*

– Pylopod of 2 or 3 articles (fig. 5.33h, d, m). Maxillula absent 9

9. Frontal border without frontal process, often rounded; cephalosome lacking paraocular ornamentation and dorsal sulcus (fig. 5.32a, h) ..... *Caecognathia*

– Frontal border with frontal processes, often transverse; cephalosome may possess paraocular ornamentation and/or a dorsal sulcus 10

10. Frontal border not deeply excavated. Mandibles not elongate (fig. 5.32d, j) ..... *Gnathia*

– Frontal border excavated. Mandibles long, lacking dentate blade (fig. 5.32i) ..... *Elaphognathia*

11. Pereon smooth, oval; pereonite 3 without dorsal, anteriorly-directed projection; pereonite 7 not visible. Pleon often folded under pereon. Antennae curved under mandibles (fig. 3.0). Mandible blade crenulate; incisor present (fig. 5.32e) ..... *Thaumastognathia*

– Pereon covered in granules and setae, rectangular; pereonite 3 with large dorsal, anteriorly-directed projection; pereonite 7 visible, small. Mandibular blade reduced or absent; incisor absent (fig. 5.32c) ..... *Gibbagnathia*

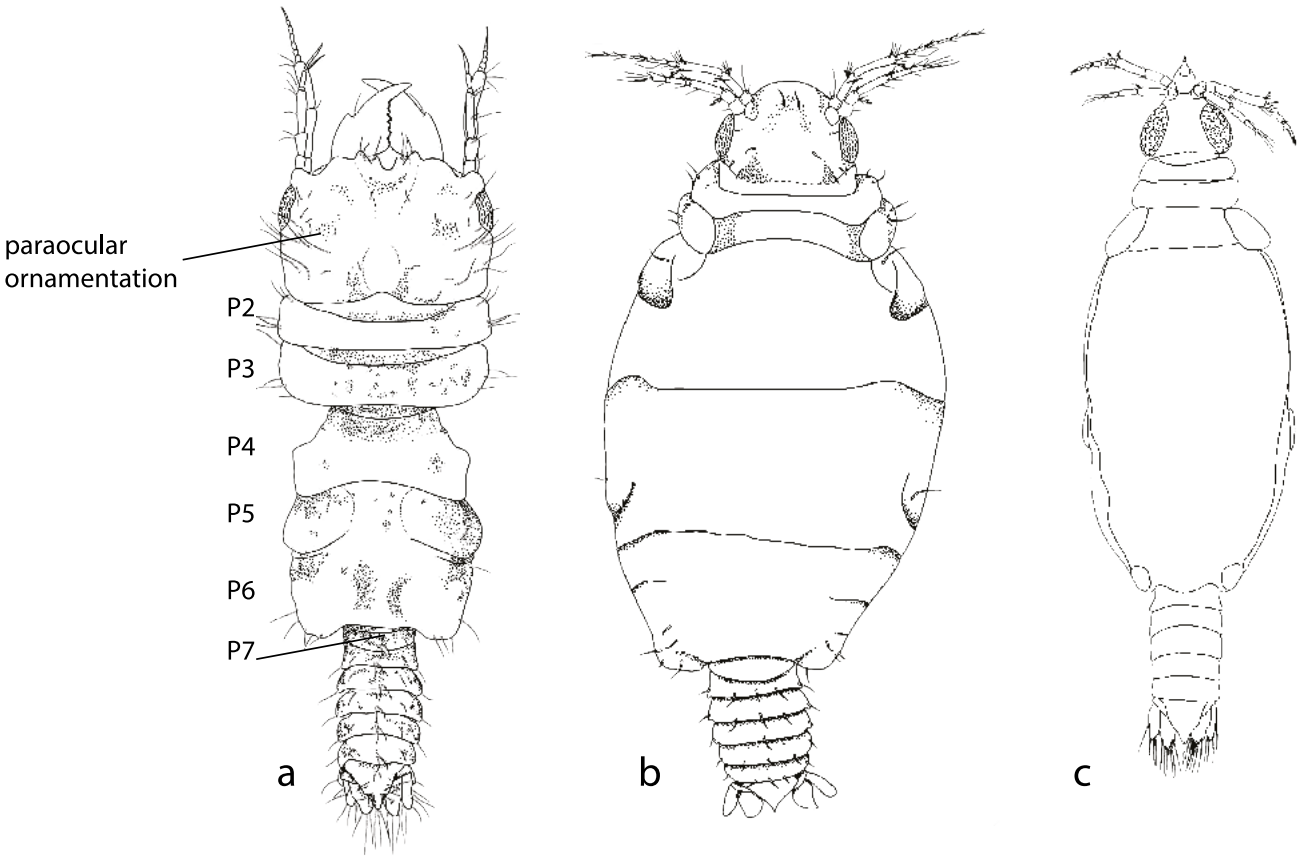


Figure 5.31. Gnathiidae. *Gnathia jimmybuffetti* Erasmus, Hadfield, Sikkel and Smit, 2023: a, adult male; b, female; c, praniza larva (not to same scale).

Afrignathia Hadfield and Smit, 2008

Diagnosis. Frontal border excavated, processes present. Mandibular blade with 2 rows of teeth. Maxillula present. Pylopod comprising singe fused article, operculate. Length of male less than 3 mm.

Shelf. Temperate Southern Africa. 1 species (Hadfield and Smit, 2008).

Bathygnathia Dolfuss, 1901

Diagnosis. Eyes present, or absent. Frontal border produced as rostrum, processes absent. Mandibular incisor slight, or absent; blade absent. Pylopod basis free, distal 3 articles triangularly operculate. Length of male 5–10 mm.

Bathyal, abyssal. North and South Atlantic, New Zealand, subantarctic, Indian Ocean basins, Central Indo-Pacific, Southern Ocean. 15 species (Cohen and Poore, 1994: rediagnosis; key to 5 species from Australia and New Zealand; Shimomura, 2008: 2 species).

Bythognathia Camp, 1988

Diagnosis. Eyes absent. Frontal border produced as rostrum, processes absent. Mandibular blade smooth. Pylopod of 4 articles, filiform. Pereonite 1 produced (partially obscuring pereonite 2). Length of male about 20 mm.

Bathyal. Caribbean. 1 species (Camp, 1988: diagnosis, description of type species; Cohen and Poore, 1994: rediagnosis).

Caecognathia Dollfuss, 1901

Diagnosis. Frontal border transverse, processes absent. Mandibular blade smooth. Pylopod basis free, remaining articles triangular operculate. Length of male less than 5 mm.

Subtidal–bathyal. Cosmopolitan. 48 species (Cohen and Poore, 1994: rediagnosis, key to 10 species from Australia; Ota et al., 2025: key to species from Japan).

Elaphognathia Monod, 1926

Diagnosis. Frontal border excavated, processes present. Mandibular blade absent. Pylopod of 2 or 3 visible articles, triangularly operculate. Length of male less than 5 mm.

Intertidal–shelf. Temperate Northern Atlantic, Temperate Northern Pacific, Western and Central Indo-Pacific, Temperate Australasia. 24 species (Cohen and Poore, 1994: rediagnosis, key to 5 species from Australia; Kensley et al., 2009: key to 6 species from Indian Ocean).

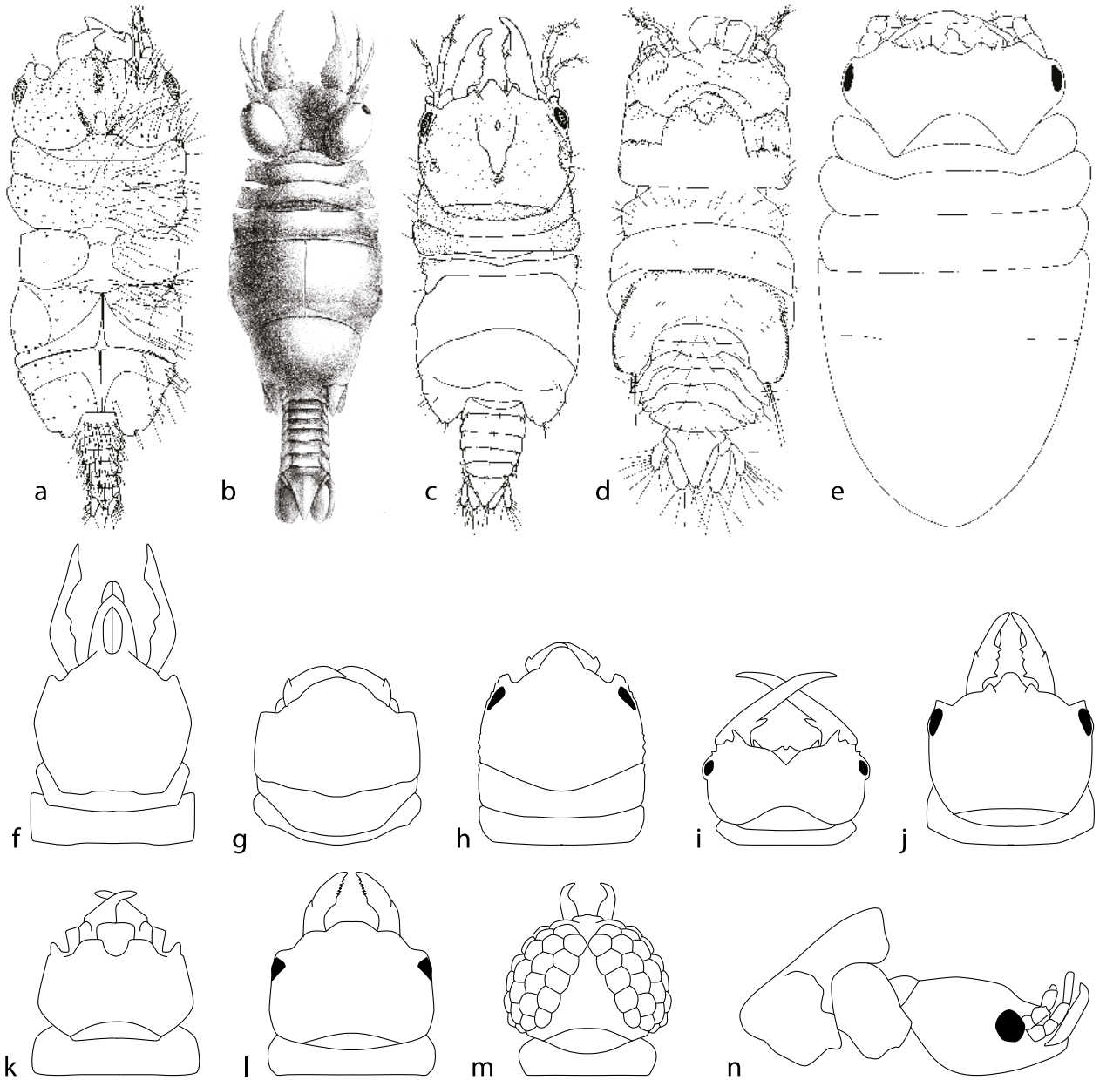


Figure 5.32. Gnathiidae. a, *Caecognathia huberia* Cohen and Poore, 1994; b, *Euneognathia gigas* (Beddard, 1886); c, *Gibbagnathia europalothrix* Cohen and Poore, 1994; d, *Gnathia camponotus* Cohen and Poore, 1994; e, *Thaumastognathia metaphone* Cohen and Poore, 1994. Pereonites 1, 2 head, mandibles: f, *Afrignathia*; g, *Bathygnathia*; h, *Caecognathia*; i, *Elaphognathia*; j, *Gnathia*; k, *Monodgnathia*; l, *Paragnathia*; m, *Tenerognathia*. n, pereonites 1–3, head, antennae, mandibles, lateral, *Bythognathia*.

Euneognathia Stebbing, 1893

Diagnosis. Frontal border transverse, processes present. Mandibular blade crenulate. Pylopod basis free, remaining 4 articles forming triangular operculum. Length of male 5–10 mm.

Shelf. Southern Ocean. 1 species (Beddard, 1886: figure of type species, *Anceus gigas* Beddard, 1886; Cohen and Poore, 1994: rediagnosis).

Gibbagnathia Cohen and Poore, 1994

Diagnosis. Frontal border slightly produced, processes absent. Mandibular blade absent. Maxilliped reduced, of 2 articles. Pylopod of 4 articles, filiform. Pereonite 3 with large anteriorly directed projection partially overhanging pereonites 1 and 2 (clear in lateral view). Length of male less than 3 mm.

Shelf. Temperate SE Australia. 1 species (Cohen and Poore, 1994).

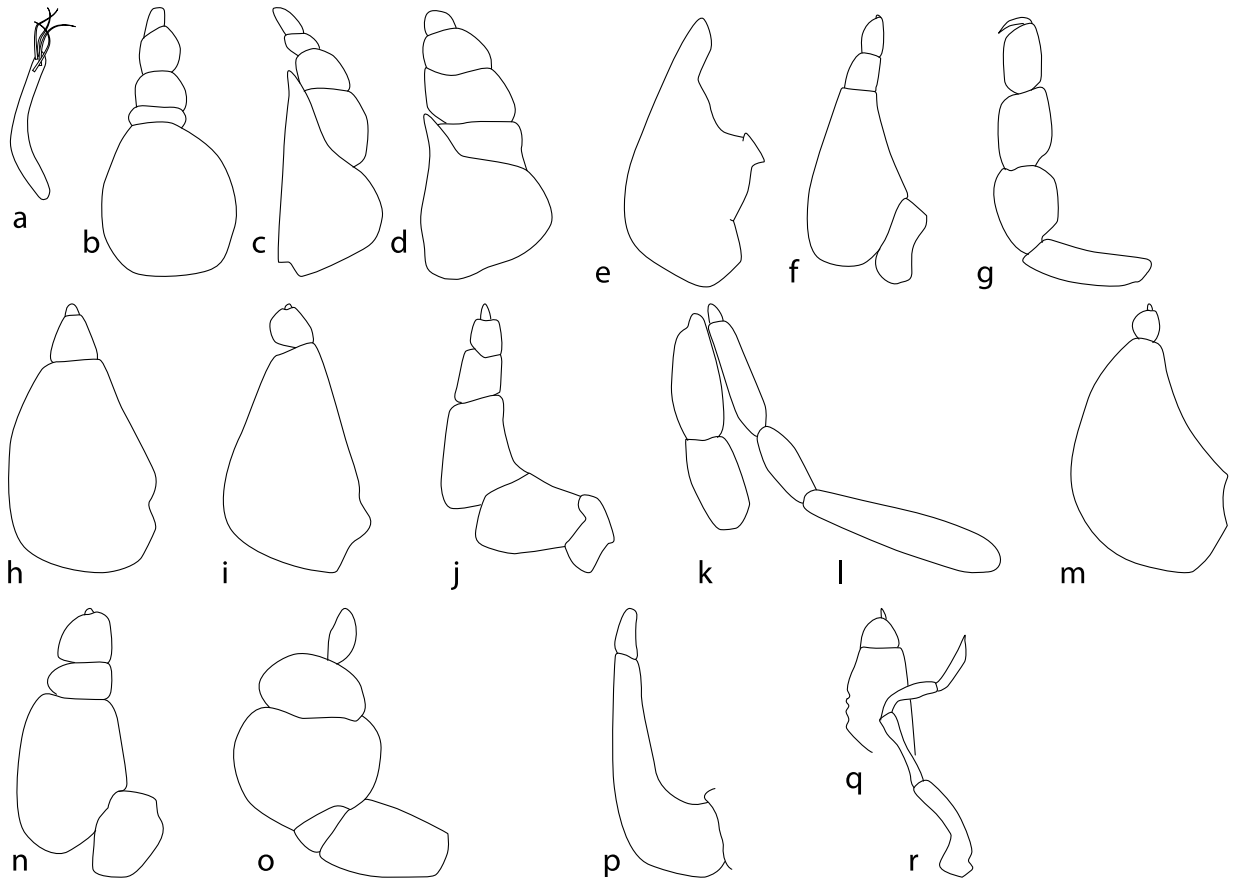


Figure 5.33. Gnathiidae. a, maxilla, *Afrignathia*. Maxilliped: b, *Afrignathia*; c, *Caecognathia*; d, *Elaphognathia*; k, *Gibbagnathia*; q, *Thaumastognathia*. Pylopod: e, *Afrignathia*; f, *Bathygnathia*; g, *Bythognathia*; h, *Caecognathia*; i, *Elaphognathia*; j, *Euneognathia*; l, *Gibbagnathia*; m, *Gnathia*; n, *Monodgnathia*; o, *Paragnathia*; p, *Tenerognathia*; r, *Thaumastognathia*.

Gnathia Leach, 1814

Diagnosis. Frontal border produced as rostrum, processes present; paraocular ornamentation on cephalosome absent, or granules posterior to eye. Mandibular incisor slight, or pronounced; blade dentate. Pylopod of 2 or 3 visible articles, triangularly operculate. Length of male less than 5 mm.

Intertidal–bathyal. Cosmopolitan. 144 species (Cohen and Poore, 1994: rediagnosis, key to 20 species from Australia; Kensley et al., 2009: key to 20 species from Indian Ocean; Svavarsson and Bruce, 2019: descriptions of 10 species; Ota et al., 2025: key to species from Japan).

Monodgnathia Cohen and Poore, 1994

Diagnosis. Eyes absent. Frontal border produced as rostrum, processes absent. Mandibular blade smooth. Pylopod basis free, distal 3 articles triangularly operculate. Length of male 5–10 mm.

Bathyal. Temperate Northern and Tropical Atlantic, Western Indo-Pacific, Temperate Australasia. 4 species (Cohen and Poore, 1994: key to 2 species from Australia).

Paragnathia Omer-Cooper and Omer-Cooper, 1916

Diagnosis. Frontal border produced as rostrum, processes absent. Mandibular blade crenulate. Pylopod ischium and merus free, distal articles oval-operculate. Length of male less than 5 mm.

Subtidal. Temperate Northern E Atlantic. 1 species (Monod, 1926: description of only species).

Tenerognathia Tanaka, 2005

Diagnosis. Eyes occupying whole of side of cephalosome. Frontal border produced as rostrum, processes absent. Mandibular blade smooth. Pylopod of 2 narrow tapering articles. Length of male less than 3 mm.

Shelf. Temperate Northern W Pacific. 2 species (Tanaka, 2005, 2024).

Thaumastognathia Monod, 1926

Diagnosis. Frontal border transverse or slightly produced, processes present or absent. Mandibular blade crenulate. Maxilliped absent, or reduced, of 2 articles. Pylopod of 4 articles, filiform. Pleon folded under pereon. Length of male less than 3 mm.

Bathyal. Temperate Northern W Pacific, Temperate Australasia. 5 species (Cohen and Poore, 1994: rediagnosis, key to 4 species; Shimomura and Tanaka, 2008: 5th species).

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Protognathiidae Wägele and Brandt, 1988

Figure 5.34

Wägele and Brandt (1988), recognising the affinities of *Cirolana bathypelagica* Schultz, 1977 to Gnathiidae and Cirolanidae, separated it as its own genus *Protognathia* and family. The mandibular incisor is acute rather than bladelike as in cirolanids; it is not held anteriorly as in Gnathiidae. Pereopod 7 is absent as in Gnathiidae.

Diagnosis. Eyes widely separated, lateral, sometimes small or absent. Mandibular incisor enlarged, distally with acute point; molar bladelike. Maxilla with 1 endite. Maxillipedal endite as long as palp article 1; palp of 5 articles. Pereopod 7 absent as adults.

Protognathia Wägele and Brandt, 1988

Meso- and bathypelagic. Southern Ocean. 2 species (Wägele and Brandt, 1988: diagnosis, redescription of type species; Kussakin and Rybakov, 1995: second species).

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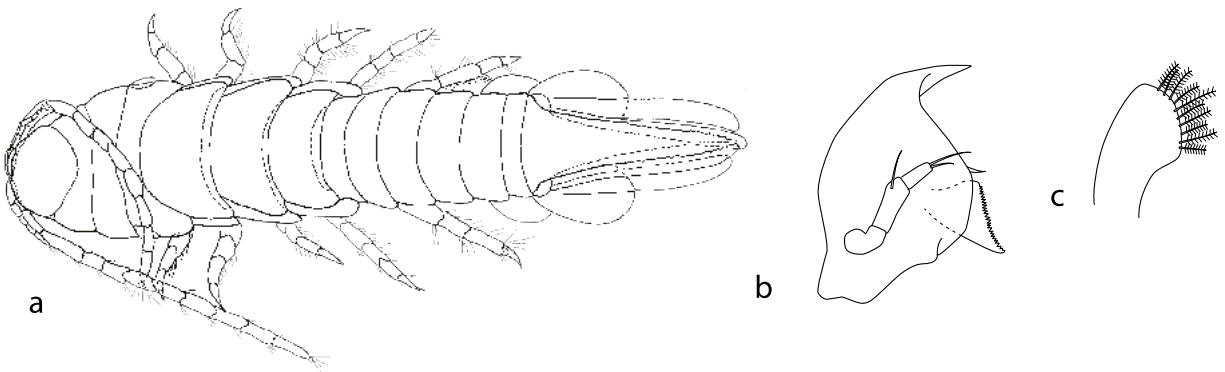


Figure 5.34. Protognathiidae. a, *Protognathia bathypelagica* (Schultz, 1977). *Protognathia*: b, mandible; c, maxilla.

Tridentellidae Bruce, 1984

Figure 5.35

The Tridentellidae are a small family with one genus (Bruce, 1984). Tridentellids are similar to the micropredatory families Aegidae and Corallanidae but are differentiated from them by an elongate maxillipedal endite that extends beyond the third palp article, and simple maxilla provided with numerous serrated scales, but without recurved spines or hooked robust setae. Many species of *Tridentella* are highly ornamented, some with cephalic processes or heavily spinose dorsal surfaces. The pleotelson often has longitudinal ridges and serrate lateral margins. Brandt and Poore (2001) listed the 16 species of *Tridentella* then known and provided a key, but several have been described since (Bruce, 2002, 2008; Bruce and Svavarsson, 2018).

Diagnosis. Eyes widely separated, lateral, sometimes small or absent (rarely contiguous). Mandibular incisor narrow; lacinia mobilis and spine row absent; molar present. Maxillula comprising 1 styliform endite with mesial and terminal robust setae. Maxilla with 1 endite, distal region with small spines or scalelike setae. Maxillipedal endite elongate; palp of 5 articles. Pereopods 1–7 ambulatory, dactyli 1–3 stout, recurved. Ectoparasitic, usually on fishes, or freeliving scavengers.

Tridentella Richardson, 1905

Shelf, slope. Temperate Northern and Tropical Atlantic, Temperate Northern W Pacific, Central Indo-Pacific, Tropical Eastern Pacific, Temperate Southern Africa, Temperate Australasia. 23 species.

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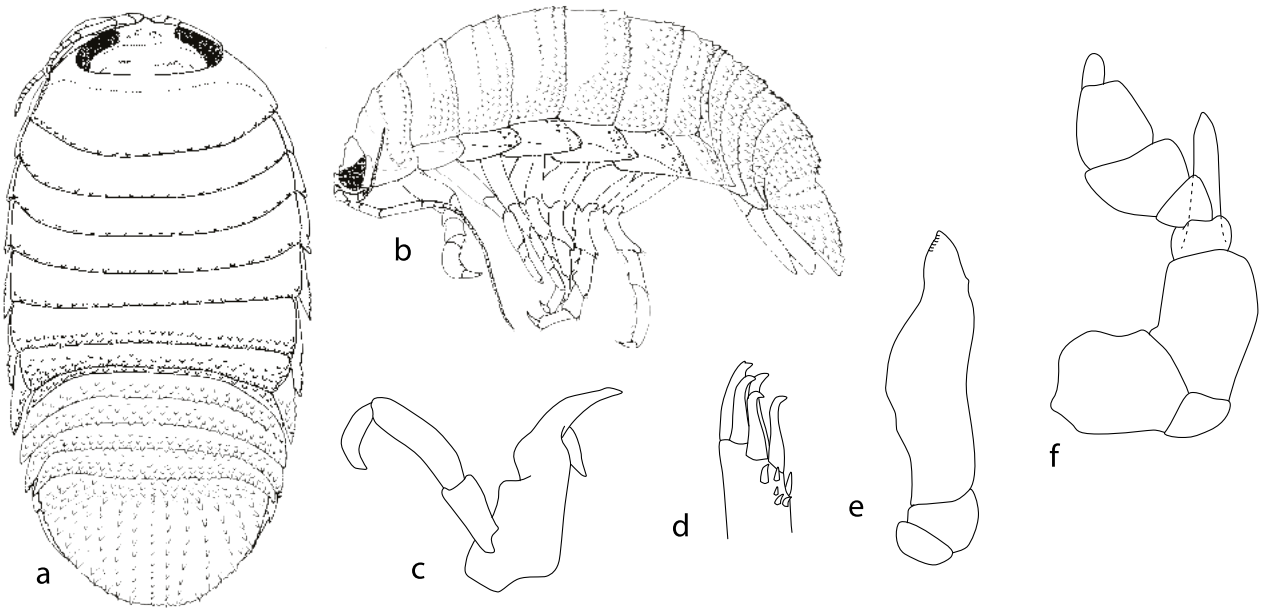


Figure 5.35. Tridentellidae. a, b, *Tridentella namibia* Brandt and Poore, 2001. *Tridentella*: c, mandible; d, maxillula apex; e, maxilla; f, maxilliped.

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Chapter 6. Suborder Epicaridea

(http://zoobank.org/urn:lsid:zoobank.org:pub:17E437E8-D068-4CDD-B8A1-5E2F45CFDACC)

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Abstract Boyko, C.B., and Williams, J.D. 2026. Chapter 6. Suborder Epicaridea. In: Poore, G.C.B. (ed.), Marine Crustacea Isopoda: guide to families and genera of the world. *Memoirs of Museum Victoria* 86: 229–354.

Diagnoses and keys are provided for 15 families, 13 subfamilies and 265 genera of epicaridean isopods. *Alaxphryxus* Boyko and Williams is diagnosed as a new genus of Hemiarthrinae. The ecology and distribution of each taxon are discussed with citation of literature critical for further investigation and identification of species.

Keywords Argeiinae, Asconiscidae, Athelginae, Bathygyginae, Bopyridae, Bopyrinae, Bopyroidea, Cabiropidae, Capitoniscidae, Crinoniscidae, Cryptoniscidae, Cryptoniscoidea, Cumoechidae, Cyproniscidae, Dajidae, Entoniscidae, Entophilidae, Hemiarthrinae, Hemioniscidae, Ionidae, Keponinae, Orbioninae, Phyllodurinae, Pleurocryptellinae, Podasconidae, Pseudioninae, Stellatoniscidae, dichotomous keys.

Introduction

Epicaridea Latreille, 1825 (c. 880 species fide Boyko et al., 2025; c. 8% of all isopods) contains species of isopods that parasitise intermediate and definitive crustacean hosts. Epicaridea is a longstanding name within Isopoda. Based on adult morphology, these parasites were formerly treated as two superfamilies (Bopyroidea Rafinesque, 1815 and Cryptoniscoidea Kossmann, 1880) within the suborder Cymothoida Wägele, 1989 (Brandt and Poore, 2003), a group that contains free-living and ectoparasitic isopods of fishes (see Dreyer and Wägele, 2001). However, molecular data has since provided support for a monophyletic Epicaridea that does not form a sister group relationship with any cymothoid (An et al., 2022; Boyko et al., 2013; Thomas Thorpe, 2024; Yu et al., 2018), calling into question the hypothesis that crustacean parasites evolved from fish parasites. Presently, Epicaridea is recognised as its own suborder of isopods (An et al., 2022).

Epicarideans are endoparasitic, mesoparasitic (with part of the female body embedded in the host) or ectoparasitic (including hyperparasites) on or in a wide range of crustacean definitive hosts; nearly all epicaridean species that have been investigated use a pelagic calanoid copepod as their intermediate host (figs 6.1a–d, 6.2c; Williams and Boyko, 2012; Williams et al., 2022). Within the epicarideans, there are presently 15 families: three in Bopyroidea (figs 6.1a, b, 6.2–6.4: Bopyridae Rafinesque, 1815, Entoniscidae Kossmann, 1881, and Ionidae H. Milne Edwards, 1840) and 12 in Cryptoniscoidea (figs 6.1c, d; 6.5, 6.6: Asconiscidae Bonnier, 1900, Cabiropidae Giard and Bonnier, 1887, Capitoniscidae Boyko and Williams, 2023, Crinoniscidae Bonnier, 1900, Cryptoniscidae Kossmann, 1880, Cumoechidae Boyko and Williams, 2023, Cyproniscidae Giard and Bonnier, 1887, Dajidae G.O. Sars, 1883, Entophilidae Richardson, 1903, Hemioniscidae Bonnier, 1900, Podasconidae Giard and Bonnier, 1895, and Stellatoniscidae Oanh and Boyko, 2020). Bopyridae is the most speciose group (650 species, Boyko et al., 2025), with ten subfamilies currently recognised: Argeiinae, Athelginae, Bathygyginae, Bopyrinae, Hemiarthrinae, Keponinae, Orbioninae, Phyllodurinae, Pleurocryptellinae and Pseudioninae (figs 6.1a, b, 6.2–6.4).

Adult female epicarideans reach sexual maturity on or in the definitive host (figs 6.1a–d, 6.2a–e, g). Typically, parasitised definitive hosts harbour one female and male pair, but several males may be found, and double infestations of mature females are known (e.g., Williams et al., 2023). The male isopods move into the brood chamber and fertilise the eggs within the marsupium of the female. The fertilised eggs develop into epicaridium larvae (figs 6.1a–d, 6.2b) and are then released into the water column to parasitise the intermediate copepod hosts. The epicaridium larva feeds on the copepod and metamorphoses into a microniscus larva (figs 6.1a–d, 6.2c), and then moults into a cryptoniscus larva (figs 6.1a–d, 6.2d) that detaches and seeks out the definitive crustacean host. The cryptoniscus larva settles on the definitive host and moves to the final attachment site on the host when ectoparasitic or penetrates the host if endoparasitic (figs 6.1a–d, 6.2a). The female cryptoniscus larva

will pierce the host and feed on its hemolymph or ovarian fluids, often shutting down reproduction of the host in the process (see review of life cycle and natural history of Epicaridea in Williams and Boyko, 2012).

The morphology of epicarideans is more highly modified than that of free-living isopods and even that of members of Cymothoida (ectoparasites of fish) (Dreyer and Wägele, 2001). All epicarideans exhibit sexual dimorphism, with larger females having more modified features than the dwarf males (figs 6.1–6.6). Bopyroids are nearly all ectoparasitic on decapod hosts (figs 6.1a, 6.2a–g), although one family (Entoniscidae: figs 6.1b, 6.4t–y) is exclusively endoparasitic. Cryptoniscoids are endoparasitic, mesoparasitic or ectoparasitic across a diverse assemblage of crustacean definitive hosts (fig. 6.1c), although one family (Dajidae: figs 6.1d, 6.5c, d) is exclusively ectoparasitic. Three families contain hyperparasites (Cabiropidae, Cryptoniscidae and Stellatoniscidae).

Bopyrids are instructive for demonstrating key morphological characters of epicarideans (figs 6.2, 6.3; see also Markham, 1985 and glossary therein, and Ribeiro and Horch, 2023), although these features (e.g. segmentation, pereopods) are further reduced or modified in many groups. Females residing in the branchial chamber of hosts may exhibit some degree of asymmetry (e.g. fig. 6.3a), whereas those ectoparasitic on the abdomens of hosts may be more symmetrical, with pereopods clustered around the head and oostegites extending beyond the margin of the head (fig. 6.2a, e). Although species in most genera exhibit five pairs of large and midventrally overlapping oostegites (fig. 6.3b), females within putatively primitive bopyrid genera (e.g., *Pleurocryptella* Bonnier, 1900) retain seven pairs of oostegites (fig. 6.3e, f). Some genera contain species that have smaller oostegites that do not meet midventrally (fig. 6.3k), thus the marsupium is partially open but eggs/larvae are retained by the host covering. The first oostegite is divided into two lobes (fig. 6.3c, m); typically, the anterior lobe is larger and rounded, whereas the posterior lobe is smaller and rounded or extended into a posterolateral point and the two lobes are divided by an internal ridge that may be smooth (fig. 6.3c) or digitate (fig. 6.3m). The maxilliped is found underneath oostegite 1 (fig. 6.3h) and is composed of two lobes: the anterior lobe, which may possess an articulated or non-articulated palp (fig. 6.3h), and the posterior lobe, exhibiting a spur-like lateral extension. The head is generally rounded and may be partially or completely divided into two lobes (figs 6.3n, 6.4e, p) and often has a frontal lamina extending beyond the anterior margin (e.g. figs 6.2a, 6.3j, 6.4e, m). Eyes are usually lacking but, if present, they are small and irregularly shaped (fig. 6.4h). Body pigmentation is also typically lacking, although some species may exhibit extensive pigmentation on the pereomeres and pleomeres. The posteroventral border of the head exhibits posterolateral projections (termed barbula; figs 6.2h, 6.3g, l) that may be smooth (fig. 6.3g) or digitate (fig. 6.3l) and the posterior margin between the lobes may likewise be smooth or digitate. The antennae (antennula = antenna 1; antenna = antenna 2) are generally reduced to 3–6 articles and often obscured by the frontal lamina and anterior structures (compare with fig. 6.3k). The seven pereomeres may exhibit dorsolateral bosses anterior to tergal projections on each segment, sometimes with coxal plates on the lateral edge (e.g., fig. 6.3a, j, n). Species in some genera exhibit middorsal projections on the posterior pereomeres and pleomeres (fig. 6.3n). The pereopods of the females are generally gnathopodal and exhibit six articles (dactylus to basis), although in some there is partial fusion of articles. The pleon is typically composed of five pleomeres plus uropods and sometimes a pleotelson extension with an anal cone. The number of pleomeres is variable due to fusion in some groups; the pleomeres may exhibit lateral extensions on the dorsal side (lateral plates), and ventrally they may exhibit pleopods that can be biramous (endopod, inner ramus and exopod, outer ramus) or uniramous (figs 6.2a, 6.3i, j, n). The uropods may also be uniramous or biramous; sometimes being similar in morphology to the pleopods or greatly extended; both pleopods and uropods may be smooth (figs 6.2a, 6.4c, k, p, r), tuberculate (figs 6.3j, k, 6.4g) or highly digitate (figs 6.3n, 6.4a, e). The pleotelson, if present, is generally small and produced into an anal cone; in species of some genera the pleotelson is elongate and large (fig. 6.4r).

Males exhibit a more typical isopod form with distinct segmentation. The head is often fused with the first pereomere (fig. 6.2f) and eyes, if present, range in size from minute to relatively large and irregularly shaped (fig. 6.4l). Body pigmentation may be present as small, scattered groups of pigment. As in females, the antennae are generally reduced to 3–6 articles, with antennulae being overall smaller and with fewer articles than the antennae (fig. 6.2l). Maxillipeds may be present or absent. The seven pereomeres may exhibit midventral projections (tubercles) on some segments (fig. 6.3o). The pereopods of males are generally gnathopodal and have six articles (basis to dactylus ; fig. 6.2k), although in some groups articles may be fused. Some species exhibit greatly enlarged anterior pereopods. The pleon exhibits variable degrees of segmental fusion, from being completely fused (figs 6.2f, 6.4d, l, s), fusion with indication of segments (fig. 6.4n), to exhibiting five clearly divided pleomeres plus pleotelson with anal cone (figs 6.2i, j, 6.3o, 6.4f, i, q); in a few groups (e.g. *Pleurocryptella*) the males exhibit "true" articulating uropods. Pleomeres are often produced laterally to a slight degree and more separated than the pereomeres (e.g. figs 6.2i, 6.4j) but some have long lateral extensions (fig. 6.4b). Pleopods may be present on the pleomeres (fig. 6.2i) and midventral tubercles likewise (fig. 6.3o). The pleotelson, if present, may be in the form of two distally rounded lobes (figs 6.2i, 6.4f, i) that in some cases may be greatly elongate (figs 6.2j, 6.4b).

The larval stages of epicarideans are more poorly known than adults for nearly all species; however, they hold key characters, especially for the cryptoniscoids (some of which are known only from the males that retain the cryptoniscus larval stage form when sexually mature; i.e. they are neotenous). The first and second larval stages, the epicaridium and microniscus larvae, are the least studied (Williams et al., 2022) and the micronisci are particularly hard to study due to their short duration and soft cuticle. *Microniscus* Müller, 1871 is also a valid genus name but is functionally a larval group with six included described and named species, all of which are based solely on the epicaridean microniscus stage and will likely not

ever be identifiable to any taxon within Epicaridea. The third and final larval stage, the cryptoniscus larva, is the best studied and can be used to distinguish between some of the groups of bopyroids and cryptoniscoids based on characters such as the antennal article count (figs 6.1a–d, 6.2d1; Boyko et al., 2013; Boyko and Williams, 2015). Additional important characters of the cryptoniscus larva include antennula morphology (fig. 6.2d1), pereopod morphology (fig. 6.2d2, d3) and pleotelson plus uropod morphology (fig. 6.1d4).

Although bopyrid morphology is a good starting point for understanding the overall morphology of epicarideans (including Ionidae and Entophilidae), their form is quite variable and becomes extremely modified in species of some genera and families. In some groups, the females may exhibit so much fusion and reduction of characters (e.g. segmentation, pereopod number) that they can only be identifiable to the species level if males or cryptoniscus larvae are present. This is the case for the bopyroid family Entoniscidae (fig. 6.3t–y) and nearly all of the cryptoniscoids (figs 6.5, 6.6). Among the cryptoniscoids, the family Entophilidae (fig. 6.5a, b) is unique in that the females and males retain a morphological form that generally matches that described for some bopyroids (e.g. with clear segmentation). Dajidae (fig. 6.5c, d) are all ectoparasitic cryptoniscoids, females of which are ovate in shape, have gnathopodal pereopods or antennae to clutch onto hosts, and retain some degree of segmentation. The rest of the cryptoniscoids (figs 6.5e–t, 6.6) have females with highly reduced bodies: from sac-like and lacking pereopods (figs 6.5e, h, k, t, 6.6a, d, f, i) to stellate-shaped bodies (fig. 6.5n) and males that retain a cryptoniscus larval-type morphology when sexually mature (figs 6.5f, g, m, o, p, r, 6.6b, e, g, j). Some groups contain hyperparasitic species, including Cabiropidae (fig. 6.6c–e) most of which parasitise bopyrid isopods, Cryptoniscidae (fig. 6.6a, b), some of which parasitise rhizocephalan barnacles, and Stellatoniscidae (fig. 6.5n, o) that parasitise entoniscid isopods. Although females of some cryptoniscoids lose all evidence of segmentation, those of Hemioniscidae (fig. 6.5e) and Asconiscidae (fig. 6.5t) retain anterior segmentation when mature.

Key to superfamilies, families and subfamilies of Epicaridea

Monotypic families and subfamilies with genus shown in parentheses

1. Cryptoniscus larva with antenna of fewer than 9 articles (fig. 6.1a, b) ..... Bopyroidea ... 2
– Cryptoniscus larva with antenna of 9 (4 basal + 5 flagellar) articles (fig. 6.1c, d) ..... Cryptoniscoidea ... 16
2. Female not vermiform, pereopods, antennulae and antennae articulated. Male with articulated antennulae and antennae. Cryptoniscus larva with antenna of 8 (4 basal + 4 flagellar) articles (fig. 6.1a). Ectoparasitic .. 4
– Female vermiform, pereopods, antennulae and antennae non-articulated. Male with antennula non-articulated, antennae lacking. Cryptoniscus larva with antenna of 7 or fewer (4 basal + 1 or 3 flagellar) articles (fig. 6.1b). Endoparasitic ..... Entoniscidae ... 14
4. Female with uropods bearing lateral plates, numerous filamentous rami extending from lateral plates. Male with long, slender lateral plates. Cryptoniscus larva with pereopodal dactyli each bearing an elongate dorsomedial seta (fig. 6.4a, b). Ectoparasitic, branchial ..... Ionidae (*Ione*) ... p. 314
– Female with uropods lacking lateral plates. Male without long, slender lateral plates. Cryptoniscus larva without pereopodal dactyli bearing an elongate dorsomedial seta. Ectoparasitic (figs 6.2, 6.3) ..... Bopyridae ... 5
5. Female with coxal plates large, first 2 pairs medially directed; second oostegites extending beyond anterior margin of head; pleon flexed anterodorsally over pereon. Male with distoventral extension on all propodi, each with slot into which dactylus inserts (fig. 6.4c, d). Ectoparasitic, branchial ..... Bathygyginae (*Bathygyge*) ... p. 249
– Female with variable coxal plates, if large, first 2 pairs not medially directed; second oostegites not extending beyond anterior margin of head; pleon not flexed anterodorsally over pereon. Male without distoventral extensions on propodi 6
6. Female with pleomeres having extended, digitate or tuberculate lateral plates, usually directed anterolaterally from pleon (fig. 6.4e, f). Ectoparasitic, branchial ..... Keponinae ... p. 270
– Female with pleomeres having short, simple, non-digitate or tuberculate lateral plates, usually directed laterally, or lateral plates lacking 7
7. Female with marsupium not much enlarged beyond margins of pereon, composed of 5 pairs of loosely fitting subequal oostegites; pleopods, when present, not pedunculate 8
– Female with marsupium enlarged beyond at least one side of pereon, formed of close-fitting oostegites, usually fewer than 5 pairs, unequal in size; pleopods and lateral plates, when present, pedunculate 12

8. Female with coxal plates and frontal lamina of head greatly enlarged, giving anterior portion of body semicircular shape (fig. 6.4g). Ectoparasitic, branchial ..... Orbioninae ... p. 280

– Female with coxal plates and frontal lamina not greatly enlarged, body more linear 9

9. Female with well-developed pleopods. 10

– Female with small tuberculiform, triangular or ovate pleopods 11

10. Male with unsegmented or reduced maxilliped. Epicaridium larvae without external yolk sac (fig. 6.4h, i). Ectoparasitic, branchial or abdominal ..... Pseudioninae ... p. 287

– Male with segmented, setose maxilliped (in some segmentation may appear indistinct). Epicaridium larvae with external yolk sac (fig. 6.4j). Ectoparasitic, branchial ..... Pleurocryptellinae ... p. 284

11. Female with head oval or fusiform, never fused with pereon; lateral plates pedunculate; pleopods knob-like, uniramous (fig. 6.4k, l). Ectoparasitic, branchial ..... Argeiinae ... p. 242

– Female with head subrectangular or subtriangular, often fully or partially fused with pereon; lateral plates, if present, not pedunculate; pleopods flap-like, usually biramous (fig. 6.4m, n). Ectoparasitic, branchial ..... Bopyrinae ... p. 250

12. Female with symmetrical to slightly asymmetrical body, brood pouch symmetrical to slightly asymmetrical (if asymmetrical then expanded on one side at posterior margin), formed by oostegites from both sides of body 13

– Female with highly asymmetrical body, brood pouch greatly expanded and formed by oostegites from one side of body (fig. 6.4o). Ectoparasitic, abdominal ..... Hemiarthrinae ... p. 260

13. Female with symmetrical body; lateral margins of head not overlapped by forward curved lateral portions of posterior pereomeres; lateral plates and pleopods falcate (fig. 6.4p, q). Ectoparasitic, abdominal ..... Phyllodurinae (*Phyllodurus*) ... p. 283

– Female with asymmetrical body; lateral margins of head overlapped by forward curved lateral portions of posterior pereomeres; lateral plates and pleopods variably foliose (thin elongate to broad) (fig. 6.4r, s). Ectoparasitic, abdominal ..... Athelginae ... p. 245

14. Female marsupium formed by close adhesion of oostegites to host membrane. Male with articulated pereopods 15

– Female oostegites free, not adhering to host membrane; pleural lamellae absent; female without pereopods. Male with non-articulated pereopods (fig. 6.4t, u). Endoparasitic ..... Entoniscinae ... p. 307

15. Parasitic in decapods other than hermit crabs. Female with well-developed pleural lamellae, with heart tubercle in pleomere 3 (fig. 6.4v, w). Endoparasitic ..... Entioninae ... p. 311

– Parasitic in hermit crabs. Female without pleural lamellae, with heart tubercle in pleomere 1 (fig. 6.4x, y). Endoparasitic ..... Diogenioninae ... p. 309

16. Mature female with segmented body; antennae lobe-like; pereopods prehensile; pleopods present. Mature male morphology distinct from cryptoniscus larval form; antennae lobe-like; pereopods prehensile. Cryptoniscus larva with isomorphic pereopods 17

– Mature female with unsegmented body; antennae absent or articulate; pereopods absent or styliform; pleopods absent. Mature male morphology similar to cryptoniscus larval form, antennae articulate; pereopods styliform. Cryptoniscus larva without isomorphic pereopods, posterior pairs elongate with long dactyli 18

17. Mature female elongate, body segments distinct in dorsal view, head distinct from pereon, 7 pairs of pereopods equally distributed along body. Male with segmented pleon. Cryptoniscus larva without oral sucker (fig. 6.5a, b). Endoparasitic, abdominal ..... Entophilidae ... p.338

– Mature female ovate, body segments indistinct in dorsal view, head and pereon fused, first 5 pairs of pereopods adjacent to each other near head, pereopod 7 usually absent. Male with fused pleomeres. Cryptoniscus larva usually[1] with oral sucker (fig. 6.5c, d). Ectoparasitic ..... Dajidae ... p. 330

18. Female parasitising thecostracan barnacles 19

– Female parasitising other hosts 20

19. Male (paedomorphic cryptoniscus) with teeth on basal article of antennula (fig. 6.5e, f). Endoparasitic ..... Hemioniscidae[2] ... p. 340

– Male (paedomorphic cryptoniscus) without teeth on basal article of antennula (fig. 6.5g–i). Endoparasitic ..... Crinoniscidae (*Crinoniscus*)[3] ... p. 322

20. Mature female with stellate body, parasitising entoniscid isopods (fig. 6.5n, o). Endoparasitic ..... Stellatoniscidae (*Stellatoniscus*) ... p. 344

– Mature female without stellate body 21

21. Female parasitising ostracods (fig. 6.5j–m). Ectoparasitic ..... Cyproniscidae ... p. 328

– Female parasitising amphipods (fig. 6.5p, q). Ectoparasitic ..... Podasconidae ... p. 342

– Female parasitising mysids (fig. 6.5r–t). Ectoparasitic ..... Asconiscidae (*Asconiscus*) ... p. 316

– Female parasitising other hosts 22

22. Cryptoniscus larva with dactylus and propodus of pereopods 6 and/or 7 fused, forming elongate rapier-like structure. Parasitising rhizocephalans and decapods (fig. 6.6a, b). Endoparasitic or mesoparasitic ..... Cryptoniscidae ... p. 324

– Cryptoniscus larva with dactylus and propodus of pereopods 6 and 7 not fused, dactylus articulating with propodus. 23

23. Cryptoniscus larva head "typical" (frontal margin not projected forward or inflated). Parasitising rhizocephalans and isopods (fig. 6.6c–e). Endoparasitic, mesoparasitic or ectoparasitic ... Cabiropidae ... p. 316

– Cryptoniscus larva head atypical (frontal margin either projected forward or inflated) 24

24. Cryptoniscus larva with conical head, posterior margin no wider than pereomere 1; antennular basal article with marginal teeth; dactylus approximately half as long as propodus. Parasitising cumaceans (fig. 6.6f–h). Ectoparasitic ..... Cumoechidae ... p. 327

– Cryptoniscus larva with inflated, rounded head, posterior margin much wider than pereomere 1; antennular basal article without marginal teeth; dactylus longer than propodus. Parasitising cumaceans (fig. 6.6i, j). Ectoparasitic ..... Capitoniscidae ... p. 322

[1] See remarks in Williams and Boyko (2021).

[2] Cryptothiridae (*Cryptothir* Dana, 1853) was poorly described from the cryptoniscus larva only and is a *nomen dubium*; based on the host barnacle, it is probably synonymous with either Crinoniscidae or Hemioniscidae.

[3] *Proteolepas* Darwin, 1854 is placed in Crinoniscidae but is a *nomen dubium*; it may be synonymous with *Crinoniscus*.

Acknowledgements

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Credits

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Fig. 6.1a, c, Williams et al. (2022); b, McDermott et al. (2019); d, Williams and Boyko (2021); insets, Boyko and Williams (2015). Fig. 6.2a–c, e–h, Cericola and Williams (2015); d, i, k, l, Williams et al. (2019); j, Bourdon and Bowman (1970). Fig. 6.3a, b, h, i, Williams et al. (2019); c–g, Boyko and Williams (2010); j–m, An et al. (2013); n, o, An et al. (2019). Fig. 6.4a, b, Trilles (1999); c, d, Markham (2016); e, f, Bourdon (1983); g, An et al. (2013); h, i, Boyko and Williams (2004); j, Williams et al. (2024); k, Williams et al. (2022); l, An et al. (2015); m, n, Williams and Boyko (2004); o, Boyko and Williams (2004); p, q, Richardson (1905); r, s, Williams and Boyko (2016); t, u, Miyashita (1940); v, w, Uyeno and Boyko (2020); x, y, DeTorre (et al. (2023). Fig. 6.5a–d, Boyko and Williams (2012); e, Trilles (1999); f, Goudeau (1970); g–i, Buhl–Mortensen et al. (2020); j–m, Shiino (1942); n, o, Oanh and Boyko (2020); p, q, Giard and Bonnier (1895); r–t, Sars (1899). Fig. 6.6a, b, Boyko (2014); c–e, Carayon (1942); f–j, Boyko and Williams (2023). Fig. 6.7a–c, An et al. (2015); d, Chopra (1923); e, Nierstrasz and Brender à Brandis (1923); f, g,

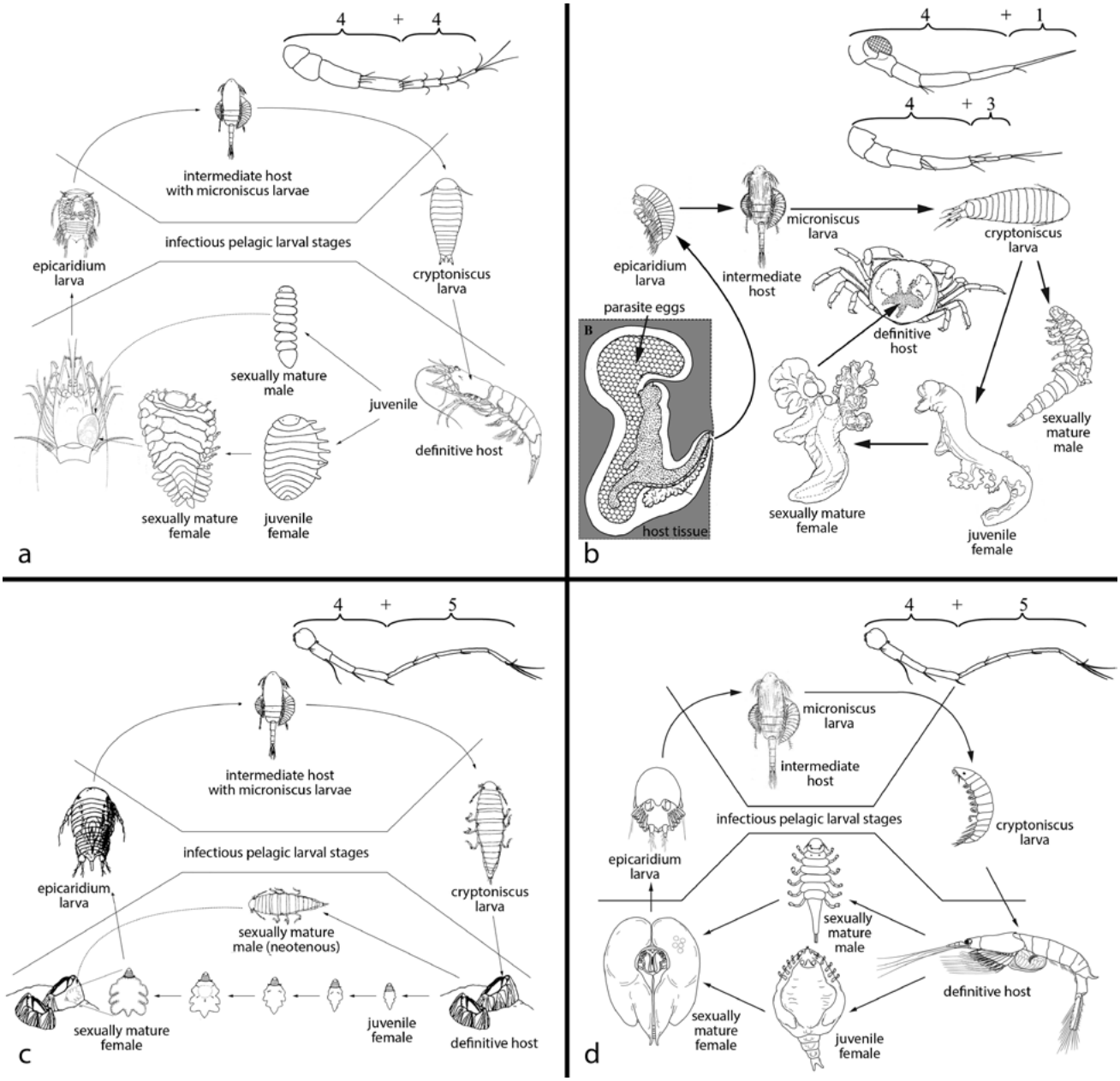


Figure 6.1. Epicaridea (Bopyroidea and Cryptoniscoidea). Representative life cycles (a–d) and antennal articulation of their respective cryptoniscus larvae. a, life cycle of *Argeia pugettensis* Dana, 1853 (Bopyridae, Argeiinae), inset shows 4 peduncular and 4 flagellar articles of cryptoniscus larval antennae. b, life cycle of *Pinnixion sexdecennia* McDermott, Williams and Boyko, 2019 (Entoniscidae, Entioninae), inset shows 4 peduncular and 1 or 3 flagellar articles of cryptoniscus larval antennae in Entoniscidae. c, life cycle of *Hemioniscus balani* Buchholz, 1866 (Cryptoniscoidea, Hemioniscidae), inset shows 4 peduncular and 5 flagellar articles of cryptoniscus larval antenna. d, life cycle of *Prodajus ostendensis* Gilson, 1909 (Cryptoniscoidea, Dajidae), inset shows 4 peduncular and 5 flagellar articles of cryptoniscus larval antenna.

Williams and Boyko (2010); h, i, An et al. (2017); j, Kensley (1974); k, l, Bourdon and Bruce (1983); m, n, Danforth (1970); n, o, Shiino (1958). Fig. 6.8a, b, Markham (1972); c, d, i–o, Williams and Boyko (2016); e–h, Boyko and Williams (2003); p, q, Cericola and Williams (2015). Fig. 6.9a, b, Markham (2016); c, d, An et al. (2015). Fig. 6.10a, b, Bourdon (1968); c, p, q, Markham (1982); d, Shiino (1933); e, Bourdon (1976); f, g, Markham (1989); h, i, Markham (1988); j, k, Richardson (1904); l, m, Ribeiro et al. (2019); n, o, t, u, Markham (1985); r, s, Adkison (1984); v, w, An et al. (2015). Fig. 6.11a, b, Nierstrasz and Brender à Brandis (1929); c, f, g, Bourdon (1983); d, e, An et al. (2015); h, i, Boyko (2004); j, Bourdon (1968); k,

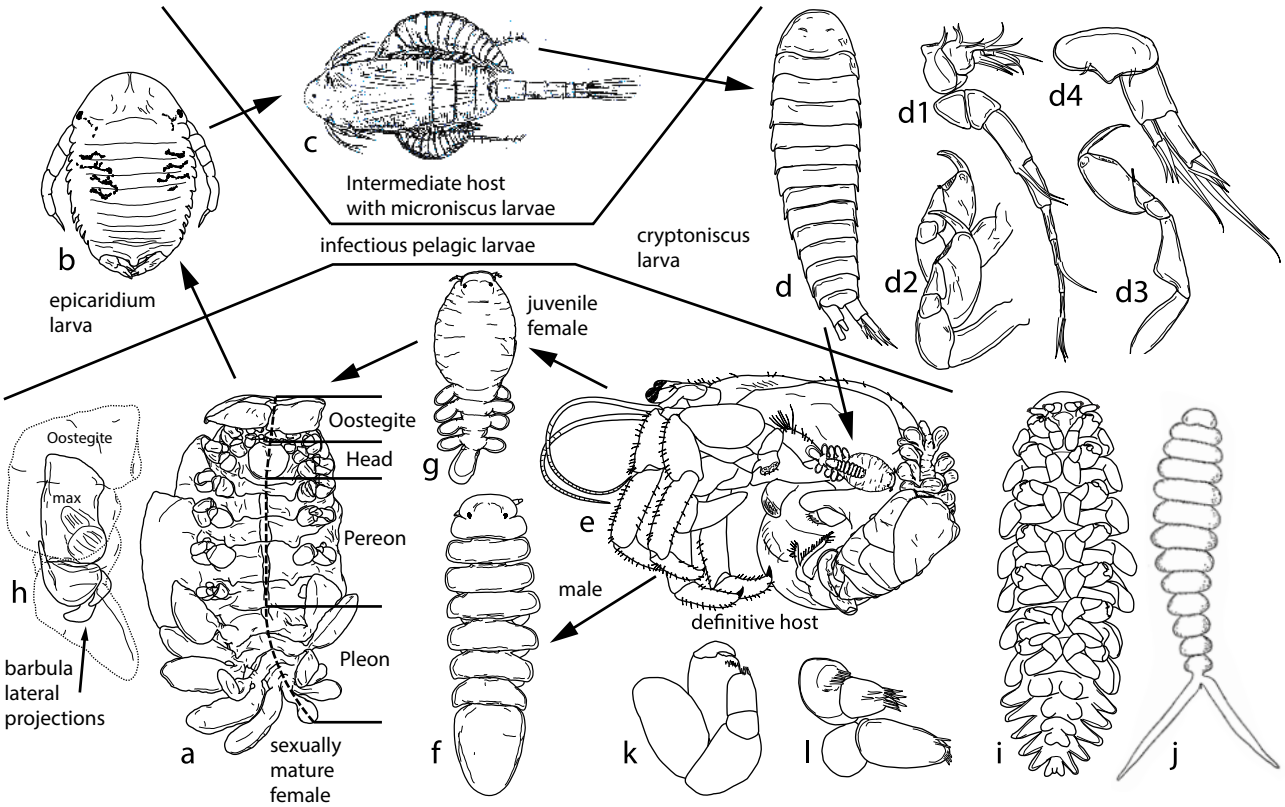


Figure 6.2. Epicaridea (Bopyridae). Life cycle stages and morphology: a, e, adult females; b, epicaridium larva; c, microniscus larva; d, cryptoniscus larva; f, i, j, adult males; g, juvenile female. a, female, ventral view; b, epicaridium larva, dorsal view; c, microniscus larvae on copepod intermediate host; d, cryptoniscus larva, dorsal view and parts (d1, antennula, antenna; d2, pereopods 1, 2; d3, pereopod 7; d4, pleotelson and right uropod); e, adult female plus juvenile female and male pair on hermit crab definitive host; f, male, dorsal view; g, juvenile female; h, maxilliped and lateral extensions of barbula shown within oostegite 1; i, male, ventral view; j, male, dorsal view; k, male, pereopod 1; l, male, antennula and antenna.

Richardson (1904); l, Shiino (1934); m, n, Bourdon and Bruce (1983); o, p, Shimomura et al. (2006); q, r, Markham (1985); s, t, Bourdon (1981); u–w, Bourdon and Markham (1980). Fig. 6.12a, b, Bruce, 1975; c, d, Bruce, 1973b; e, Bruce, 1972b; f, Shiino, 1937; g, Nierstrasz and Brender à Brandis, 1932; h, i, Bruce, 1974; j, Markham, 1985; k, q, r, Shiino, 1934; l, Richardson, 1904; m, Saito, 2020; n, Boyko, 2012; o, Saito, 2015; p, Nierstrasz and Brender à Brandis, 1931; s, An et al., 2015; t, u, Markham, 1972; v, Bruce, 1973a. Fig. 6.13a–d, Markham, 1990; e, Markham, 1972; f, n, Markham, 1985; g, Nierstrasz and Brender à Brandis, 1931; h, i, Saito and Shimomura, 2015; j, Barnard, 1955; k, Markham, 1992; l, Nierstrasz and Brender à Brandis, 1932; m, Boyko and Williams, 2004; o, p, Chopra, 1923. Fig. 6.14a, b, Shiino (1936b); c, Nobili (1906); d, Tattersall (1905); e, f, An et al. (2012); g, h, Bourdon (1968); i, p q, Shiino (1937); j, k, Shiino (1951); l, An et al. (2019); m, u, Nierstrasz and Brender à Brandis (1931); n, An et al. (2018); o, Shiino (1936b); r, s, Bourdon (1977); t, Nierstrasz and Brender à Brandis (1930a); v, An et al. (2007); w, Uyeno and Boyko (2020); x, Williams et al. (2023). Fig. 6.15a, b, g, h, Nierstrasz and Brender à Brandis (1931); c, d, Shiino (1936a); e, f, Brasil Lima (1980); i, j, q, r, Danforth (1972); k, Nierstrasz and Brender à Brandis (1930b); l, m, An et al. (2006a); n, o, Bourdon and Bowman (1970). Fig. 6.16a, b, h, Bourdon (1981); c, d, Bourdon (1968); e, Boyko (2003); f, g, k, l, An et al. (2013a); i, j, Bourdon (1982); m, n, Shiino (1950); o, p, Richardson (1904). Fig. 6.17a–c, Richardson (1905). Fig. 6.18a–h, Bourdon (1981); i, Boyko et al. (2024); j–o, Williams et al. (2024); p, q, Bourdon (1979); r, s, Boyko and Williams (2010); t, u, Bourdon (1972b); v, Nierstrasz and Brender à Brandis (1929). Fig. 6.19a, Saito and Moritaki, 2020; b, c, Pérez, 1920; d, e, Boyko and van der Meij, 2018; f, g, Bourdon and Boyko, 2005; h, i, l, o, Shiino, 1933; j An et al., 2010; k Markham, 2010; m, n, Williams et al., 2019; p, q, Shiino, 1949. Fig. 6.20a, Dollfus and Carayon, 1942; b, c, An et al., 2016a; d, e, Markham and Boyko, 1999; f, Kensley, 1974; g, Markham, 1979; h, Bourdon, 1972a; i, An et al., 2015; j, Markham, 1999; k, Markham, 1994; l, Van Name, 1920; m, n, Adkison and Heard, 1995; o, An et al., 2016b; p, Bourdon, 1983; q, An et al., 2009; r, Williams and An, 2009; s, t, Markham, 1985; u, SOSA et al., 2025; v, Bourdon, 1968; w, Nobili, 1906. Fig. 6.21a, Nobili, 1906; b, c, Bourdon, 1968; d, e, n, Nierstrasz and Brender à Brandis, 1929; f, Markham, 1978a; g, h, Bourdon,

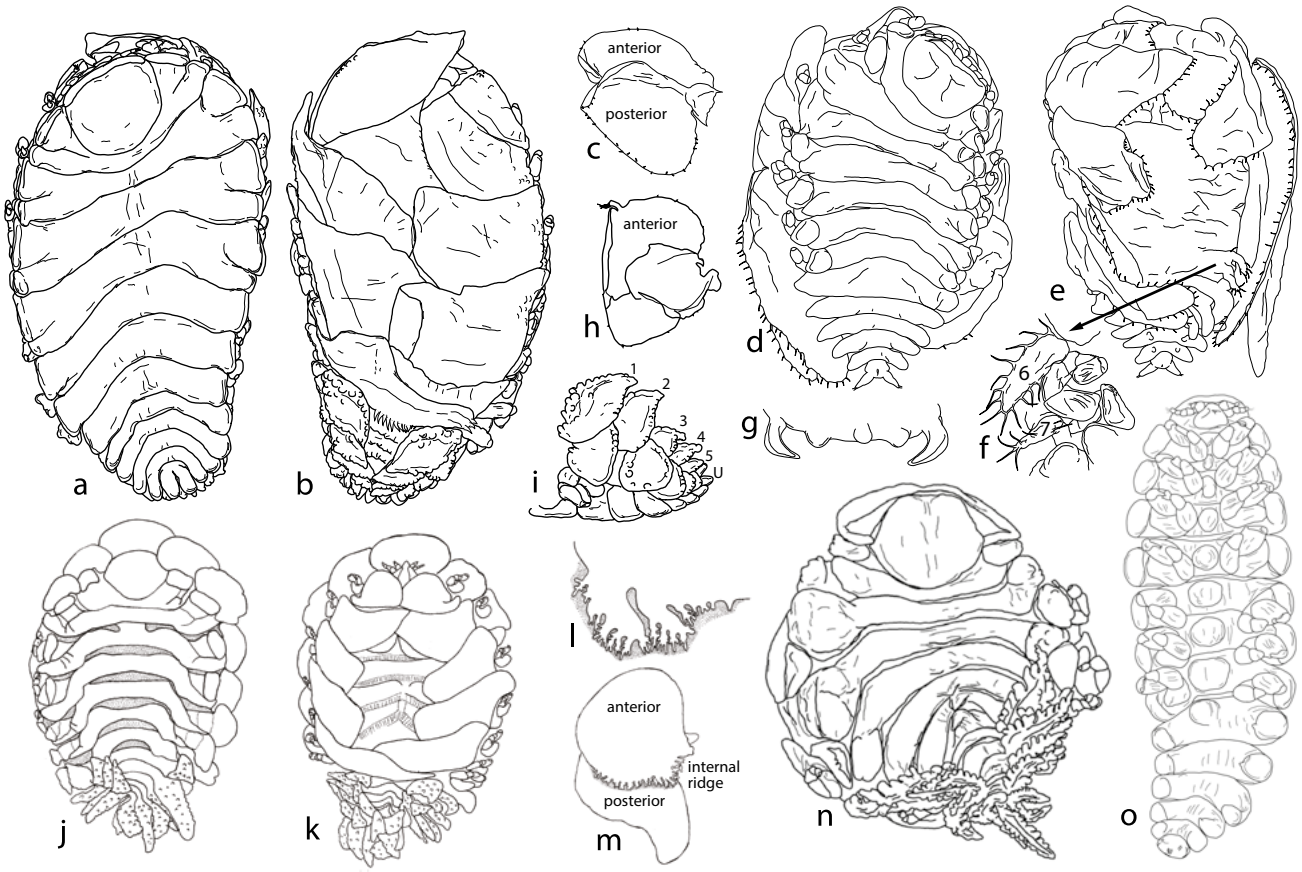


Figure 6.3. Epicaridea (Bopyridae). Representative adult females and males. a, female, dorsal view; b, female, ventral view; c, oostegite 1, internal view; d, female, dorsal view; e, female, ventral view showing oostegites 6 and 7; f, close up of oostegites 6, 7 and pereopod 7; g, barbula, both sides shown; h, maxilliped with palp; i, lateral view of pleon; j, female, dorsal view; k, female, ventral view; l, barbula, only one side shown; m, oostegite 1, internal view; n, female, dorsal view; o, male, ventral view.

1976; i, j, Markham, 1974; k, Richardson, 1910; l, Markham, 2008; m, Román-Contreras and Soto, 2002; n, Román-Contreras, 2008. Fig. 6.22a, Nierstrasz and Brender à Brandis, 1923; b, Román-Contreras and Boyko, 2007; c, d, Shiino, 1934; e, f, Markham, 1988; g, h, Boyko et al., 2018; i, j, Markham, 1975b; k, l, Shiino, 1958; m, n, Markham, 1975a; o, Richardson, 1904; p, Williams and Madad, 2010; q, An et al., 2020; r, Nierstrasz and Brender à Brandis, 1929. Fig. 6.23a, b, Miyashita (1940); c, d, Reinhard (1945); e, f, Codreanu et al. (1960); g–l, Uyeno and Boyko (2020); m–o, McDermott et al. (2019); p, Williams et al. (2023). Fig. 6.24a–g, Bourdon (1968). Fig. 6.25a–g, Sars (1899). Fig. 6.26a, Boyko (2013); b, c, Caullery and Mesnil (1920); d, e, Shiraki and Kakui (2024); f, p, Giard and Bonnier (1895); g, Sars (1883); h–l, Pillai (1966); m, Barnard (1925); n, o, Nierstrasz and Brender à Brandis (1931); q–t, Sassaman (1985); u, v, Hansen (1916); w, x, Rybakov (1990). Fig. 6.27a–f, Bourdon (1972); g–l, Schultz (1977). Fig. 6.28a–h, Buhl–Mortensen et al. (2020). Fig. 6.29a, Pérez (1920); b, c, Peresan and Roccatagliata (2005); d, Fraisse (1878); e–n, Boyko (2014); o, Boyko and van der Meij (2018). Fig. 6.30a–h, Hansen (1916). Fig. 6.31a–c, Sars (1883); d–i, Shiino (1942). Fig. 6.32a–d, Williams and Boyko (2021); e, f, Shields and Gómez–Gutiérrez (1996); g, p, q, Sars (1885); h, i, Boyko and Williams (2012); j–l, Shimomura et al. (2005); m, Richardson (1909); n. o, Koehler (1911). Fig. 6.33a, f, Richardson (1908a); b–d, Nierstrasz and Brender à Brandis (1923); e, G.O. Sars (1883); g, Schultz (1978); h, Williams and Boyko (2021); i–k, Boyko and Williams (2021b); l–n, Jones and Smaldon (1986); o–q, Nierstrasz and Brender à Brandis (1931). Fig. 6.34a, b, f, g, Markham and Dworschak (2005); c–e, Boyko and Williams (2015); h–j, Richardson (1903); k–n, Bourdon (1976). Fig. 6.35a–d, Grygier (1981a); e, Goudeau (1977); f, g, Goudeau (1970); h, Hosie (2008); i, j, Grygier (1981b). Fig. 6.36a, d–j, Giard and Bonnier (1885); b, c, Giard and Bonnier (1899). Fig. 6.37a–i, Oanh and Boyko (2020). Fig. 6.38a–h, Bourdon (1983); i–q, Schultz (1977). Fig. 6.39a–i, p–s, Schultz (1977); j, k, Nielsen (1967); l–o, Bourdon (1981); t–w, Williams et al. (2022). Fig. 6.40a–d, Bourdon (1967); g–k, Bourdon (1981); l–s, Schultz (1977); t–w, Williams et al. (2024). Fig. 6.41a–m, Schultz (1977); n–q, Schädel et al. (2019).

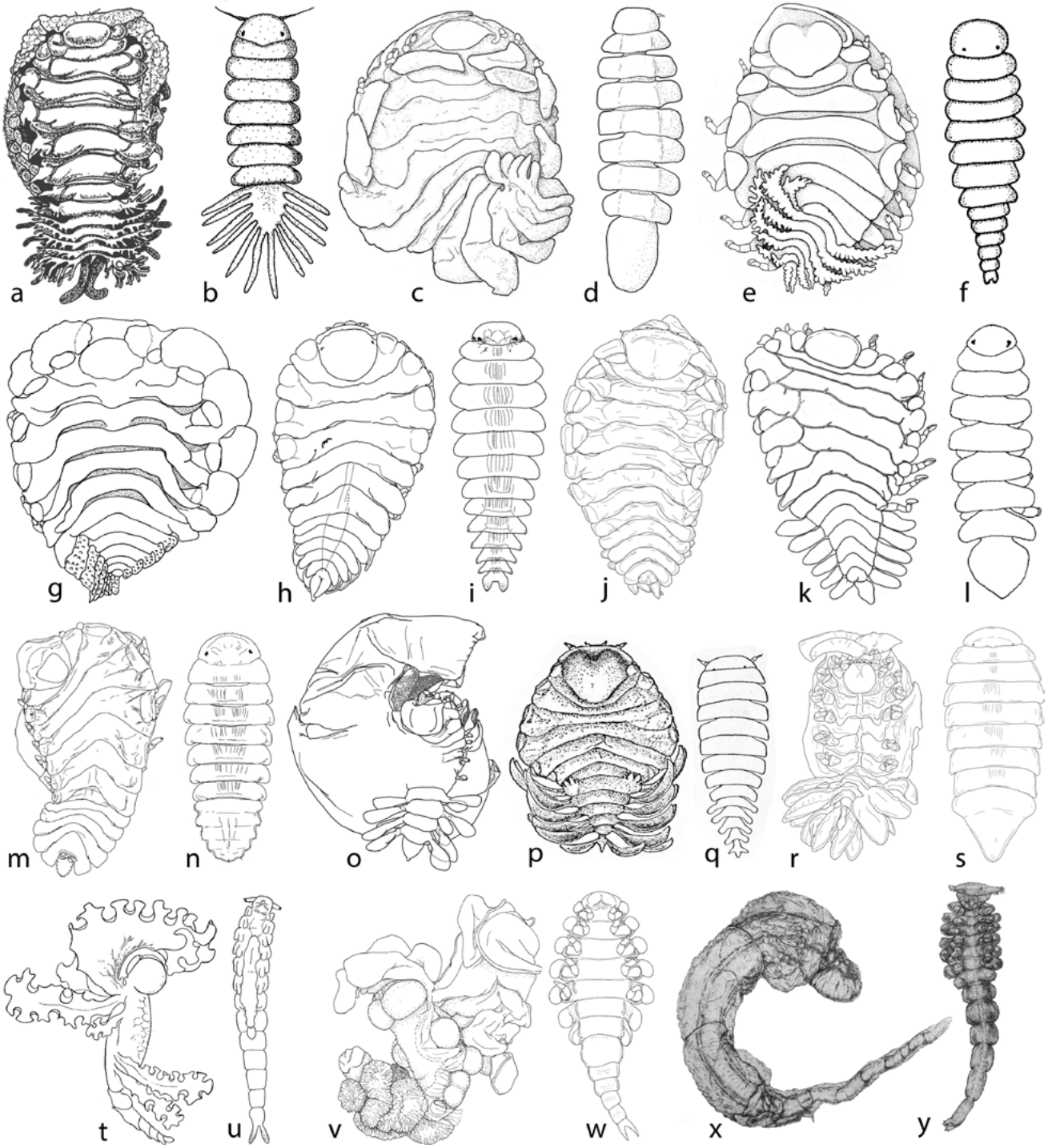


Figure 6.4. Epicaridea (Ionidae, Bopyridae, and Entoniscidae). Representative adult females and males. a, b, Ionidae: *Ione thoracica* (Montagu, 1808); c, d, Bathygyginae: *Bathygyge grandis* Hansen, 1897; e, f, Keponinae: *Dactylokepon semipennatus* Bourdon, 1983; g, Orbioninae: *Parasymmetrorbione bicauda* An, Boyko and Li, 2013; h, i, Pseudioninae: *Pseudione quasimodo* Boyko and Williams, 2004; j, Pleurocryptellinae: *Pleurocryptella poseidon* Williams and Boyko in Williams, Boyko and Stewart, 2024; k, l, Argeiinae: *Argeia pugettensis* Dana, 1853; m, n, Bopyrinae: *Schizobopyrina bombyliaster* Williams and Boyko, 2004; o, Hemiarthrinae: *Hemiarthrus surculus* Boyko and Williams, 2004; p, q, Phyllodurinae: *Phyllodurus abdominalis* Stimpson, 1857; r, s, Athelginae: *Allathelges alisonae* Williams and Boyko, 2016; t, u, Entoniscinae: *Entoniscoides okadai* Miyashita, 1940; v, w, Entioninae: *Allocancrion yunnu* Uyeno and Boyko, 2020; x, y, Diogenioninae: *Diogenion vermifactus* Codreanu, Codreanu and Pike, 1960. a, c, e, g, h, j, k, m, o, p, r, mature female, dorsal view; t, v, x, mature female, lateral view; b, d, f, i, l, n, q, s, male, dorsal view; u, w, y, male, ventral view.

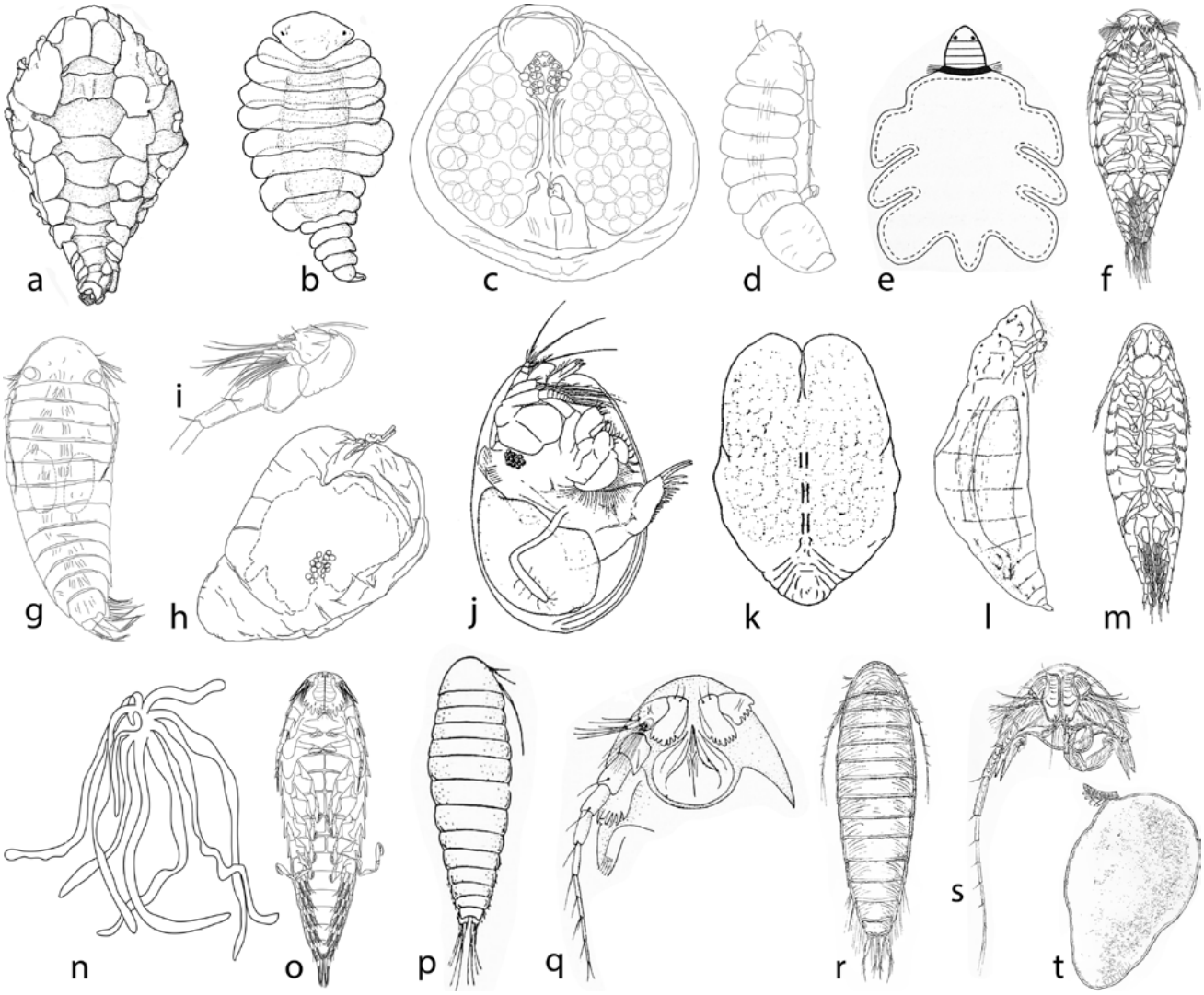


Figure 6.5. Epicaridea (Cryptoniscoidea). Representative adult females and males. a, b, Entophilidae: *Entophilus mirabiledictu* Markham and Dworschak, 2005; c, d, Dajidae: *Aspidophryxus discoformis* Boyko and Williams, 2012; Hemioniscidae: e, f, *Hemioniscus balani* Buchholz, 1866; g–i, *Crinoniscus stroembergi* Buhl-Mortensen, Williams and Boyko, 2020; Cyproniscidae: j–m, *Onisocryptus ovalis* (Shiino, 1942); n, o, Stellatoniscidae: *Stellatoniscus tentaculus* Oanh and Boyko, 2020; p, q, Podasconidae: *Parapodascon stebbingi* (Giard and Bonnier, 1895); r–t, Asconiscidae: *Asconiscus simplex* G.O. Sars, 1899. a, k, mature female, ventral view; b, d, g, p, r, male, dorsal view; c, ovigerous female, ventral view; e, mature female, dorsal view; f, m, o, male, ventral view; h, ovigerous female, lateral view; i, antennula of male; j, mature female within ostracod host; l, immature female, lateral view; n, mature female; q, mouthparts, antennulae, and antenna of male; s, antennulae, antenna, and pereopod 1 of male; t, immature female, lateral view.

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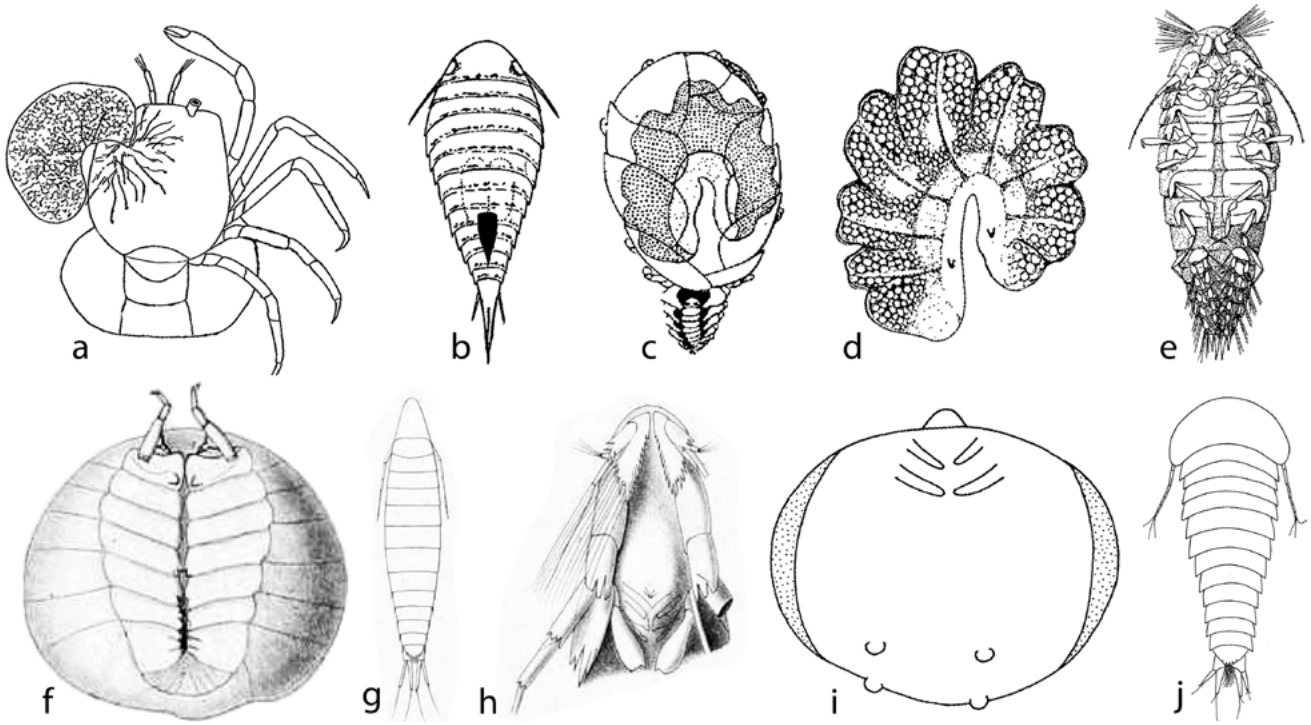


Figure 6.6. Epicaridea (Cryptoniscoidea). Representative adult females and males. a, b, Cryptoniscidae: *Danalia hapalocarcini* Fize, 1955; c–e, Cabiropidae: *Cabirops perezi* Carayon, 1942; f–h, Cumoechidae: *Cumoechus insignis* Hansen, 1916; i, j, Capitoniscidae: *Capitoniscus cumacei* Bourdon, 1972. a, mature females attached to host crab; b, male, ventral view; c, mature female within brood chamber of host; d, ovigerous female, lateral view; e, male, ventral view; f, mature female, ventral view; g, male, dorsal view; h, antennulae and antennae of male; i, mature female, ventral view; j, male, dorsal view.

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Superfamily Bopyroidea Rafinesque, 1815

The superfamily Bopyroidea contains three families (Bopyridae Rafinesque, 1815, Entoniscidae Kossmann, 1881, and Ionidae H. Milne Edwards, 1840), with bopyrids and ionids composed of ectoparasitic (branchial and abdominal) species and entoniscids of solely endoparasitic species. However, it is difficult to diagnose Bopyroidea effectively. Trilles (1999) indicated the following characters as unique to bopyroids: sexually dimorphic with females being much larger than males, often symmetrical, with large broods and oostegites; males being symmetrical and dwarf; the cryptoniscus larva developing into a fourth stage (bopyridium). However, Trilles' (1999) concept of Bopyroidea included Dajidae and Entophilidae, which were subsequently shown to be part of Cryptoniscoidea (Boyko et al., 2013). Therefore, characters of significant sexual dimorphism, hypertrophic, often symmetrical and usually hyperfertile with oostegites apply to members of Bopyroidea and Cryptoniscoidea. In addition, there are symmetrical, dwarf males in both groups, although no species of bopyroids have neotenous males as found in many cryptoniscoids. The "bopyridium" (sometimes referred to as the fourth larval stage) is found in all bopyroids as well as dajids and entophilids.

The only morphological character that appears to be a synapomorphy for bopyroids is the number of articles on the antennae of the cryptoniscus larval stage (four basal plus four or fewer flagellar articles (Boyko and Williams, 2015). This is supported by molecular data that distinguishes the two superfamilies (Boyko et al., 2013). Schädel et al. (2019) stated that "two supposed species of Bopyridae, *Probopyrus pandalicola* and *Probopyrus floridensis*, have five antennal flagellum elements (Dale and Anderson, 1982)." This, however, is not correct. Dale and Anderson (1982) did state in the text, without comment that the numbers were odd, that both species had five flagellar articles on the antennae, but examination of their illustrations shows that both species clearly have four flagellar articles and do not deviate from the 4+4 or fewer pattern of bopyroid cryptoniscus larvae antennae.

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Family Bopyridae Rafinesque, 1815

Bopyridae as currently diagnosed is a diverse and heterogeneous taxon (see below) composed of ten subfamilies. Further molecular studies are required to more adequately define the family and some of the subfamilies (e.g. Pseudioninae; Boyko et al., 2017). It is likely that some subfamilies are not monophyletic, whereas others may be raised to family level. All subfamilies are ectoparasitic (branchial or abdominal) on a range of hosts.

Diagnosis. **Female** body ovate to elongate; pereomeres distinct or fused; head shape variable. Frontal lamina present or absent. Eyes present or absent. Barbular lobes present or absent. Antenna and antennula articulated or fused. Maxilliped with or without palp. Marsupium open or closed. 5 or 7 pairs of oostegites; oostegite 1 with anterior and posterior lobes; internal ridge smooth or digitate. Coxal plates present or absent. Dorsolateral bosses present or absent. Middorsal projections present or absent. 1 to 7 pairs of pereopods. Pleomeres distinct or fused; lateral plates present or absent. Pleopods present or absent. Uropods present or absent. **Male** body elongate; head distinct or fused with pereomere 1. Eyes present or absent. Antennae and antennulae articulated. Midventral tubercles present or absent. 7 pairs of pereopods. Pleomeres distinct or fused; pleopods and uropods present or absent. Ectoparasites. **Cryptoniscus** larva body teardrop shaped, eyes present or absent. Antennula without denticles on basal segment. Oral sucker present or absent. Pereomeres without toothed coxal plates. Pereopods 1–7 subequal in size and shape. 5 biramous pleopods. Uropodal exopod larger and longer than endopod. Pleotelson without teeth.

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Subfamily Argeiinae Markham, 1977

Figure 6.7

Females of species in Argeiinae are all ectoparasites in the branchial chambers of shrimps and have the posterior lobe of the first oostegite of two main shapes: rounded or with a triangular projection. Males are all similar in shape, with the main differences being seen in the shape of the pleotelson, including: short rounded (fig. 6.7i), short triangular (fig. 6.7o), and elongate (fig. 6.7g). The genus *Bopyrosa* Nierstrasz and Brender à Brandis, 1923 was based solely on a single, clearly immature, female (now lost) from an unknown host. Markham (1977) placed *Bopyrosa* in Argeiinae but it could also belong to Keponinae based on the morphology of the pleon. The family diagnosis and key to genera are modified from An et al. (2017). Males representative of some genera are figured.

Diagnosis. **Female** body rounded, subtriangular to nearly circular; weakly distorted, up to 30°; pereomeres usually distinct; head wider than long, oval to triangular, head entire or bilobed. Frontal lamina present or absent. Eyes present or absent. Barbula smooth, with 2 or 3 smooth, tapered lobes on each side. Antenna and antennula articulated. Maxilliped with articulated palp or tuft of setae in palp area. Marsupium open or almost closed. 5 pairs of oostegites; oostegite 1 with low rounded or extended triangular posterior lobe; internal ridge smooth. Coxal plates present. Dorsolateral bosses present or absent. Middorsal projections absent. 5 pairs of pereopods. Pleon of 6 pleomeres, lateral plates present or absent. Pleopods uniramous or biramous, 3–5 pairs, tuberculiform, triangular or ovate flaps. Uropods uniramous or biramous. **Male** pereomeres subequal in width, head wider than long. Eyes present or absent. Antenna and antennula articulated. Midventral tubercles absent. 7 pairs of pereopods. Pleomeres fused into single segment, pleopods and uropods absent. Branchial parasites.

Key to females of genera of Argeiinae

1.	Pleomeres with lateral plates	2
–	Pleomeres without lateral plates	6
2.	Pleopods biramous	3
–	Pleopods uniramous	4
3.	Body longer than broad (fig. 6.7a, b)	*Argeia*
–	Body broader than long (fig. 6.7d)	*Stegoalpheon*
4.	Pereon much wider than pleon	5
–	Pereon approximately as wide as pleon (fig. 6.7e)	*Bopyrosa*
5.	Pleon quadrate, approximately as long as pereon (fig. 6.7f, g)	*Eragia*
–	Pleon triangular, much shorter than pereon (fig. 6.7h, i)	*Paraeragia*
6.	Uropods uniramous	7
–	Uropods biramous (fig. 6.7j)	*Argeiopsis*
7.	Pleomeres fused (fig. 6.7k, l)	*Gareia*
–	Pleon segmented	8
8.	Brood pouch closed. Maxilliped with articulated palp (fig. 6.7m)	*Parargeia*
–	Brood pouch open (fig. 6.7n, o). Maxilliped without palp or with non-articulated palp	*Stegoargeia*

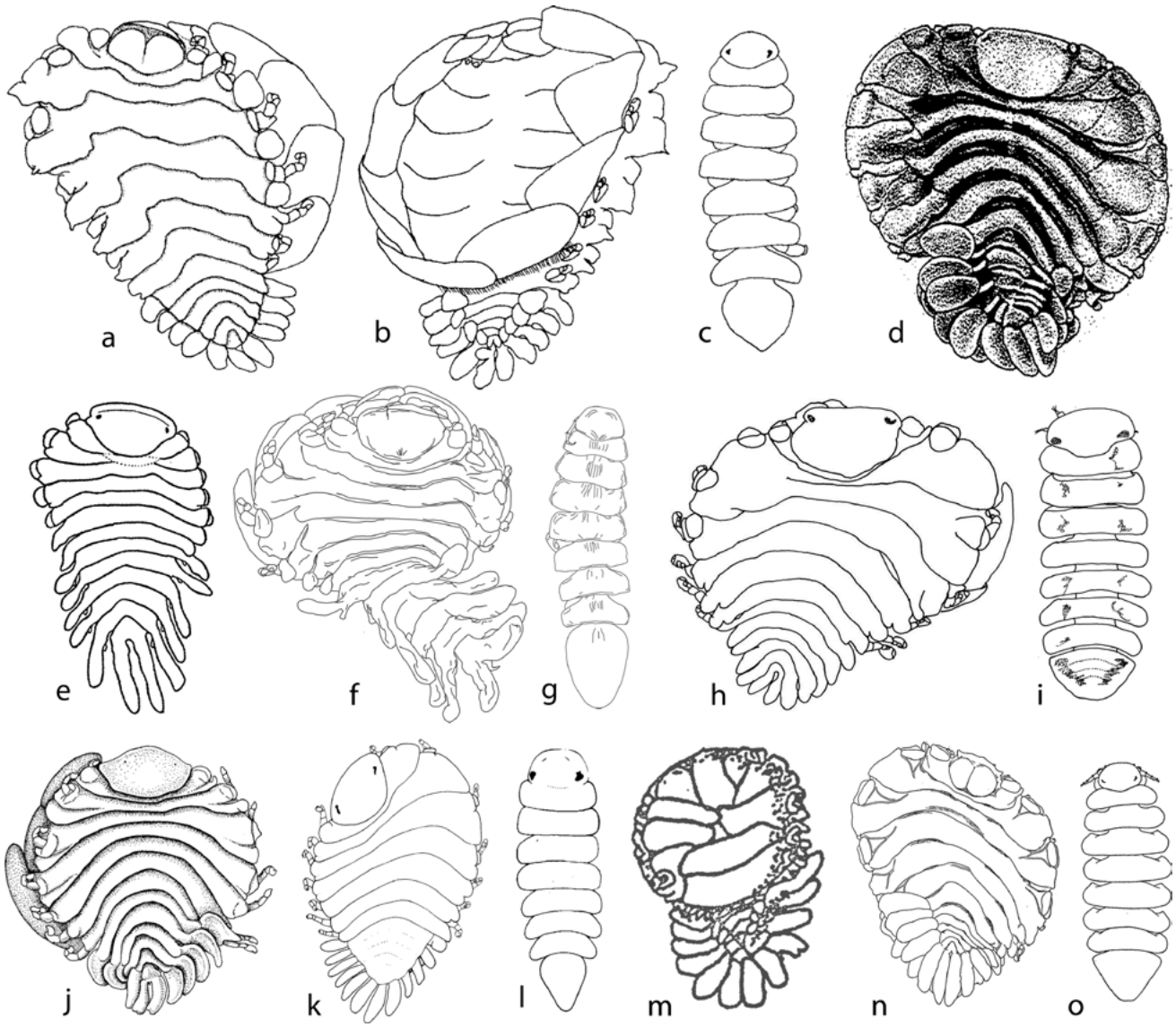


Figure 6.7. Argeiinae. *Argeia pugettensis* Dana, 1853: a, female dorsal view; b, female ventral view; c, male dorsal view. *Stegoalpheon kempi* Chopra, 1923: d, female dorsal view. *Bopyrosa phryxiformis* Nierstrasz and Brender à Brandis, 1923: e, female dorsal view. *Eragia profunda* Markham, 1994: f, female dorsal view; g, male dorsal view. *Paraeragia kiribatiensis* An, Zhang and Paulay, 2017: h, female dorsal view; i, male dorsal view. *Argeiopsis inhacae* Kensley, 1974: j, female dorsal view. *Gareia arafurae* Bourdon and Bruce, 1983: k, female dorsal view; l, male dorsal view. *Parargeia ornata* Hansen, 1897: m, female ventral. *Stegoargeia lowisi* (Chopra, 1923): n, female dorsal view; o, male dorsal view.

Argeia Dana, 1853

Diagnosis. **Female** body ovoid, approximately 3/4 as wide as long, pereomeres distinct; head subrectangular, wider than long, bilobed, not distorted. Frontal lamina present, narrow. Eyes absent. Maxillipedal palp setose, sometimes articulated. Marsupium open. Oostegite 1 with low rounded posterior lobe. Dorsolateral bosses present. Pereopods subequal. Pleon with 5 pairs of uniramous oval to lanceolate lateral plates. 4 or 5 pairs of uniramous knob-like to ovate uniramous pleopods. Uropods uniramous. **Male** with eyes. All pereopods subequal.

Shelf-slope, parasitising crangonid shrimps. Temperate Northern Pacific, Temperate Northern and Tropical Atlantic. 2 species and 1 *taxon inquirendum* (An et al., 2015; Markham, 1977).

Argeiopsis Kensley, 1974

Diagnosis. **Female** body nearly circular to triangular in outline; pereonites distinct; head triangular, not bilobed, not distorted. Frontal lamina present, thin. Eyes present. Barbula with 2 smooth, tapered lobes on each side. Maxilliped with setose,

non-articulated palp. Marsupium open. Oostegite 1 with extended triangular posterior lobe. Dorsolateral bosses present. Pereopods subequal. Pleon without lateral plates. 5 pairs of biramous pleopods as large triangular flaps. Uropods biramous. **Male** head narrower than first pereonite. Eyes present or absent. First pair of pereopods larger than others.

Subtidal, parasitising stenopodid and alpheid shrimps. Western Indo-Pacific. 3 species (An et al., 2017; Boyko and Kazmi, 2005).

Bopyrosa Nierstrasz and Brender à Brandis, 1923

Diagnosis. **Female** body outline subrectangular, first 3 pereomeres fused medially; head ovate, not bilobed, distorted 15°. Frontal lamina present, thin. Eyes present. Barbula, antenna, antennula, maxilliped unknown. Marsupium open. Oostegite 1 unknown. Dorsolateral bosses absent. Pereopods unknown. Pleon with 5 pairs of uniramous, elongate lateral plates. 5 pairs of uniramous pleopods as minute flaps. Uropods uniramous. **Male** unknown.

Subtidal, host unknown. Central Indo-Pacific. 1 species (Nierstrasz and Brender à Brandis, 1923).

Eragia Markham, 1994

Diagnosis. **Female** pereon rounded, pleon distorted 30°; pereomeres distinct; head quadrilateral in shape, embedded in pereon, not bilobed, not distorted. Frontal lamina present, thin. Eyes absent. Barbula with 2 short, smooth lobes on each side. Maxilliped with setose articulated palp. Marsupium open. Oostegite 1 with extended triangular posterior lobe. Dorsolateral bosses present. Pereopods 1 and 2 smaller than others. Pleon with 5 pairs of uniramous, elongate lateral plates. 5 pairs of uniramous pleopods as minute knobs. Uropods apparently as single uniramous structure. **Male** without eyes. Pereopod 7 with much longer basis and ischium than others.

Bathyal, parasitising crangonid shrimps. Central Indo-Pacific. 1 species (Williams and Boyko, 2010).

Gareia Bourdon and Bruce, 1983

Diagnosis. **Female** body ovate, pereomeres distinct; head ovate, not bilobed, distorted approximately 30°. Frontal lamina absent. Eyes present. Barbula with 2 pairs of lobes on each side. Maxilliped with setose non-articulated palp. Marsupium open. Oostegite 1 with low rounded posterior lobe. Coxal plates present but reduced. Dorsolateral bosses indistinct. Pleomeres almost completely fused dorsally, lateral plates absent. 5 pairs of biramous pleopods (exopods ovate, endopods tuberculiform). Uropods uniramous. **Male** with eyes present. Pereopods subequal in size.

Intertidal, parasitising alpheid shrimps. Central Indo-Pacific. 1 species (Bourdon and Bruce, 1983).

Paraeragia An, Zhang and Paulay, 2017

Diagnosis. **Female** body ovate, pereomeres distinct; head subquadrate, not bilobed, distorted approximately 10°. Frontal lamina absent. Eyes present. Barbula with 2 short tapered lobes on each side. Maxilliped with setose articulated palp. Marsupium open. Oostegite 1 with extended triangular posterior lobe. Dorsolateral bosses present. Pleomeres distinct, 5 pairs of lateral plates. 5 pairs of uniramous tuberculiform pleopods. Uropods uniramous. **Male** with eyes present. Pereopods subequal in size. Pleomeres fused but with faint dorsal indications of segmentation.

Subtidal, parasitising alpheid shrimps. Eastern Indo-Pacific. 1 species (An et al., 2017).

Parargeia Hansen, 1897

Diagnosis. **Female** body (exclusive of lateral plates) subtriangular, pereomeres distinct; head ovate, distorted approximately 15°. Frontal lamina thin. Eyes absent. Barbula unknown. Maxilliped with setose articulated palp. Marsupium closed. Oostegite 1 with ovate posterior lobe bearing small distolateral projection. Dorsolateral bosses present. Pleomeres distinct, 5 pairs of lateral plates. 5 pairs of uniramous ovate pleopods. Uropods uniramous. **Male** with eyes absent. Pereopods becoming gradually smaller posteriorly. Pleon much broader than pereon, bearing anterior middorsal tubercle.

Slope, parasitising crangonid shrimps. Tropical Eastern Pacific. 1 species (Hansen, 1897).

Stegoalpheon Chopra, 1923

Diagnosis. **Female** body ovate, pereomeres distinct; head ovate, distorted approximately 10°. Frontal lamina present, subquadrate. Eyes absent. Barbula with 2 long tapered lobes on each side. Maxilliped with setose non-articulated palp. Marsupium open. Oostegite 1 with extended triangular posterior lobe. Dorsolateral bosses present. Pleomeres distinct, 5 pairs of uniramous lateral plates. 5 pairs of biramous pleopods. Uropods uniramous. **Male** with eyes present. Pereopods 1 and 2 larger than others.

Intertidal, parasitising alpheid shrimps. Western Indo-Pacific, Temperate Northern Pacific. 1 species (An et al., 2015).

Stegoargeia An, Boyko and Li, 2015

Diagnosis. **Female** body ovate, pereomeres distinct; head bilobed, distorted approximately 5°. Frontal lamina present, subquadrate. Eyes absent. Barbula with 3 long tapered lobes on each side. Maxilliped with setose non-articulated palp. Marsupium open. Oostegite 1 with extended triangular posterior lobe. Dorsolateral bosses present. Pleomeres distinct, lateral plates absent. 5 pairs of biramous pleopods. Uropods uniramous. **Male** with eyes. Pereopod proportions unknown. Pleon triangular.

Intertidal, parasitising alpheid shrimps, Western Indo-Pacific, Temperate Northern Pacific. 2 species (An et al., 2015; Shiino, 1958).

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Subfamily Athelginae Codreanu and Codreanu, 1956

Figure 6.8

The genera of Athelginae can be distinguished from other epicarideans in that the females are abdominal ectoparasites of calcinid, diogenid and pagurid hermit crabs, as well as one species recorded from the abdomen of a hapalogastrid anomuran. No other epicarideans are known as abdominal parasites of hermit crabs or their close relatives. The heads of females are not distorted relative to the pereon but the pleon may be distorted up to 90°, one or more oostegites are typically extended anterior to the head, forming a funnel for aerating the brood and releasing the larvae, and the abdomen usually lacks lateral plates and has biramous ovate or foliose pleopods on four or five pleomeres. All males have fused pleomeres lacking any appendages. The key is modified from Boyko and Williams (2003) and Williams and Boyko (2016). Males of representative genera are figured.

Diagnosis. **Female** body longer than wide, linear or distorted up to 90°; head wider than long or length and width subequal, with subparallel margins, posterior margin convex or straight; barbula of 1–4 smooth or digitate lobes on each side. Oostegites 1, 2 or 3 extended over head or not anteriorly produced; oostegite 1 with long or short, triangular, recurved or rounded posterior lobe; other oostegites forming large, enclosed marsupium. One or more pereopods anterior to head, at least some pairs adjacent to head, last 2 pairs evenly spaced or distant from first 5 pairs. Pleomeres 1–4 or 1–5 with biramous pleopods arising from common peduncle, lateral plates present or absent. Pleotelson with or without uropods. **Male** body length approximately 2–6 times width, lateral margins of all pereomeres subequal or with some larger, rounded or laterally tapered. Head wider than long, anterior margin rounded. Pereomeres closely approximated or with posterior pereonites more widely spaced. Pleomeres fused into single segment without indication of segmentation or with weak indication of first pleomere, triangular, broadest anteriorly, tapering distally to rounded or subacute tip. Pleopods and uropods absent. Abdominal ectoparasites of anomurans.

Key to females of genera of Athelginae

1.	Lateral plates present	2
–	Lateral plates absent	7
2.	Lateral plates on pleomeres 1–5	3
–	Lateral plates only on pleomeres 1–3 (fig. 6.8a, b)	*Stegias*
3.	Lateral plates on pleomere 5 similar to lateral plates on other pleomeres.	4
–	Lateral plates on pleomere 5 reduced, globular or scar-like (fig. 6.8c, d)	*Pseudostegias*

4.	Pereopods 5 and 6 widely separated (broad pereomeres)	5
–	Pereopods 5 and 6 not widely separated (narrow pereomeres)	6
5.	Pleopods uniramous (fig. 6.8e, f)	*Minimathelges*
–	Pleopods biramous (fig. 6.8g, h)	*Anathelges*
6.	5 pleomeres (fig. 6.8i)	*Claustrathelges*
–	6 pleomeres (fig. 6.8j, k)	*Falsanathelges*
7.	Uropods uniramous, articulated with terminal pleomere (fig. 6.8l, m)	*Parathelges*
–	Uropods absent or as reduced unsegmented lobes	8
8.	Pleopods on pleomere 5 present (fig. 6.8n, o)	*Allathelges*
–	Pleopods on pleomere 5 absent (fig. 6.8p, q)	*Athelges*

Allathelges Kazmi and Markham, 1999

Diagnosis. **Female** body longer than broad, not distorted; head wider than long, posterior margin slightly convex; barbula of 4 smooth lobes on each side. First oostegites extended over head and reflexed, posterior lobe elongate, triangular. Pereomeres 1, 2 anteriorly concave, posteriorly convex; pereomeres 3–6 anteriorly medially straight and laterally narrowly convex, posteriorly straight and laterally with narrow posteriorly directed lobes; pereomere 5 or 6 largest; pereomere 7 with convex anterior margin and concave posterior margin. Pereopods 1–3 anterior to head, 4–7 evenly spaced. Pleomeres 1–5 with lamellar biramous pleopods arising from common peduncle, lateral plates absent. Pleotelson tapering, uropods absent. **Male** body length approximately 2–3 times width, lateral margins of all pereomeres subequal, rounded. Pereomeres closely approximated. Pleomeres fused into single segment without indication of segmentation or with weak indication of first segment, triangular, broadest anteriorly, tapering distally to rounded tip.

Intertidal–subtidal, parasitising calcinid and diogenid hermit crabs. Western and Central Indo-Pacific. 2 species (Williams and Boyko, 2016).

Anathelges Bonnier, 1900

Diagnosis. **Female** body distorted sinistrally; head longer than wide, posterior margin slightly convex; barbula of 3 smooth short lobes on each side. First 3 oostegites extended over head, first pair forming conical projection, posterior lobe elongate, triangular. Pereomeres 1–5 anteriorly concave, posteriorly convex; pereomere 6 largest, anterior and posterior margins concave; pereomere 7 with convex anterior margin and concave posterior margins; pereomere 7 similar to 6 but smaller. Pereopods 1, 2 anterior to head, 3–5 parallel to head, 4 and 5 at posterior margin of pereon. Pleomeres 1–5 with lamellar or subovate biramous pleopods and uniramous lateral plates arising from common peduncle. Pleotelson with uniramous, nonpedunculate, uropods. **Male** body length approximately 3 times width, lateral margins of all pereomeres subequal, rounded. Pereomeres separated at lateral margins, especially 5–7. Pleomeres fused into single elongate segment without indication of segmentation or with weak indications of segmentation, broadest anteriorly, tapering distally to rounded or subacute tip.

Intertidal–subtidal, parasitising pagurid hermit crabs. Temperate Northern and Tropical Atlantic, Tropical Eastern Pacific, Temperate Northern Pacific, Temperate South America. 4 species (Boyko and Williams, 2003).

Athelges Gerstaecker, 1862

Diagnosis. **Female** body linear or distorted at 90°; head length and width subequal, posterior margin convex; barbula of 2 smooth short lobes on each side. Second pair of oostegites extended over head, oostegite 1 posterior lobe elongate, triangular. Pereomere 1 anteriorly concave, posteriorly convex; pereomeres 2–5 anteriorly medially straight and laterally narrowly convex, posteriorly straight and laterally with narrow posteriorly directed lobes; pereomere 6 largest, anterior margin straight, posterior margin concave; pereomere 7 similar to 6 but shorter. Pereopod 2 anterior to head, pereopods 2 and 3 parallel to head, 6 and 7 at posterior margin of pereon. Pleomeres 1–4 with subovate biramous pleopods, lateral plates absent. Pleotelson without uropods, distal tip slender, rounded or with 2–4 small knobs. **Male** body length approximately 3 times width, lateral margins of all pereomeres subequal, rounded. Pereomeres closely approximated. Pleomeres fused into single elongate segment without indication of segmentation, broadest anteriorly, tapering distally to rounded tip.

Intertidal–slope, parasitising diogenid and pagurid hermit crabs. Temperate Northern Atlantic, Temperate Southern Africa, Temperate Northern Pacific, Central Indo-Pacific, Temperate Australasia. 14 species (Boyko et al., 2024; Shinoda et al., 2026).

Claustrathelges Williams and Boyko, 2016

Diagnosis. **Female** pereon not distorted, pleon weakly distorted, head length and width subequal, anterior margin weakly convex, posterior margin convex; barbula with 2 digitate lobes on each side. No oostegites extended over head or produced posteriorly; oostegite 1 with short rounded posterior lobe. Pereomeres 1–4 anteriorly concave and posteriorly convex, pereomere 5 with margins nearly straight, pereomeres

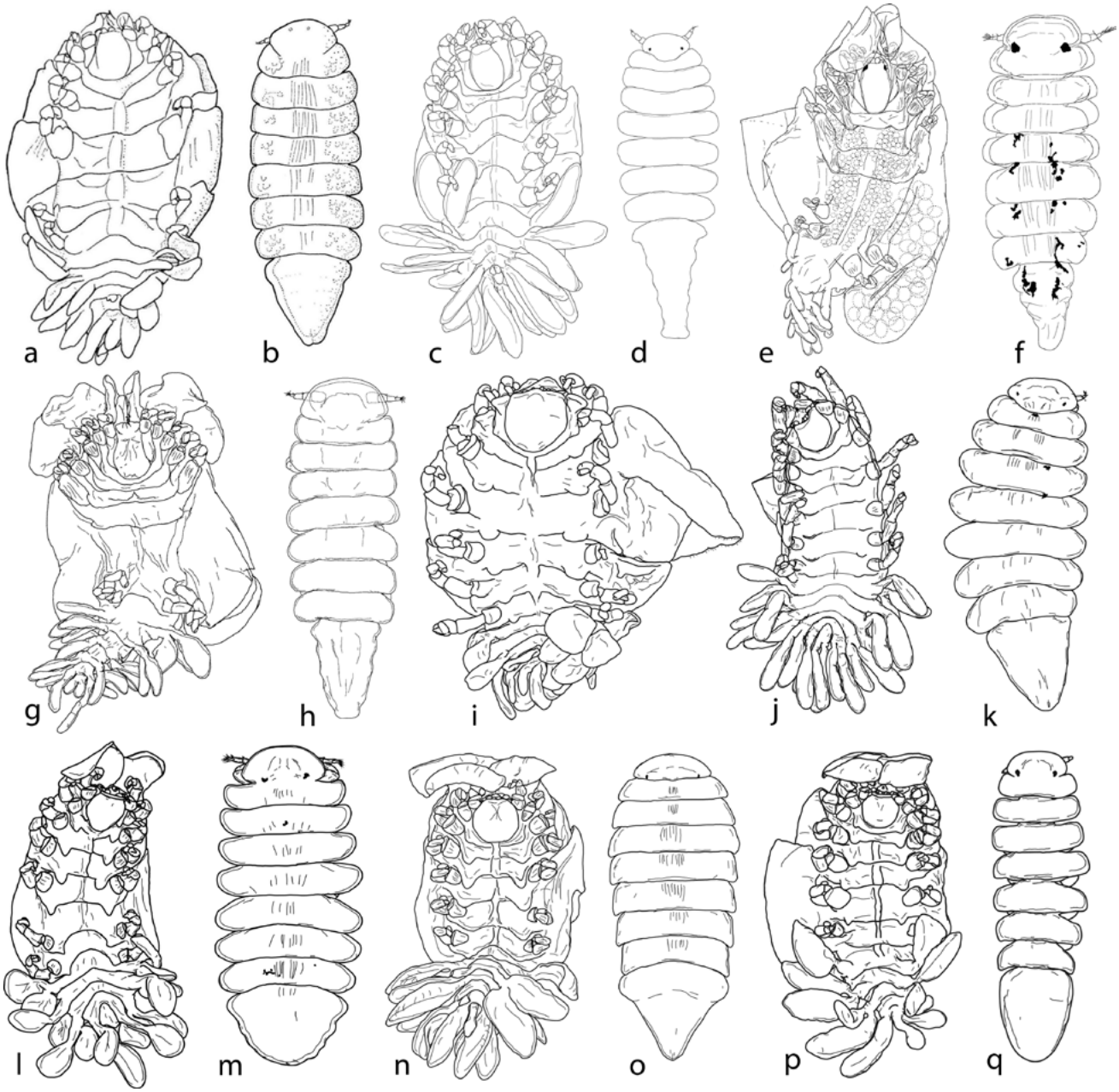


Figure 6.8. Athelginae. *Stegias clibanarii* Richardson, 1904: a, female dorsal view; b, male dorsal view. *Pseudostegias dulcilacuum* Markham, 1982: c, female dorsal view; d, male dorsal view. *Minimathelges nanus* Boyko and Williams, 2003: e, female dorsal view; f, male dorsal view. *Anathelges hyptius* (Thompson, 1902): g, female dorsal view; h, male dorsal view. *Claustrathelges macdermotti* Williams & Boyko, 2016: i, female dorsal view. *Falsanathelges mariae* Williams and Boyko, 2016: j, female dorsal view; k, male dorsal view. *Parathelges aniculi* (Whitelegge, 1897): l, female dorsal view; m, male dorsal view. *Allathelges alisonae* Williams and Boyko, 2016: n, female dorsal view; o, male dorsal view. *Athelges takanoshimensis* Ishii, 1914: p, female dorsal view; q, male dorsal view.

6 and 7 anteriorly convex, posteriorly concave; pereomere 4 broader than other pereomeres. Pereopod 1 anterior to head, pereopods 2 and 3 parallel to head, no large gaps between pereopods 4–7. Dorsal surface of first oostegites with pattern of ridges. Pleomeres 1–5 with elongate-ovate biramous pleopods and uniramous lateral plates, all arising from common peduncle. Pleotelson absent; pleon of 5 pleomeres. **Male** unknown.

Subtidal, parasitizing diogenid hermit crabs. Temperate Australasia. 1 species (Williams and Boyko, 2016).

Falsanathelges Boyko and Williams, 2003

Diagnosis. **Female** body not distorted, head broader than long with convex lateral margins, anterior margin concave, posterior margin convex; barbula of 2 digitate lobes on each side. No oostegites extended over head or produced posteriorly; oostegite 1 with short recurved posterior lobe. Pereomeres 1–3 anteriorly concave and posteriorly convex, pereomere 4 only slightly so, pereomere 5 with more or less straight margins, pereomeres 6 and 7 anteriorly convex and posteriorly concave; pereomeres 3–5 subequal in size and larger than others. Pereopod 1 anterior to head, 2 parallel to head, no large gaps between 4–7. Pleomeres 1–5 with elongate-ovate biramous pleopods and uniramous lateral plates, all arising from common peduncle. Pleotelson with biramous, pedunculate, elongate-ovate uropods. **Male** body length approximately 3.5 times width, lateral margins of pereomeres 3–7 almost parallel, 1, 2 shorter. Pereomeres widely separated. Pleomeres fused into single segment, broadest anteriorly, lateral margins showing residual segmentation, tapering posteriorly to rounded distal tip.

Intertidal–subtidal, parasitizing calcinid and diogenid hermit crabs. Central Indo-Pacific. 3 species (Boyko and Williams, 2003; Shinoda et al., 2025; Williams and Boyko, 2016).

Minimathelges Boyko and Williams, 2003

Diagnosis. **Female** body distorted sinistrally with right side longest; head longer than wide, posterior margin convex; barbula unknown. First two oostegites extended over head, oostegite 1 with long triangular lobe. Pereomeres 1–5 anteriorly concave and posteriorly convex; pereomere 6 largest, anterior and posterior margins subparallel. Pereopod 1 anterior to head, 3 and 4 parallel to head, 6 and 7 at posterior margin of pereon. Pleomeres 1–5 with lamellar uniramous pleopods and uniramous lateral plates, not arising from common peduncle. Pleotelson with uniramous lamellar uropods. **Male** body length approximately 3.1 times width, lateral margins of pereomeres 3–6 almost parallel, 1, 2, 7 shorter. Pereomeres closely approximated. Pleomeres fused into single segment with partial demarcation of at least first pleomere ventrally, broadest anteriorly, lateral margins showing residual segmentation, tapering posteriorly to rounded distal tip.

Intertidal, parasitising pagurid hermit crabs. Central Indo-Pacific. 2 species (Boyko and Williams, 2003).

Parathelges Bonnier, 1900

Diagnosis. **Female** body slightly to c. 30° distorted dextrally with left side longest; head approximately as long as wide, posterior margin slightly convex; barbula of 2 smooth lobes on each side. First oostegites extended over head, posterior lobe long, triangular, second and third pairs adjacent to head. Pereomere 1 anteriorly concave, posteriorly convex; pereomeres 2–5 anteriorly medially straight and laterally narrowly convex, posteriorly straight and laterally with narrow posteriorly directed lobes; pereomere 6 largest, anterior margin straight, posterior margin concave; pereomere 7 similar to 6 but not as long. Pereopod 1 anterior to head, 2 and 3 parallel to head, 4 and 7 at posterior margin of pereon. Pleomeres 1–4 with lamellar biramous pleopods arising from common peduncle, lateral plates absent. Pleotelson with uniramous lamellar uropods. **Male** body length approximately 2–3 times width, lateral margins of all pereomeres subequal, rounded. Pereomeres closely approximated. Pleomeres fused into single segment without indication of segmentation, triangular, broadest anteriorly, tapering distally to rounded tip.

Intertidal–subtidal, parasitising calcinid, diogenid and pagurid hermit crabs. Temperate Northern and Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific. 10 species (Kazmi and Markham, 1999; Markham, 1972).

Pseudostegias Shiino, 1933

Diagnosis. **Female** body not distorted to weakly distorted; head longer than wide, posterior margin straight; barbula of 1–4 smooth or digitate lobes on each side. First oostegites not extended over head, with long triangular posterior lobe. Pereomere 1 anteriorly concave, posteriorly convex; pereomeres 2–5 anteriorly medially straight and laterally narrowly convex, posteriorly straight and laterally with narrow posteriorly directed lobes; pereomere 6 largest, anterior margin straight, posterior margin concave; pereomere 7 similar to 6 but not as long. Pereopod 1 anterior to head, 2 and 3 parallel to head, 6 and 7 at posterior margin of pereon. Pleomeres 1–4 with elongate lateral plates and biramous pleopods; pleomere 5 with pair of rounded or triangular medially positioned lateral plates and biramous pleopods. Pleotelson with uniramous elongate uropods. **Male** body length approximately 3 times width, lateral margins of all pereomeres rounded, pereomere 4 broadest. Pereomeres not closely approximated. Pleomeres fused into single segment with or without indication of segmentation, triangular, broadest anteriorly, tapering distally to rounded or truncate tip.

Intertidal–subtidal, parasitizing calcinid and diogenid hermit crabs and hapalogastrids. Tropical Atlantic, Western and Central Indo-Pacific, Temperate Australasia, Temperate Northern Pacific. 7 species (Williams and Boyko, 2016).

Stegias Richardson, 1904

Diagnosis. **Female** body slightly distorted sinistrally with right side longest or straight; head longer than wide, posterior margin convex; barbula with 2 short lobes bearing few digitations. First oostegites not extended over head, oostegite 1 with long triangular posterior lobe. Pereomeres 1 and 2 anteriorly concave and posteriorly convex; pereomeres 3–5 anteriorly concave and posteriorly straight; pereomere 6 largest, anterior margin straight, posterior margin concave. Pereopod 1 anterior to head, 3 and 4 parallel to head, 6 and 7 at posterior margin of pereon. Pleomeres 1–3 with lamellar biramous pleopods and uniramous lateral plates, not arising from common peduncle; pleomeres 4 and 5 with biramous pleopods, without lateral plates. Pleotelson with uniramous lamellar uropods. **Male** body length approximately 6 times width, lateral margins of pereomeres 1–4 subequal, straight, those of 5–7 wider and tapered laterally. Pereomeres closely approximated in anterior

half of body. Pleomeres fused into single segment without indication of segmentation, broadest anteriorly, tapering distally and slightly expanded at rounded distal tip.

Subtidal, parasitising diogenid hermit crabs. Tropical Atlantic, Central Indo-Pacific, Tropical Eastern Pacific. 3 species (Nierstrasz and Brender à Brandis, 1931).

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Subfamily Bathygyginae Markham, 2016

Figure 6.9

The sole genus and species of Bathygyginae is ectoparasitic in the branchial chambers of shrimps. It can be distinguished from other epicarideans in that the females have oostegite 2 extending beyond the anterior margin of the head, the coxal plates of at least pereomeres 1 and 2 extending medially over the pereomeres, and the pleon distorted at approximately 70° (Markham, 2016). The males possess propodal sockets into which the tips of the dactyli are inserted; this character is known from species in a few other genera (e.g. *Asymmetrione* Codreanu, Codreanu and Pike, 1965). The cryptoniscus larval stage was figured but not described by An et al. (2015).

Diagnosis. **Female** body nearly circular; pereomeres distinct; head much wider than long, oval, deeply embedded in first pereomere and overlapped by second oostegites. Head entire, not distorted. Frontal lamina absent. Eyes absent. Barbula with 2 smooth, tapered lobes on each side. Antenna and antennula articulated. Maxilliped with articulated palp. Marsupium closed. 5 pairs of oostegites; oostegite 1 with extended

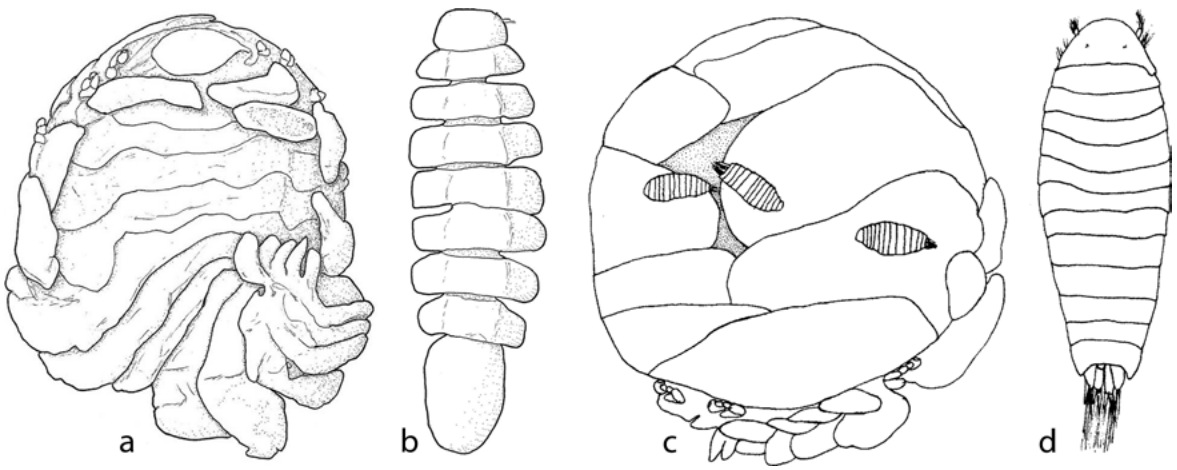


Figure 6.9. Bathygyginae. *Bathygyge grandis* Hansen, 1897: a, female dorsal view; b, male dorsal view; c, female ventral view, with three cryptoniscus larvae; d, cryptoniscus larva dorsal view.

triangular posterior lobe; internal ridge smooth. Coxal plates present, those of pereomeres 1 and 2 (sometimes 3) extending medially over pereomeres. Dorsolateral bosses absent. Middorsal projections absent. 5 pairs of subequal pereopods. Pleon of 6 segments, partially fused, distorted approximately 70°; 5 pairs of uniramous lateral plates present. Pleopods absent. Uniramous uropods present. **Male** body with pereomeres subequal in width; head wider than long, narrower than pereomere 1. Eyes absent. Antenna and antennula articulated. Midventral tubercles absent. 7 pairs of pereopods, dactyli on 1–5 longer than those on 6 and 7; all propodi with sockets for insertion of dactyli. Pereomeres fused into single segment, pleopods and uropods absent. Branchial parasites.

Bathygyge Hansen, 1897

Diagnosis. As for family.

Bathypelagic, parasitising glyphocrangonid shrimps. Temperate Northern Atlantic, Temperate Southern Africa, Central Indo-Pacific, Temperate Northern Pacific. 1 species (Hansen, 1897; Markham, 2016).

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Subfamily Bopyrinae Rafinesque, 1815

Figures 6.10, 6.11

Species in the genera of Bopyrinae are all ectoparasitic in the branchial chambers of caridean shrimps, primarily in alpheid and palaemonid hosts. Bodies of females are generally dorsoventrally flattened with slight to moderate distortion of the head relative to the body, weakly developed (or absent) coxal plates and dorsolateral bosses, and a pleon with small, flap-like pleopods; lateral plates, if present, are not pedunculate. Males typically have a fused or partly fused pleon and if pleopods are present, they are sessile and uropods are absent. The key is modified from those in Markham (1985) and An et al. (2015). Males of some representative genera are figured.

Diagnosis. **Female** body linear, elongate or ovate, body not distorted to moderately distorted; head distinct from or fused with pereon; frontal lamina present or absent. Eyes present or absent. Antennula and antenna articulated or indistinct. Maxilliped without palp or with articulated or non-articulated palp. Barbula with 1 or 2 smooth short lobes on each side. Pereomeres distinct or medially fused dorsally. 5 or 7 pairs of oostegites. Oostegites 1 symmetrical or asymmetrical with triangular or ovate posterior lobe, smaller or larger than anterior lobe; internal ridges smooth or digitate. Marsupium open or closed. Coxal plates, dorsolateral bosses and tergal projections present or absent. 5 pairs of pereopods. Pleon narrower or not narrower than pereon, 4–6 distinct or fused pleomeres; 3–5 pairs (sometimes asymmetrical) of smooth uniramous or biramous pleopods; uropods uniramous or absent. **Male** approximately 2–4 times as long as wide, pereomeres narrower or not narrower posteriorly. Head narrower than or subequal in width to pereon. Eyes present or absent. Antennula and antenna articulated or not articulated. Pereopods moderate to large compared to body, subequal or smaller posteriorly. Midventral tubercles present or absent. Pleon fused or of 6 segments; pleopods present or absent. Uropods absent.

Key to females of genera of Bopyrinae

1.	Uropods present	2
–	Uropods absent	5
2.	Uropods biramous, with long, thin rami (fig. 6.10a, b)	*Urobopyrus*
–	Uropods uniramous, with long, wide rami	3
3.	Maxilliped without palp (fig. 6.10c)	*Litobopyrus*
–	Maxilliped with palp	4
4.	Palp without setae; oostegite 1 posterior lobe ovate (fig. 6.10d)	*Bopyrinina*
–	Palp with setae; oostegite 1 posterior lobe triangular (fig. 6.10e)	*Parapleurocrypta*

5.	All pleopods biramous	6
–	Some or all pleopods uniramous	13
6.	Head distinctly extended into anterolateral horns (fig. 6.10j, k)	*Capitetragonia*
–	Head not anterolaterally extended	7
7.	Head and pereomere 1 separate	8
–	Head and pereomere 1 fused at least medially	11
8.	Body heart-shaped, barbula with 2 pairs of projections on each side (fig. 6.10l, m)	*Probopyrus*
–	Body not heart-shaped, barbula with 1 pair of projections on each side	9
9.	Oostegite 1 without posterolateral point (fig. 6.10n, o)	*Parabopyriscus*
–	Oostegite 1 with posterolateral point	10
10.	Pleomeres distinct, separated laterally on both sides (fig. 6.10p, q)	*Probopyriscus*
–	Pleomeres distinct on long side only (fig. 6.10r, s)	*Probopyrinella*
11.	Head fused with pereomere 1 medially. Body oval (fig. 6.10t, u)	*Ovobopyrus*
–	Head completely fused with pereomere 1. Body elongate	12
12.	Pleomeres of at least one side fused (fig. 6.10v, w)	*Bopyrella*
–	Pleomeres distinct on both sides (fig. 6.11a, b)	*Parabopyrella*
13.	Pleopods on one side of pleon (fig. 6.10f, g)	*Palaemonellione*
–	Pleopods on both sides of pleon	14
14.	Some pleopods biramous	15
–	All pleopods uniramous	16
15.	Pleopods 1–3 biramous, fourth uniramous (fig. 6.11c)	*Allobopyrus*
–	Pleopods on one side of pleon biramous, on other side uniramous (fig. 6.10h, i)	*Ogyridione*
16.	5 pairs of pleopods	17
–	Fewer than 5 pairs of pleopods	24
17.	5 pairs of oostegites	18
–	7 pairs of oostegites (fig. 6.11d, e)	*Septembopyrina*
18.	Coxal plates absent (fig. 6.11f, g)	*Probopyrione*
–	Coxal plates present	19
19.	Coxal plates on pereomeres 1–4	20
–	Coxal plates on pereomeres 2–4	23
20.	Pleopods reduced to tubercles (fig. 6.11h)	*Bopyroides*
–	Pleopods flap-like, not reduced	21
21.	Body ovate (fig. 6.11i)	*Discorsobopyrus*
–	Body elongate	22
22.	Oostegites 1 symmetrical (fig. 6.11j)	*Bopyrus*
–	Oostegites 1 asymmetrical (fig. 6.11k)	*Bopyrinella*
23.	Pleomeres fused (fig. 6.11l)	*Parabopyrus*
–	Pleomeres distinct (fig. 6.11m, n)	*Probynia*

24.	Pleomeres fused on one side (fig. 6.11o, p)	*Bopyrina*
–	Pleomeres distinct on both sides	25
25.	Oostegites 1 asymmetrical (fig. 6.11q, r)	*Schizobopyrina*
–	Oostegites 1 symmetrical	26
26.	Head fused with pereomere 1 at least medially (fig. 6.11s, t)	*Synsynella*
–	Head separate from pereomere 1 (fig. 6.11u–w)	*Bopyrione*

Allobopyrus Bourdon, 1983

Diagnosis. **Female** linear, body distorted; head distinct from pereon; frontal lamina present. Eyes present. Antennulae and antennae articulated. Maxilliped with setose, non-articulated palp. Barbula with 1 smooth short lobe on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegites 1 slightly asymmetrical with triangular posterior lobe, larger than anterior lobe; internal ridges smooth. Marsupium open. Coxal plates and dorsolateral bosses present, tergal projections absent. Pleon not narrower than pereon, 6 pleomeres, fused except at lateral margins; 4 pairs of smooth pleopods: 3 pairs biramous and 1 pair uniramous; uropods absent. **Male** unknown.

Intertidal, parasitising palaemonid shrimps. Central Indo-Pacific. 1 species (Bourdon, 1983).

Bopyrella Bonnier, 1900

Diagnosis. **Female** ovate, body slightly distorted; head fused with pereon medially, subquadrate; frontal lamina absent. Eyes present. Antennula and antenna articulated. Maxilliped with setose articulated palp. Barbula with 2 smooth lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with ovate posterior lobe bearing distal recurved lobe, smaller than anterior lobe; internal ridge smooth. Marsupium open. Coxal plates present and dorsolateral bosses usually present, tergal projections absent. Pleon not narrower than pereon, 4 indistinct pleomeres mostly fused; 5 pairs of smooth biramous pleopods; uropods absent. **Male** approximately twice as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles present. Pleon of 6 segments; pleopods absent.

Intertidal–subtidal, parasitising alpheid shrimps. Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific. 7 species (An et al., 2015).

Bopyrina Kossmann, 1881

Diagnosis. **Female** elongate, body distorted; head distinct from pereon; frontal lamina present. Eyes present or absent. Antennula and antenna indistinct. Maxilliped without palp. Barbula with 1 smooth lobe on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with posterior elongate ovate lobe larger than anterior lobe; internal ridges smooth. Marsupium open. Coxal plates present, dorsolateral bosses and tergal projections absent. Pleon narrower than pereon, 5 pleomeres fused on one side or medially; 3 or 4 pairs of smooth uniramous pleopods; uropods absent. **Male** approximately 4 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula articulated; antenna not articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon of 6 segments mostly fused with faint indications of segmentation or distinct; pleopods absent.

Subtidal–shelf, parasitising chlorotocellid, hippolytid and palaemonid shrimps. Temperate Northern Atlantic, Tropical Atlantic, Western and Central Indo-Pacific. 5 species (Markham, 1985).

Bopyrinella Nierstrasz and Brender à Brandis, 1925

Diagnosis. **Female** elongate, body distorted; head fused with pereon medially; frontal lamina present. Eyes present. Antennula and antenna articulated. Maxilliped with setose articulated palp. Barbula with 1 smooth lobe on each side. Pereomeres fused medially in dorsal view. 5 pairs of oostegites. Oostegites 1 asymmetrical, that on long side of body with triangular posterior lobe, larger than anterior lobe; that on short side of body with ovate or triangular posterior lobe, smaller than anterior lobe; internal ridges smooth. Marsupium open. Small coxal plates, dorsolateral bosses and tergal projections present on short side. Pleon not narrower than pereon, 6 pleomeres fused medially or laterally; 5 pairs of smooth uniramous pleopods; uropods absent. **Male** approximately twice as long as wide, pereomeres narrower posteriorly. Head narrower than pereon. Eyes present or absent. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon of 6 segments fused medially; 5 pairs of sessile pleopods present.

Intertidal–subtidal, parasitising alpheid, ogyridid and thorid shrimps. Tropical Atlantic, Western Indo-Pacific, Temperate Northern Pacific. 7 species (An et al., 2021). This diagnosis is based only on the type species, *Bopyrinella antillensis* Nierstrasz and Brender à Brandis, 1925 (= *B. thorii* (Richardson, 1904)) because the genus does not appear to be monophyletic.

Bopyrinina Shiino, 1933

Diagnosis. **Female** elongate ovate, body distorted; head distinct from pereon; frontal lamina present. Eyes absent. Antennula not articulated; antenna articulated. Maxilliped with non-setose unsegmented palp. Barbula with 2 smooth lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with ovate posterior lobe, smaller than anterior

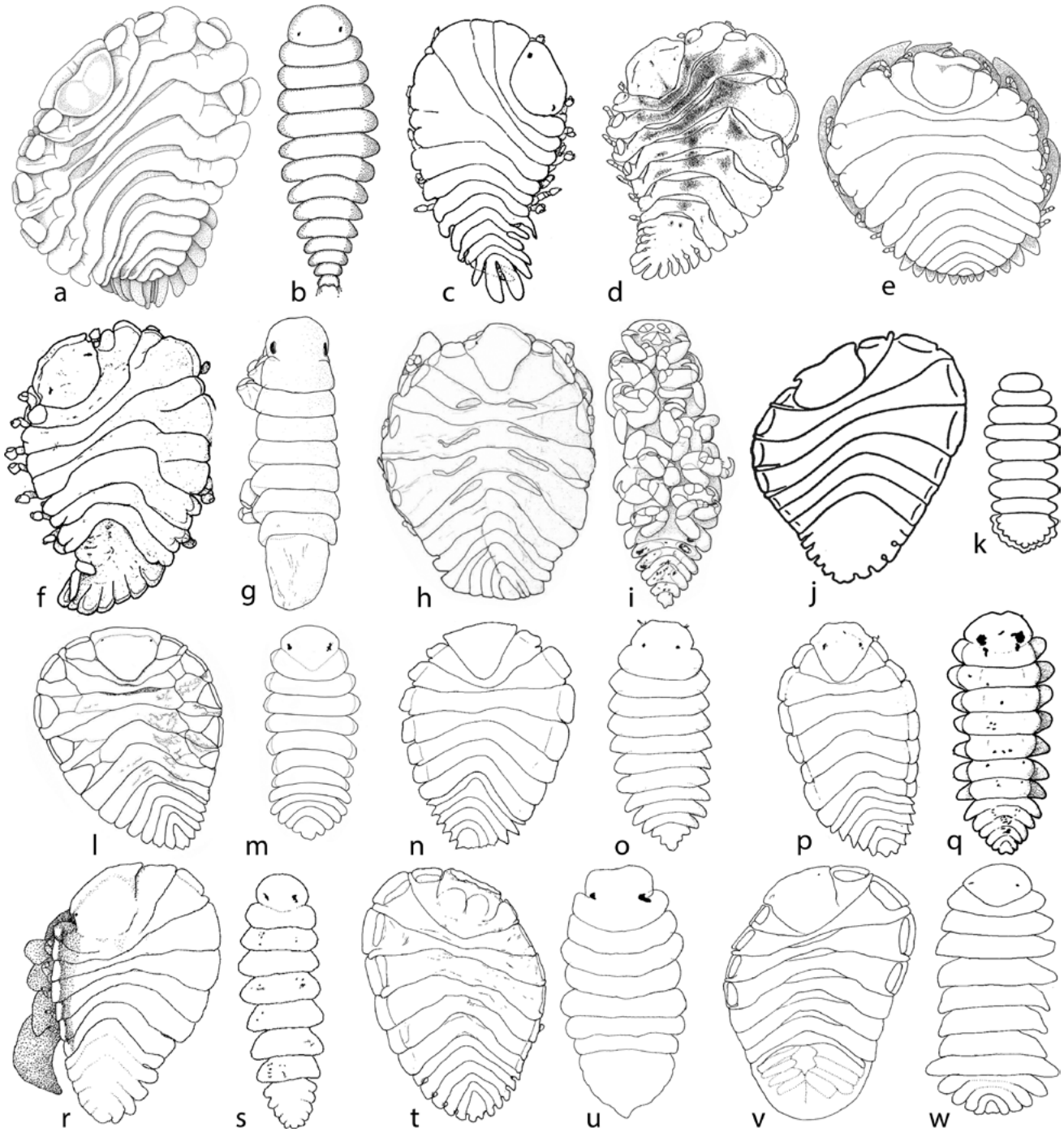


Figure 6.10. Bopyrinae. *Urobopyrus processae* Richardson, 1904: a, female dorsal view; b, male dorsal view. *Litobopyrus longicaudatus* Markham, 1982: c, female dorsal view. *Bopyrinina dorsimaculata* Shiino, 1933: d, female dorsal view. *Parapleurocrypta digitata* Bourdon, 1976: e, female dorsal view. *Palaemonellione cebuensis* Markham, 1989: f, female dorsal view; g, male dorsal view. *Ogyridione caroliniana* Markham, 1988: h, female dorsal view; i, male ventral view. *Capitetragonia alphei* (Richardson, 1900): j, female dorsal view; k, male dorsal view. *Probopyrus* cf. *pandalicola* (Packard, 1879): l, female dorsal view; m, male dorsal view. *Parabopyriscus stellatus* Markham, 1985: n, female dorsal view; o, male dorsal view. *Probopyriscus novempalensis* Markham, 1982: p, female dorsal view; q, male dorsal view. *Probopyrinella heardi* Adkison, 1984: r, female dorsal view; s, male dorsal view. *Ovobopyrus alphezemiotes* Markham, 1985: t, female dorsal view; u, male dorsal view. *Bopyrella articulata* An, Boyko and Li, 2015: v, female dorsal view; w, male dorsal view.

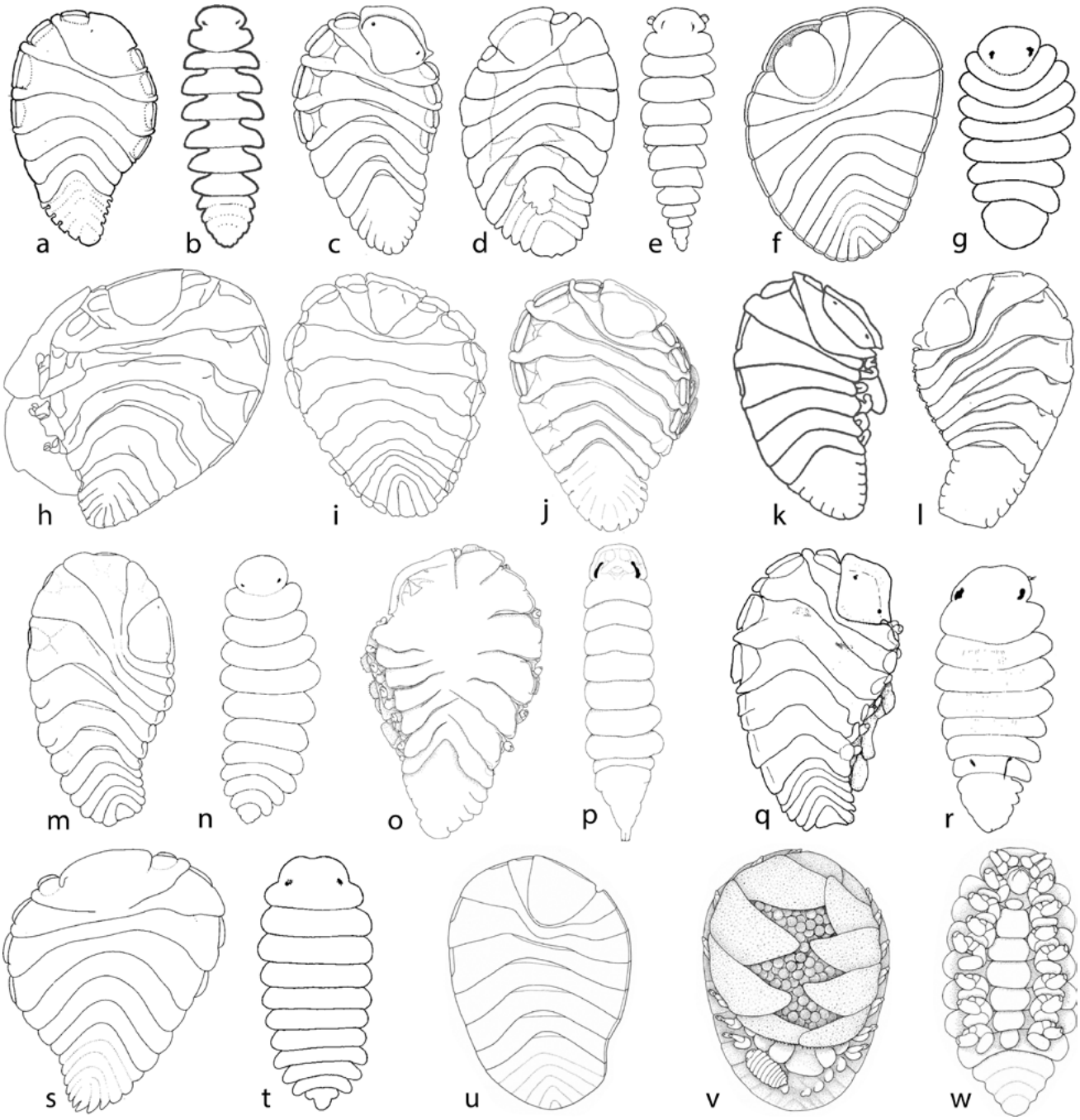


Figure 6.11. Bopyrinae. *Parabopyrella mortenseni* (Nierstrasz and Brender à Brandis, 1929): a, female dorsal view; b, male dorsal view. *Allobopyrus rumphiusi* Bourdon, 1983: c, female dorsal view. *Septembopyrina tozeumaophila* An, Boyko and Li, 2015: d, female dorsal view; e, male dorsal view. *Probopyrione plana* Bourdon, 1983: f, female dorsal view; g, male dorsal view. *Bopyroides hippolytes* (Kröyer, 1838): h, female dorsal view. *Discorsobopyrus stebbingi* (Nierstrasz and Brender à Brandis, 1923): i, female dorsal view. *Bopyrus crangorum* (Fabricius, 1798): j, female dorsal view. *Bopyrinella thorii* (Richardson, 1904): k, female dorsal view. *Parabopyrus kiiensis* Shiino, 1934: l, female dorsal view. *Probynia obstipa* Bourdon and Bruce, 1983: m, female dorsal view; n, male dorsal view. *Bopyrina ocellata* (Czerniavsky, 1868): o, female dorsal view; p, male dorsal view. *Schizobopyrina urocaridis* (Richardson, 1904): q, female dorsal view; r, male dorsal view. *Synsynella choprai* (Pearse, 1932): s, female dorsal view; t, male dorsal view. *Bopyrione synalphei* Bourdon and Markham, 1980: u, female dorsal view; v, female ventral view, with male attached and eggs shown in brood chamber; w, male ventral view.

lobe; internal ridge smooth. Marsupium open. Coxal plates present; dorsolateral bosses and tergal projections absent. Pleon narrower than pereon; 6 pleomeres, separated laterally, fused medially; 3 or 4 pairs of smooth uniramous pleopods; uropods present. **Male** approximately 3 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon fused; pleopods absent.

Subtidal–slope, parasitising palaemonid shrimps. Central Indo-Pacific, Temperate Northern Pacific. 3 species (An et al., 2021). This diagnosis is based on two of the three described species because *Bopyrinina articulata* An, Xi and Paulay, 2021 does not appear to belong to this genus.

Bopyrione Bourdon and Markham, 1980

Diagnosis. **Female** ovate, body slightly distorted; head distinct from pereon, triangular; frontal lamina absent. Eyes present or absent. Antennula and antenna articulated. Maxilliped without palp. Barbula with 2 smooth lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with triangular posterior lobe, larger or smaller than anterior lobe; internal ridge smooth. Marsupium open or closed. Coxal plates present; dorsolateral bosses and tergal projections absent. Pleon not narrower than pereon, 5 or 6 indistinct pleomeres; 4 or 5 pairs of smooth uniramous pleopods; uropods absent. **Male** approximately twice as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles present. Pleon with 1 or more segments laterally indicated and medially fused, ventrally segmented; pleopods absent.

Subtidal–shelf, parasitising alpheid shrimps. Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific. 5 species (An et al., 2015).

Bopyroides Stimpson, 1864

Diagnosis. **Female** ovate, body slightly distorted; head distinct from pereon; frontal lamina present. Eyes absent. Antennula and antenna articulated. Maxilliped with setose non-articulated palp. Barbula with 2 smooth lobes on each side. Pereomeres distinct. 5 pairs of oostegites. Oostegite 1 with ovate posterior lobe, smaller than anterior lobe; internal ridge smooth. Marsupium open. Coxal plates and dorsolateral bosses present, tergal projections absent. Pleon narrower than pereon, 6 pleomeres, distinct laterally, fused medially or distinct; 4 or 5 pairs of tubercular uniramous pleopods; uropods absent. **Male** approximately 4 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon fused; pleopods absent.

Subtidal–slope, parasitising hippolytid and pandalid shrimps. Arctic Ocean, Temperate Northern Atlantic, Central Indo-Pacific, Temperate Northern Pacific. 3 species (Boyko, 2004).

Bopyrus Bosc, 1801

Diagnosis. **Female** ovate, body distorted; head distinct from pereon; frontal lamina present. Eyes absent. Antennula and antenna articulated. Maxilliped with setose non-articulated palp. Barbula with 2 smooth lobes on each side. Pereomeres distinct. 5 pairs of oostegites. Oostegite 1 with ovate posterior lobe bearing triangular distal projection; internal ridge digitate. Marsupium open. Coxal plates, tergal projections and dorsolateral bosses present. Pleon narrower than pereon, 6 pleomeres fused medially, distinct laterally; 5 pairs of smooth uniramous pleopods; uropods absent. **Male** approximately 2.5 times as long as wide, pereomeres narrower posteriorly. Head narrower than pereon. Eyes present or absent. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon of 6 segments fused medially with only lateral indications; 4 pairs of sessile pleopods.

Subtidal, parasitising palaemonid shrimps. Temperate Northern Atlantic, Western Indo-Pacific, Temperate Northern Atlantic. 2 species (Bourdon, 1968).

Capitetragonia Pearse, 1953

Diagnosis. **Female** ovate, body slightly distorted; head distinct from or fused with pereon medially; frontal lamina present. Eyes present or absent. Antennula and antenna indistinct. Maxilliped with setose non-articulated palp. Barbula with 2 smooth lobes on each side. Pereomeres distinct. 5 pairs of oostegites. Oostegite 1 with ovate posterior lobe bearing triangular distal projection; internal ridge smooth. Marsupium open. Coxal plates and tergal projections present; dorsolateral bosses absent. Pleon not narrower than pereon, 6 pleomeres; 4 or 5 pairs of smooth uniramous pleopods; uropods absent. **Male** approximately 3 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present or absent. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon of 6 segments fused medially with only lateral indications; 4 or 5 pairs of sessile pleopods present.

Subtidal, parasitising alpheid shrimps. Tropical Atlantic, Central Indo-Pacific. 2 species (An et al., 2015; Markham, 1992).

Discorsobopyrus Boyko, 2004

Diagnosis. **Female** ovate, body slightly distorted; head distinct from pereon, triangular; frontal lamina present. Eyes present. Antennula and antenna not articulated. Maxilliped without palp. Barbula with 2 smooth lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with triangular posterior lobe, smaller than anterior lobe; internal ridge smooth. Marsupium closed. Coxal plates and dorsolateral bosses present; tergal projections absent. Pleon not narrower than pereon; 6 pleomeres; 5 pairs of smooth uniramous pleopods; uropods absent. **Male** approximately as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna not articulated. Pereopods of moderate size, subequal. Midventral tubercles present. Pleon fused; pleopods absent.

Slope, parasitising pandalid shrimps. Central Indo-Pacific. 1 species (Boyko, 2004).

***Litobopyrus* Markham, 1982**

Diagnosis. **Female** elongate ovate, body distorted; head distinct from pereon; frontal lamina indistinct. Eyes present. Antennula and antenna articulated. Maxilliped without palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with ovate posterior lobe, smaller than anterior lobe; internal ridge smooth. Marsupium open. Coxal plates, dorsolateral bosses and tergal projections absent. Pleon narrower than pereon, 6 pleomeres, separated laterally; 5 pairs of smooth biramous pleopods; uropods present. **Male** approximately 3 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon fused; pleopods absent.

Intertidal, parasitising alpheid shrimps. Central Indo-Pacific. 1 species (Markham, 1982).

***Ogyridione* Markham, 1988**

Diagnosis. **Female** ovate, body not distorted; head distinct from pereon; frontal lamina indistinct. Eyes present. Antennula and antenna not described. Maxilliped with setose articulated palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with triangular posterior lobe, larger than anterior lobe; internal ridge smooth. Marsupium open. Coxal plates and dorsolateral bosses present on some pereomeres; tergal projections present or absent. Pleon not narrower than pereon, 6 pleomeres, overlapping laterally; 5 pairs of asymmetrical smooth pleopods (biramous one side, uniramous on other); uropods absent. **Male** approximately twice as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of large size, subequal. Midventral tubercles absent. Pleon of 6 segments; sessile pleopods present on pleomeres 1–5.

Intertidal, parasitising ogyridid shrimps. Temperate Northern Atlantic. 1 species (Markham, 1988).

***Ovobopyrus* Markham, 1985**

Diagnosis. **Female** body ovate, length approximately 1.5 times maximum width, head distinct from pereon laterally, fused posteriorly, medially bilobed. Eyes absent. Antennula and antenna each of 2 articles. Maxilliped with non-setose, non-articulating palp. Barbula with 1 smooth short lobe on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with triangular posterior lobe, larger than anterior lobe, internal ridge smooth. Marsupium open. Coxal plates, dorsolateral bosses, and tergal projections larger on long side of pleomeres 1–4, short side of pleomeres 1–4 with reduced coxal plates and tergal projections, dorsolateral bosses absent. Pleon of 6 pleomeres, separated by lateral notches; 5 pairs of biramous smooth pleopods; uropods absent. **Male** approximately twice as long as wide, pereomeres subequal in width. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods large compared to body. Midventral tubercles absent. Pleon without lateral indication of segmentation; 5 pairs of discoid sessile pleopods.

Shelf, parasitising alpheid shrimps. Tropical Western Atlantic. 2 species (Markham, 1985; Modesto et al., 2025).

***Palaemonellione* Markham, 1989**

Diagnosis. **Female** body elongate ovate, moderately distorted; head distinct from pereon; frontal lamina present. Eyes present. Antennula and antenna articulated. Maxilliped with non-setose articulating palp. Barbula not described. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with rounded posterior lobe, smaller than anterior lobe, internal ridge smooth. Marsupium open. Tergal projections present on long side of body; coxal plates and dorsolateral bosses absent. Pleon narrower than pereon, 5 pleomeres, fused medially; pleopods asymmetrical (3 uniramous smooth pleopods on long side, none on short side); uropods absent. **Male** approximately 3 times as long as wide, pereomeres subequal in width. Head as wide as pereon. Eyes present. Antennula and antenna articulated. Pereopods not large compared to body. Midventral tubercles absent. Pleon fused; pleopods absent.

Subtidal, parasitising palaemonid shrimps. Central Indo-Pacific. 1 species (Markham, 1989).

***Parabopyrella* Markham, 1985**

Diagnosis. **Female** body linear to ovate, slightly to moderately distorted; head almost entirely fused with pereon; thin frontal lamina present. Eyes absent. Antennula and antenna articulated. Maxilliped with setose (usually) articulating palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with triangular posterior lobe, larger than anterior lobe, internal ridge smooth. Marsupium open. Coxal plates, dorsolateral bosses, and tergal projections usually present on pleomeres 1–4. Pleon subequal in width to pereon or markedly narrower; 6 pleomeres, separated by lateral notches; 5 pairs of biramous smooth pleopods; uropods absent. **Male** approximately twice as long as wide, pereomeres subequal in width. Head slightly to markedly narrower than pereon. Eyes present or absent. Antennula and antenna articulated. Pereopods large compared to body. Midventral tubercles absent. Pleon partly to completely fused; 5 pairs of sessile pleopods.

Intertidal–shelf, parasitising alpheid, hippolytid and lysmatid shrimps. Tropical Atlantic, Temperate Southern Africa, Western and Central Indo-Pacific, Temperate Northern Pacific. 29 species (An et al., 2015; Markham, 1985; Modesto et al., 2026).

***Parabopyriscus* Markham, 1985**

Diagnosis. **Female** ovate, body not distorted; head distinct from pereon; frontal lamina absent. Eyes absent. Antennula and antenna articulated. Maxilliped with setose, non-articulating palp. Barbula with 1 smooth short lobe on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with rounded posterior lobe, subequal in size to anterior lobe, internal ridge smooth. Marsupium open. Coxal plates present on pereomeres 1–6, dorsolateral bosses and tergal projections absent. Pleon subequal in width to pereon; 6 pleomeres, separated by lateral notches; 5 pairs of biramous smooth pleopods; uropods absent.

Male approximately twice as long as wide, pereomeres subequal in width. Head markedly narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size. Midventral tubercles absent. Pleon partly fused with lateral indications of segmentation; 5 pairs of sessile pleopods.

Shelf, parasitising alpheid shrimps. Tropical Western Atlantic. 1 species (Markham, 1985).

Parabopyrus Shiino, 1934

Diagnosis. **Female** elongate ovate, body distorted; head not fused with pereon; frontal lamina present. Eyes absent. Antennula and antenna articulated. Maxilliped without palp. Barbula with 1 smooth short lobe on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegites 1 asymmetrical, that on short side of body with triangular posterior lobe, much larger than anterior lobe, that on long side of body with ovate lobe, slightly larger than anterior lobe; internal ridges smooth. Marsupium open. Coxal plates present, dorsolateral bosses and tergal projections absent. Pleon not narrower than pereon; 6 pleomeres, separated laterally, fused medially; 5 pairs of smooth uniramous pleopods; uropods absent. **Male** approximately 4 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present or absent. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles present. Pleon of 6 segments; pleopods present.

Subtidal, parasitising alpheid and lysmatid shrimp. Central Indo-Pacific, Temperate Northern Pacific. 1 species (Bourdon and Bruce, 1983b).

Parapleurocrypta Chopra, 1923

Diagnosis. **Female** elongate ovate, body slightly asymmetrical; head not fused with pereon; frontal lamina present or absent. Eyes absent or present. Antennula and antenna articulated. Maxilliped with setose non-segmented palp. Barbula with 1 or 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with triangular posterior lobe, larger than anterior lobe; internal ridge smooth. Marsupium open. Coxal plates absent or present, dorsolateral bosses present, tergal projections absent. Pleon not narrower than pereon, 6 pleomeres; 5 pairs of smooth uniramous pleopods or pleopods absent; uropods uniramous. **Male** approximately twice as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon fused; pleopods and uropods absent.

Subtidal–slope, parasitising alpheid shrimps. Western Atlantic, Western Indo-Pacific. 3 species (Bourdon, 1976; Horch et al., 2024).

Probopyrinella Nierstrasz and Brender à Brandis, 1929

Diagnosis. **Female** elongate ovate, body slightly distorted; head fused or not fused with pereon; frontal lamina present. Eyes absent. Antennula and antenna articulated. Maxilliped with setose non-articulated palp. Barbula with 1 smooth short lobe on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with triangular posterior lobe, larger than anterior lobe; internal ridge smooth. Marsupium open. Coxal plates, dorsolateral bosses and tergal projections absent. Pleon not narrower than pereon, 6 pleomeres, separated laterally, fused medially; 4 pairs of smooth biramous pleopods and 1 pair of smooth uniramous pleopods; uropods absent. **Male** approximately 3 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon of 6 segments; 5 pairs of uniramous pleopods.

Pelagic, parasitising hippolytid shrimps. Temperate Northern Atlantic, Tropical Atlantic. 2 species (Adkison, 1984; Markham, 1985).

Probopyrione Bourdon, 1983

Diagnosis. **Female** ovate, body slightly distorted; head not fused with pereon; frontal lamina present. Eyes absent. Antennula and antenna not articulated. Maxilliped without palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with triangular posterior lobe, larger than anterior lobe; internal ridge smooth. Marsupium closed. Coxal plates, dorsolateral bosses and tergal projections absent. Pleon not narrower than pereon, 6 pleomeres, separated laterally, fused medially; 5 pairs of smooth uniramous pleopods; uropods absent. **Male** approximately twice as long as wide, pereomeres narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna not articulated. Pereopods of moderate size, subequal. Midventral tubercles present. Pleon fused; pleopods absent.

Subtidal, parasitising alpheid shrimps. Central Indo-Pacific. 1 species (Bourdon, 1983).

Probopyriscus Markham, 1982

Diagnosis. **Female** elongate, body not distorted; head distinct from pereon; frontal lamina present. Eyes present. Antennula and antenna articulated. Maxilliped with setose palp. Barbula with 2 smooth very short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegites 1 asymmetrical, triangular posterior lobe on one side larger than anterior lobe, on other side subequal to anterior lobe; internal ridges smooth. Marsupium open. Coxal plates, dorsolateral bosses and tergal projections present. Pleon narrower than pereon, 6 pleomeres, separated laterally; 5 pairs of smooth biramous pleopods; uropods absent. **Male** approximately twice as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon of 6 segments; 5 pairs of uniramous pleopods.

Subtidal, parasitising alpheid shrimps. Central Indo-Pacific. 1 species (Markham, 1982).

Probopyrus Giard and Bonnier, 1888

Diagnosis. **Female** ovate, body slightly distorted; head distinct from pereon; frontal lamina small or absent. Eyes absent. Antennula and antenna articulated. Maxilliped with setose

non-articulated palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with ovate posterior lobe bearing distal triangular projection, larger than anterior lobe; internal ridge smooth or digitate. Marsupium open. Coxal plates and dorsolateral bosses present; tergal projections absent. Pleon not narrower than pereon, 6 pleomeres, distinct or fused medially; 5 pairs of biramous smooth pleopods; uropods present or absent. **Male** approximately 2–3 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon of 5 or 6 segments; 3–5 pairs of tuberculiform to globose pleopods.

Subtidal, parasitising palaemonid and thorid shrimp. Temperate Northern Atlantic, Tropical Atlantic, Temperate South American, Western and Central Indo-Pacific, Tropical Eastern Pacific. 29 species (Dale and Anderson, 1982; Markham, 1985).

Probynia Bourdon and Bruce, 1983

Diagnosis. **Female** elongate ovate, body strongly distorted; head distinct from pereon; frontal lamina present. Eyes present or absent. Antennula and antenna articulated. Maxilliped with setose articulated palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with ovate posterior lobe bearing distal triangular projection, larger than anterior lobe; internal ridge smooth. Marsupium open. Coxal plates present on some pereomeres; dorsolateral bosses and tergal projections present or absent. Pleon narrower than pereon, 6 pleomeres, overlapping laterally; 4 or 5 pairs of uniramous smooth pleopods; uropods absent. **Male** approximately 3 times as long as wide, pereomeres slightly narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon of 3 free segments and fourth segment fused with lateral indications of segmentation; pleopods present on pleomeres 1 and 2 or 1–3.

Subtidal, parasitising palaemonid shrimp. Tropical Atlantic, Western and Central Indo-Pacific. 3 species (Bourdon and Bruce, 1983a; Romero-Rodríguez and Álvarez, 2021).

Schizobopyrina Markham, 1985

Diagnosis. **Female** ovate, body distorted; head distinct from pereon; frontal lamina present. Eyes present or absent. Antennula and antenna articulated. Maxilliped with setose, articulating palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegites 1 asymmetrical, that on short side of body with recurved triangular posterior lobe, larger than anterior lobe, that on long side of body with rounded posterior lobe, subequal to anterior lobe; internal ridges smooth. Marsupium open. Dorsolateral bosses present on pereomeres 1–4, coxal plates and tergal projections absent. Pleon narrower than pereon, 6 pleomeres, overlapping laterally; 4 pairs of uniramous smooth pleopods; uropods absent. **Male** approximately 2–3 times as long as wide, pereomeres subequal in width. Head subequal in width to pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size. Midventral tubercles absent. Pleon partly fused with lateral indications of segmentation; 3 or 4 pairs of sessile pleopods.

Subtidal, parasitising hippolytid, palaemonid and thorid shrimps. Temperate Northern Atlantic, Tropical Atlantic, Indo-West Pacific, Temperate Northern Pacific. 13 species, including *Schizobopyrina platylobae* (Bourdon *in* Bourdon and Bruce, 1983), which Boyko and Williams (2023) listed erroneously under *Bopyrina* (Campos and Campos, 1990; Markham, 1985; Williams and Boyko, 2004).

Septembopyrina An, Boyko and Li, 2015

Diagnosis. **Female** elongate ovate, body slightly distorted; head fused with pereon; frontal lamina present. Eyes absent. Antennula and antenna articulated. Maxilliped without palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 7 pairs of oostegites. Oostegite 1 with elongate triangular posterior lobe, larger than anterior lobe; internal ridge smooth. Marsupium open. Dorsolateral bosses present on pereomere 1, coxal plates and tergal projections absent. Pleon slightly narrower than pereon, 5 pleomeres, separated laterally with notches; 5 pairs of uniramous smooth pleopods; uropods absent. **Male** approximately 3 times as long as wide, pereomeres narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, smaller posteriorly. Midventral tubercles absent. Pleon fused with lateral indications of segmentation; pleopods absent.

Shelf, parasitising hippolytid shrimps. Central Indo-Pacific. 1 species (An et al., 2015).

Synsynella Hay, 1917

Diagnosis. **Female** elongate ovate, body weakly distorted; head fused with pereon; frontal lamina present. Eyes absent. Antennula and antenna articulated. Maxilliped with setose articulated or non-articulated palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1with ovate posterior lobe bearing triangular posterior projection, larger than anterior lobe; internal ridge smooth. Marsupium open. Coxal plates and dorsolateral bosses present, tergal projections absent. Pleon narrower than pereon, 6 pleomeres, approximated laterally; 4 pairs of smooth uniramous pleopods; uropods absent. **Male** approximately twice as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present or absent. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon of 3 free segments and 2 fused segments; 3 or 4 pairs of uniramous pleopods present or absent.

Subtidal–shelf, parasitising alpheid shrimps. Temperate Northern Atlantic, Tropical Atlantic, Temperate Northern Pacific. 5 species (Markham, 1985).

Urobopyrus Richardson, 1904

Diagnosis. **Female** ovate, body not distorted; head distinct from pereon; frontal lamina present. Eyes absent. Antennula and antenna articulated. Maxilliped with setose non-articulated palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with triangular

posterior lobe, larger than anterior lobe; internal ridge smooth. Marsupium open. Coxal plates and dorsolateral bosses present, tergal projections absent. Pleon narrower than pereon, 6 pleomeres, separated laterally; 5 pairs of smooth biramous pleopods; uropods biramous. **Male** approximately 3 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes absent. Antennula and antenna articulated. Pereopods of moderate size, first 2 pairs much larger than others. Midventral tubercles absent. Pleon of 6 segments; 1 pair of uniramous pleopods.

Shelf, parasitising processid shrimps. Tropical Atlantic, Temperate Northern Atlantic. 1 species (Markham, 1985).

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Subfamily Hemiarthrinae Markham, 1972

Figures 6.12, 6.13

Genera of Hemiarthrinae can be distinguished from those of other bopyrid subfamilies in that females have slight to extreme distortion of the head relative to the body and have one side of the body formed by greatly expanded oostegites, giving the body a strongly asymmetrical appearance. Species in Hemiarthrinae are ectoparasites of caridean shrimps. Females of most species are found attached to the ventral surface of the abdomen but those in some genera are found in unusual positions: attached to the buccal region (*Orophryxus*), attached to the dorsal or lateral surface of the abdomen (*Filophryxus*, *Metaphrixus*), or in the branchial chamber (*Sigyn*). The key is modified from that of An et al. (2020). *Pliophrixus* Caroli, 1930 is very poorly described and is not included in the key. Representative males are figured.

Diagnosis. **Female** body linear or subovate, elongate or compact, asymmetrical and expanded on convex side, distorted approximately 10–110°; head rounded or elongated, anterolateral margins not produced or produced into anteriorly or anterolaterally directed lobes. Eyes present or absent. Antennula articulated or non-articulated or absent. Antenna articulated or non-articulated or absent. Barbula with 1–8 smooth short lobes on each side. Maxilliped without palp. Pereomeres distinct on concave side, fused on convex side (sometimes with 1–4 anterior segments distinct), distinct or indistinct dorsally. Marsupium closed. Oostegites 1 asymmetrical; internal ridge smooth; oostegites 2–5 usually present but variable; oostegite 2 recurved over head and covered with cup-like discs or not recurved and smooth. Coxal plates and dorsolateral bosses present or absent. 1–7 pereopods present on concave and convex sides. Pleon of 1–5 pleomeres; 2–5 pairs of uniramous or biramous smooth lateral plates and 2–5 pairs of uniramous or biramous smooth pleopods present or absent. Uropods uniramous or absent. **Male** pereomeres subequal in width or anterior, middle, or posterior pereomeres wider; midventral tubercles absent. Head wider than long. Eyes present or absent. Antennula and antenna articulated or non-articulated. 7 pairs of subequal pereopods. Pleomeres fused into single segment with or without lateral indication of segmentation; pleopods absent. Uropods present or absent.

Key to genera of Hemiarthrinae

1.	Pleon of female without appendages (fig. 6.12a, b)	*Orophryxus*
–	Pleon of female with appendages	2
2.	Coxal plates of female with filiform extensions	3
–	Coxal plates of female without filiform extensions	4
3.	Female with 3 pairs of uniramous pleopods (fig. 6.12e)	*Filophryxus*
–	Female with 3 pairs of uniramous pleopods and 4th uniramous pleopod on one side (fig. 6.12o)	*Izuohshimaphryxus*
4.	Female without lateral plates	5
–	Female with lateral plates	7
5.	Female with 5 pleomeres	6
–	Female with pleon fused, 2 pereopods on convex side of body (fig. 6.12f)	*Anomophryxus*
6.	Female with 1 pereopod on convex side of body, male without pleonal extensions (fig. 6.12c, d)	*Neophryxus*
–	5 pereopods on convex side of body, male with 2 pairs of pleonal extensions (fig. 6.13o, p)	*Alaxphryxus* n. gen.
7.	Female with fewer than 5 pleomeres	8

– Female with 5 pleomeres 16

8. Female with fewer than 4 pleomeres 9

– Female with 4 pleomeres 12

9. Female with 1 pleomere 10

– Female with 3 pleomeres 11

10. Female with 3 pairs of uniramous lateral plates (fig. 6.12v) ..... *Mesophryxus*

– Female with 4 pairs of uniramous lateral plates (fig. 6.12p) ..... *Apophrixus*

11. Female with 3 pairs of uniramous lateral plates (fig. 6.13k, l) ..... *Anchiarthrus*

– Female with 2 pairs of uniramous lateral plates (fig. 6.13j) ..... *Miophrixus*

12. Female with 4 lateral plates on convex side, 3 on concave side (fig. 6.13n) ..... *Azygopleon*

– Female with all lateral plates paired 13

13. Female with 3 pairs uniramous lateral plates (fig. 6.13l) ..... *Hypohyperphrixus*

– Female with 4 pairs uniramous lateral plates 14

14. Female with biramous pleopods (fig. 6.12m) ..... *Quadripediphryxus*

– Female with uniramous pleopods 15

15. Female with 4 pereopods on convex side (fig. 6.12h, i) ..... *Hemiphryxus*

– Female with 2 pereopods plus stub on convex side (fig. 6.13c, d) ..... *Mediophrixus*

16. Female with fewer than 5 pereopods on convex side 17

– Female with 5 or 7 pereopods on convex side 25

17. Female with lateral plates biramous to quadriramous 18

– Female with lateral plates uniramous 20

18. Female with oostegite 2 not reflexed over head, 4 biramous pleopods on one side of pleon (fig. 6.12j) 19

– Female with oostegite 2 reflexed over head, 4 biramous pleopods on both sides of pleon (fig. 6.12l) ..... *Diplophryxus*

19. Female with 4 biramous pleopods on one side of pleon (fig. 6.12j) ..... *Allodiplophryxus*[1]

– Female with 4 biramous pleopods on both sides of pleon (fig. 6.12n) ..... *Micropodiphryxus*

20. Female with oostegite 2 reflexed over head 21

– Female with oostegite 2 not reflexed over head 22

21. Female with 4 pairs of biramous pleopods (fig. 6.13f) ..... *Hyperphrixus*[1]

– Female with 4 pairs of uniramous pleopods (fig. 6.13m) ..... *Hemiarthrus*

22. Female with pleotelson divided (fig. 6.13e) ..... *Dicropleon*

– Female with pleotelson undivided 23

23. Female with 5 pairs of lateral plates, uropods present (fig. 6.12g) ..... *Epiphrixus*

– Female with 4 pairs of lateral plates, uropods absent 24

24. Female with head c. 80–90° distorted (fig. 6.13g) ..... *Metaphrixus*

– Female with head c. 20–30° distorted (fig. 6.13a) ..... *Eriphrixus*

25. Female found in host branchial chamber (fig. 6.12s) ..... *Sigyn*

– Female found on ventral abdomen 26

26.	Male with 1 pair of pleonal extensions	*Hypophryxus*
–	Male without pleonal extensions	27
27.	Female with biramous lateral plates (fig. 6.12k)	*Cataphryxus*[2]
–	Female with uniramous lateral plates	28
28.	Female with terminal pleomere entire or indented but without elongate uropods (figs 6.12q, r, 6.13h, i)	*Anisarthrus*/*Eophrixus*[3]
–	Female with elongate uropods (fig. 6.12t, u)	*Loki*

[1] Type species only (genus likely not monophyletic)

[2] Females of *Cataphryxus fiedleri* Markham, 2025 have only 3 pereopods on the convex side of the body; the other two species in the genus have 7 pairs of pereopods; otherwise all three species appear congeneric.

[3] Type species of *Eophrixus* and *Anisarthrus* are very similar; the type species of *Eophrixus* is incompletely described/illustrated and the genus is likely not monophyletic.

Alaxphryxus Boyko and Williams n. gen.

(http://zoobank.org/urn:lsid:zoobank.org:act:40AA0134-BBE7-4167-8D3C-BC1699A94CFB)

Type species. *Hemiarthrus filiformis* Chopra, 1923 (by original designation and monotypy).

Diagnosis. **Female** body linear, distorted approximately 30°. Eyes absent. Antennula, antenna, barbula and oostegite 1 not described. Pereomeres distinct dorsally only on concave side. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 5 pereopods on convex side. Pleon of 5 pleomeres, lateral plates absent, 4 pairs of smooth biramous pleopods; uropods absent. **Male** with pereomeres subequal in width. Eyes present. Antennula and antenna articulated. Pleon with segmentation laterally indicated, with 2 pairs of pleonal extensions at anterior end; uropods absent.

Subtidal, parasitising alpheid shrimps, Western Indo-Pacific. 1 species (Chopra, 1923).

Etymology. The new genus is named (*ala* = wing + x + *phryxus*, a common suffix in hemiarthrine taxa) after the male's pleopodal extensions, which resemble the wings of an X-wing starfighter in the *Star Wars* films.

Remarks. The two pairs of extensions on the pleon of the male are unique among hemiarthrine taxa and warrant the erection of a new genus; males in *Hypophryxus* have a single pair of pleonal extensions, but the females in that genus have lateral plates that are lacking in *Alaxphryxus*. There is a record of "*Hypophryxus filiformis* (Chopra, 1923)" from Markham (1992) where the male has two pleonal extensions but the female has lateral plates; this is not likely to be conspecific with *Alaphryxus filiformis* n. comb. and may not belong to the genus.

Allodiplophryxus Markham, 1985

Diagnosis. **Female** body linear, elongate, distorted approximately 90°; head elongated, anterolateral margins not produced. Eyes present. Antennula of 1 or 2 articles; antenna absent. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. Oostegite 1 on convex side with ovate posterior lobe, larger than anterior lobe, that on concave side with elongate posterior lobe, larger than anterior lobe. Coxal plates and dorsolateral bosses absent. 5 pereopods present on concave side, 2 plus basal scar of 3 present on convex side. Pleon of 5 pleomeres; 4 pairs of biramous smooth lateral plates and 4 pairs of biramous smooth pleopods on both sides or 4 biramous smooth pleopods on one side only; uropods absent. **Male** with pleomeres subequal in width. Eyes present. Antennula and antenna articulated. Pleon without lateral indication of segmentation; uropods absent.

Subtidal, parasitising palaemonid shrimps. Tropical Western Atlantic, Central Indo-Pacific. 2 species (An et al., 2020; Markham, 1985).

Anchiarthrus Markham, 1992

Diagnosis. **Female** body subovate, distorted approximately 60°; head embedded in pereon. Eyes absent. Antennae and antennulae absent. Barbula with 1 smooth lobe on each side. Pereomeres indistinct dorsally. Oostegite 1 on concave side with small bilobed posterior lobe, that on convex side larger. Oostegites 2–4 present on both sides. Coxal plates and dorsolateral bosses absent. 7 pereopods present on concave side, 3–6 present on convex side. Pleomeres fused but with indication of 3 pleomeres; 3 pairs of uniramous smooth lateral plates and 3 pairs of biramous smooth pleopods present; uropods absent. **Male** with pereomeres subequal in width. Eyes present. Antenna and antennula articulated. Posterior pairs of pereopods slightly longer. Pleon with lateral indications of segmentation; uropods absent.

Intertidal, parasitising alpheid shrimps. Central Indo-Pacific. 1 species (An et al., 2015).

Anisarthrus Giard, 1907

Diagnosis. **Female** body linear, elongate, distorted approximately 40°; head rounded, anterolateral margins produced as anterolaterally directed lobes. Eyes absent. Antennula and antenna articulated. Barbula with 1 smooth short lobe on each side. Pereomeres distinct dorsally. Oostegite 1 on convex side with ovate posterior lobe, smaller than anterior lobe, that on concave side without posterior lobe. Coxal plates absent; dorsolateral bosses present on concave side. 7 pereopods present on both sides. Pleon of 5 pleomeres; pleomeres 1 and 2 with

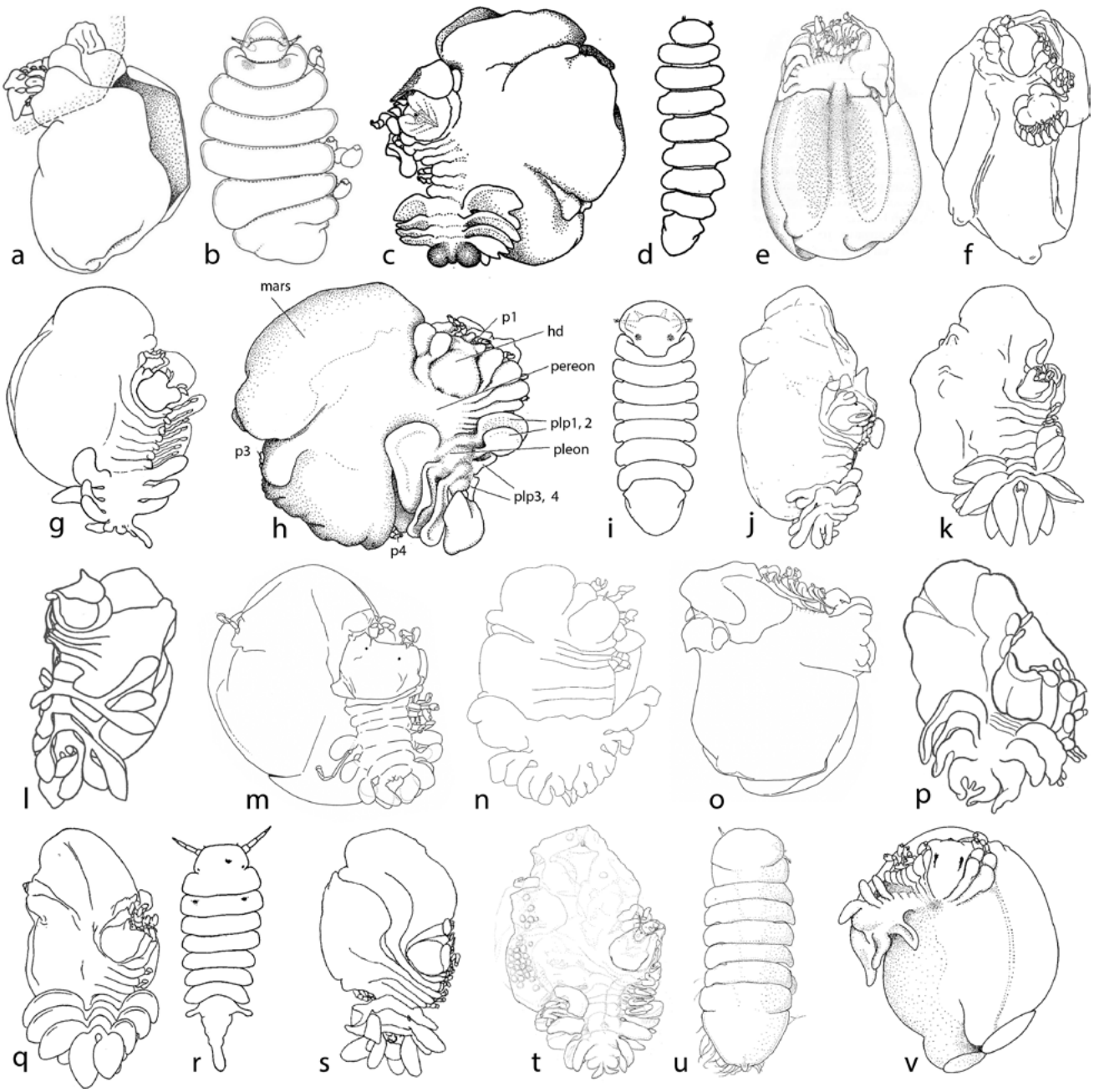


Fig. 6.12. Hemiarthrinae. *Orophryxus shiinoi* Bruce, 1972: a, female dorsal view, host's carapace indicated by broken line; b, male dorsal view. *Neophryxus globicaudatus* (Bruce, 1973): c, female dorsal view; d, male dorsal view. *Filophryxus dorsalis* Bruce, 1972: e, female dorsal view. *Anomophryxus deformatus* Shiino, 1937: f, female dorsal view with male attached. *Epiphrixus adriaticus* Nierstrasz and Brender à Brandis, 1932: g, female dorsal view. *Hemiphryxus malindiae* (Bruce, 1974): h, female dorsal view; i, male dorsal view. *Allodiplophryxus floridanus* Markham, 1985: j, female dorsal view. *Cataphryxus primus* (Shiino, 1934): k, female dorsal view. *Diplophryxus jordani* Richardson, 1904: l, female dorsal view. *Quadripediphryxus mayuzumii* Saito, 2020: m, female dorsal view. *Micropodiphryxus richardsonae* (Chopra, 1930): n, female dorsal view. *Izuohshimaphryxus hoshinoi* Saito, 2015: o, female dorsal view. *Apophrixus philippinensis* Nierstrasz and Brender à Brandis, 1931: p, female dorsal view. *Eophrixus yusakiensis* (Shiino, 1934): q, female dorsal view; r, male dorsal view. *Sigyn branchialis* An, Boyko and Li, 2015: s, female dorsal view. *Loki circumsaltanus* Markham, 1972: t, female dorsal view; u, male dorsal view. *Mesophryxus ventralis* Bruce, 1973: v, female dorsal view. Abbreviations: hd, head; mars, marsupium, p, pereopod; plp, pleopod.

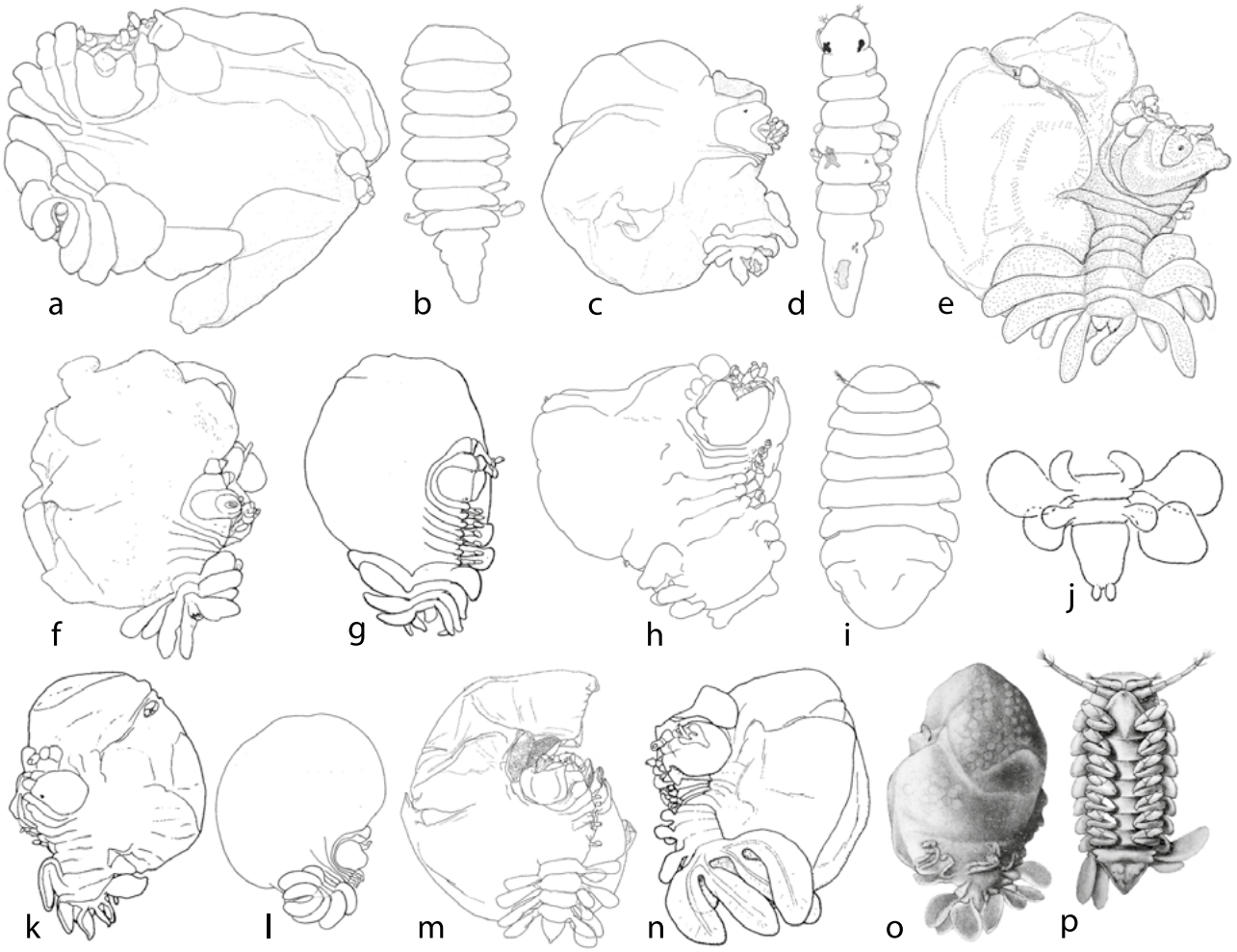


Fig. 6.13. Hemiarthrinae. *Eriphrixus obesus* Markham, 1990: a, female dorsal view; b, male dorsal view. *Mediophrixus pinuum* Markham, 1990: c, female dorsal view; d, male dorsal view. *Dicropleon periclimenis* Markham, 1972: e, female dorsal view. *Hyperphrixus castrensis* Markham, 1985: f, female dorsal view. *Metaphrixus carolii* Nierstrasz and Brender à Brandis, 1931: g, female dorsal view. *Anisarthrus okunoi* Saito and Shimomura, 2015: h, female dorsal view; i, male dorsal view. *Miophrixus latreutidis* Barnard, 1955: j, terminal segments of female pleon. *Anchiarthrus derelictus* Markham, 1992: k, female dorsal view. *Hypohyperphrixus latilamellaris* Nierstrasz and Brender à Brandis, 1932: l, female dorsal view. *Hemiarthrus surculus* Boyko and Williams, 2004: m, female dorsal view. *Azygopleon schmitti* (Pearse, 1932): n, female dorsal view. *Alaxphryxus filiformis* (Chopra, 1923) n. comb.: o, female dorsal view; p, male ventral view.

midventral tubercles; 4 pairs of uniramous smooth lateral plates present; 4 pairs of uniramous smooth pleopods present; uropods absent. **Male** with pereomeres wider posteriorly, pereomeres 7 medially fused with pleon. Eyes absent. Antennula and antenna articulated. Pleon fused with pereomere 7 with slight lateral indication of segmentation; uropods absent.

Subtidal, parasitising alpheid and rhynchocinetid shrimps. Temperate Northern Atlantic, Temperate Northern Pacific. 2 species (Saito and Shimomura, 2015).

Anomophryxus Shiino, 1937

Diagnosis. **Female** body compact, distorted approximately 60°; head elongate, medially constricted, anterolateral margins not produced. Eyes absent. Antennula papilliform, antenna articulated. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally and on first 2 pereomeres of convex side. Marsupium formed of 4 oostegites on convex side, 3 on concave side. Oostegite 1 on convex side with ovate posterior lobe, as large as anterior lobe, that on concave side without posterior lobe. Coxal plates and dorsolateral bosses absent. 7 pereopods present on concave side, 2 present on convex side. Pleon of fused segments; lateral plates absent; 4 pairs of uniramous smooth pleopods, anterior 2 pairs much larger than posterior ones; uropods present. **Male** with pereomeres subequal in width except 7 narrower. Eyes absent. Antennula and antenna articulated. Pleon without lateral indication of segmentation; uropods absent.

Shelf, parasitising pandalid shrimps. Temperate Northern Pacific. 1 species (Shiino, 1937).

Apophrixus Nierstrasz and Brender à Brandis, 1931

Diagnosis. **Female** body linear, elongate, distorted approximately 30°; head subquadrate, anterolateral margins produced as anterolaterally directed lobes. Eyes absent. Antennula and antenna articulated. Barbula with 1 smooth short lobe and 1 low blunt lobe on each side. Pereomeres indistinct dorsally. Oostegite 1 on convex side with triangular posterior lobe, smaller than anterior lobe, that on concave side with ovate posterior lobe, larger than anterior lobe. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 6 or 7 on convex side. Pleon of single fused segment; 4 pairs of uniramous smooth lateral plates; 4 pairs of uniramous smooth pleopods; uropods present. **Male** with pereomeres subequal in width, pereomeres 6 and 7 fused with pleon in one species. Eyes present or absent. Antennula and antenna articulated. Posterior pairs of pereopods longer. Pleon sometimes fused with pereomeres 6 and 7, with slight lateral indication of segmentation; uropods absent.

Subtidal, parasitising alpheid shrimps. Central Indo-Pacific. 2 species (An et al., 2015).

Azygopleon Markham, 1985

Diagnosis. **Female** body linear, compact, distorted approximately 40–90°; head rounded, anterolateral margins not produced. Eyes absent. Antennulae fused, displaced onto dorsal surface of head, antennae as non-articulated lobes. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. Oostegite 1 on convex side with ovate posterior lobe, as large as anterior lobe, that on concave side with small finger-like posterior lobe, much smaller than anterior lobe. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 1 on convex side. Pleon usually of 4 pleomeres, pleotelson absent; concave side with 4 uniramous smooth lateral plates and 4 uniramous smooth pleopods, convex side with 3 lateral plates and uniramous pleopod on pleomere 4 only; uropods absent. **Male** with pereomeres subequal in width but posterior pereomeres longer than anterior. Eyes absent. Antennula and antenna articulated. Pleon fused without lateral indication of segmentation; uropods absent.

Subtidal–shelf, parasitising alpheid shrimps. Temperate Northern and Tropical Atlantic. 1 species (Markham, 1985).

Cataphryxus Shiino, 1936

Diagnosis. **Female** body linear, distorted approximately 35–50°; head ovate, anterolateral margins produced anteriorly. Eyes absent. Antennula and antenna articulated. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. Marsupium formed of 4 or 5 oostegites on both sides. Oostegite 1 on convex side with slender ovate posterior lobe, as large as or smaller than anterior lobe, that on concave side with minute to large posterior lobe. Coxal plates and dorsolateral bosses absent. 7 pereopods on both sides or 3 on one side and 7 on the other. Pleon of 5 pleomeres; 4 pairs of biramous smooth lateral plates; 4 pairs of biramous pleopods, those on pleomeres 2–4 with additional papilla-like appendage; uropods absent but pleotelson with posterior digitiform processes. **Male** with pereomeres subequal in width. Eyes absent. Antennula and antenna articulated. Pleon without lateral indication of segmentation; uropods absent.

Subtidal, parasitising lysmatid shrimps. Temperate Northern Pacific, Tropical Eastern Pacific. 3 species (Romero Rodríguez and Álvarez, 2023; Markham, 2025).

Dicropleon Markham, 1972

Diagnosis. **Female** body linear, elongate, distorted approximately 30–50°; head rounded, anterolateral margins produced as anteriorly directed lobes. Eyes absent. Antennula and antenna articulated. Barbula with 2 smooth lobes on each side. Pereomeres distinct dorsally. Oostegite 1 on convex side with ovate posterior lobe, as large as anterior lobe, that on concave side with small finger-like lobe. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 2 or 3 on convex side. Pleon of 5 pleomeres; pleotelson subdivided; 4 pairs of uniramous smooth lateral plates, 4 pairs of uniramous or biramous or 3 pairs and 1 pair uniramous smooth pleopods; uropods absent. **Male** with pereomeres subequal in width. Eyes present. Antennulae and antennae articulated. Posterior pairs of pereopods longer. Pleon without indication of segmentation, distal tip cleft; uropods absent.

Subtidal, parasitising palaemonid and processid shrimps. Tropical Atlantic, Western and Central Indo-Pacific. 4 species (An et al., 2015).

Diplophryxus Richardson, 1904

Diagnosis. **Female** body linear, compact, distorted approximately 30–100°; head ovate, anterolateral margins not produced. Eyes absent. Antennula non-articulated or articulated; antenna non-articulated. Barbula with 2 smooth lobes on each side. Pereomeres distinct dorsally. Oostegite 1 on convex side with ovate elongate posterior lobe, larger than anterior lobe, that on concave side with ovate posterior lobe, smaller than anterior lobe. Oostegite 2 reflexed over head, covered in cup-shaped discs. Pereopods 3–7 on concave side; 1 or 2 on convex side. Pleon of 5 pleomeres, pleotelson elongate with terminal point; 4 pairs of biramous to quadriramous smooth lateral plates and 4 pairs of smooth biramous to quadriramous pleopods; uropods absent. **Male** with pereomeres subequal in width. Eyes absent. Antennula and antenna articulated. Pleon without indication of segmentation; uropods absent.

Intertidal–shelf, parasitising alpheid and palaemonid shrimps. Temperate Northern Atlantic, Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific, Temperate South America. 8 species (Boyko, 2012; Markham, 1985).

Eophrixus Caroli, 1930

Diagnosis. **Female** body linear, compact, not distorted or distorted approximately 40–80°; head bilobate or ovate, anterolateral margins not produced or produced into anteriorly directed lobes. Eyes absent. Antennula articulated or non-articulated; antenna articulated. Barbula with 2 smooth lobes on each side. Pereomeres distinct dorsally. Oostegite 1 on convex side with ovate posterior lobe, smaller than anterior lobe, that on

concave side with ovate posterior lobe, smaller (sometimes markedly so) than anterior lobe. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 5 or 7 pereopods on convex side. Pleon of 5 pleomeres; 4 pairs of uniramous smooth lateral plates and 3 or 4 pairs of smooth uniramous or biramous pleopods; uropods present or absent. **Male** with pereomeres subequal in width. Eyes present. Antennula and antenna articulated. Pleon without indication of segmentation or with segmentation laterally indicated; uropods absent or present but not elongate.

Subtidal, parasitising alpheid, hippolytid, lysmatid, palaemonid and pasiphaeid shrimps. Temperate Northern Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific. 11 species (An et al., 2015).

Epiphrixus Nierstrasz and Brender à Brandis, 1932

Diagnosis. **Female** body linear, distorted approximately 30°; anterolateral margins of head produced into anteriorly directed lobes. Eyes absent. Antenna and antennula present (non-articulated?). Barbula unknown. Pereomeres distinct dorsally. Oostegites 1 posterior lobes unknown. Oostegites 2–4 present. Coxal plates on pereomeres 1 and 2 of convex side and 1–7 of concave side; dorsolateral bosses absent. 7 pereopods on concave side, 2 on convex side. Pleon of 5 pleomeres; 5 uniramous lateral plates, 5 pairs of uniramous pleopods; uropods present. **Male** unknown.

Intertidal, parasitising alpheid shrimps. Temperate Northern Atlantic. 1 species (Nierstrasz and Brender à Brandis, 1932).

Eriphrixus Markham, 1990

Diagnosis. **Female** body ovate, compact, distorted approximately 40°; head rounded, anterolateral margins produced as anteriorly directed lobes. Eyes absent. Antennulae absent; antenna non-articulated. Barbula with 1 smooth short lobe on each side. Pereomeres weakly distinct dorsally. Oostegite 1 on convex side with ovate posterior lobe, smaller than anterior lobe, that on concave side unknown. Coxal plates present on concave side; dorsolateral bosses absent. 7 pereopods on concave side, pereopods 1–3 on convex side. Pleon of 5 pleomeres; pleotelson globose; 4 pairs of uniramous smooth lateral plates and 4 pairs of uniramous smooth pleopods; uropods absent. **Male** with anterior pereomeres wider than posterior. Eyes absent. Antennula and antenna articulated. Posterior pairs of pereopods longer. Pleon with lateral indication of segmentation; uropods absent.

Slope, parasitising palaemonid shrimps. Central Indo-Pacific. 1 species (Markham, 1990).

Filophryxus Bruce, 1972

Diagnosis. **Female** body linear, compact, distorted approximately 90°; head fused with pereon, anterolateral margins produced as laterally directed lobes. Eyes absent. Antennulae absent; antenna non-articulated. Barbula with 1 smooth short lobe on each side. Pereomeres distinct dorsally, first 2 pereomeres distinct on convex side. Oostegite 1 on convex side with ovate posterior lobe, nearly as large as anterior lobe, that on concave side with ovate posterior lobe, much smaller than anterior lobe. Filiform coxal plates on pereomeres 1–6 of concave side; dorsolateral bosses absent. 3 pereopods on concave side, 2 pereopods on convex side. Pleon of 1 fused segment; lateral plates absent; 3 pairs of uniramous smooth pleopods; uropods absent. **Male** with anterior pereomeres wider than posterior. Eyes absent. Antennula and antenna articulated. Pleon without lateral indication of segmentation; uropods absent.

Slope, parasitising palaemonid shrimps. Temperate Australasia. 1 species (Bruce, 1972a).

Hemiarthrus Giard and Bonnier, 1887

Diagnosis. **Female** body linear, elongate, distorted approximately 35–60°; head ovate, anterolateral margins produced into anteriorly directed lobes. Eyes absent. Antennulae and antennae non-articulated. Barbula with 2–4 smooth lobes on each side. Pereomeres distinct dorsally. Oostegite 1 on convex side with ovate posterior lobe, larger than anterior lobe, that on concave side with finger-like posterior lobe, smaller than anterior lobe. Oostegite 2 reflexed over head and covered with cup-shaped discs; oostegites 3 and 4 with cup-shaped discs on lateral margins. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side; 1 pereopod on convex side. Pleon of 5 pleomeres; 4 pairs of uniramous smooth lateral plates and 4 pairs of smooth uniramous pleopods; uropods absent. **Male** with pereomeres subequal in width. Eyes present. Antennulae and antennae articulated. Pleon without indication of segmentation or with segmentation laterally indicated; uropods absent.

Subtidal–slope, parasitising alpheid, nematocarcinid, and thorid shrimps. Temperate Northern Atlantic, Tropical Atlantic, Temperate Southern Africa, Eastern Indo-Pacific. 5 species (An et al., 2020; Markham, 1985).

Hemiphryxus Bruce, 1978

Diagnosis. **Female** body linear, compact, distorted approximately 90°; head rounded, anterolateral margins produced as anterolaterally directed lobes. Eyes absent. Antennula as papillae; antenna articulated. Barbula with 1 smooth short lobe on each side. Pereomeres distinct dorsally, first 2 distinct on convex side. Oostegite 1 on convex side with triangular posterior lobe, larger than anterior lobe, that on concave side with ovate posterior lobe, smaller than anterior lobe. Coxal plates present; dorsolateral bosses absent. 7 pereopods on concave side, 4 pereopods on convex side. Pleon of 4 pleomeres; 4 pairs of uniramous smooth lateral plates; 4 pairs of uniramous smooth pleopods; uropods absent. **Male** with pereomeres subequal, head distally expanded and recurved. Eyes present. Antennula and antenna articulated. Pleon with lateral indication of segmentation; uropods absent.

Subtidal, parasitising palaemonid shrimps. Western Indo-Pacific. 1 species (Bruce, 1974).

Hyperphrixus Nierstrasz and Brender à Brandis, 1931

Diagnosis. **Female** body linear, elongate, distorted approximately 90°–110°; head elongate-ovate, anterolateral margins not produced. Eyes absent. Antennula and antenna

unknown. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side; 1 or 2 pereopods on convex side. Pleon of 5 pleomeres; 4 pairs of uniramous smooth lateral plates; 4 pairs of biramous smooth pleopods; uropods absent. **Male** with pereomeres subequal in width. Eyes present. Antennula and antenna articulated. Posterior pairs of pereopods shorter. Pleon without lateral indication of segmentation; uropods absent.

Subtidal, parasitising alpheid and palaemonid shrimps. Tropical Atlantic, Western and Central Indo-Pacific. 3 species (An et al., 2015).

Hypohyperphrixus Nierstrasz and Brender à Brandis, 1932

Diagnosis. **Female** body linear, compact, not distorted; head rounded, anterolateral margins not produced. Eyes absent. Antennula and antenna unknown. Barbula unknown. Pereomeres distinct dorsally, 1–4 distinct on convex side. Coxal plates and dorsolateral bosses absent. 7 Pereopods on concave side, 1 on convex side. Pleon of 4 pleomeres; 3 pairs of uniramous smooth lateral plates; 3 pairs of biramous smooth pleopods; uropods present. **Male** unknown.

Subtidal, parasitising alpheid shrimps. Western Indo-Pacific. 1 species (Nierstrasz and Brender à Brandis, 1932).

Hypophryxus Shiino, 1934

Diagnosis. **Female** body linear, compact, not distorted or distorted approximately 15°; head bilobate, anterolateral margins produced into anteriorly directed lobes. Eyes absent. Antennula articulated; antenna articulated. Barbula unknown. Pereomeres distinct dorsally. Oostegite 1 unknown. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 7 pereopods on convex side. Pleon of 5 pleomeres; 4 pairs of uniramous smooth lateral plates and 4 pairs of smooth biramous pleopods; uropods present. **Male** with anterior pereomeres widest. Eyes present. Antennula and antenna articulated. Pleon fused with segmentation laterally indicated and pair of pleonal extensions at anterior end; uropods absent.

Subtidal, parasitising alpheid shrimps. Temperate Northern Pacific. 1 species (Shiino, 1934). Markham (1992) confounded the genera *Hypophryxus* and *Hyperphrixus* when trying to resurrect *Hypophryxus* from synonymy with *Eophrixus* (see Caroli, 1949) and An et al. (2015) decided that Caroli's synonym was correct. Re-examination of the description of *H. yusakiensis* Shiino, 1934 and comparison with all hemiarthrine taxa leads us to conclude that Markham (1992) was correct in his intent, if not execution, and we reinstate *Hypophryxus* as a valid genus herein.

Izuohshimaphryxus Saito, 2015

Diagnosis. **Female** body subovate, distorted approximately 40°; lateral sides of head produced into expanded lobes. Eyes absent. Antenna absent; antennula non-articulated. Barbula with 2 smooth lobes on each side. Pereomere 1 dorsally distinct on convex side. Oostegite 1 on concave side with minute posterior lobe, that on convex side with posterior lobe subequal in size to anterior lobe. Oostegites 2–4 present. Coxal plate and dorsolateral boss only on pereomere 1 of convex side. 7 pereopods on concave side, 2 pereopods on convex side; filiform coxal plates at base of pereopods on concave side, stout extensions on convex side. Pleon of 1 fused segment. Lateral plates absent; 4 uniramous pleopods on concave side, 3 on convex side; uropods absent. **Male** unknown.

Shelf, parasitising palaemonid shrimps. Temperate Northern Pacific. 1 species (Saito, 2015).

Loki Markham, 1972

Diagnosis. **Female** body linear, compact, not distorted or distorted approximately 40°; head rounded, anterolateral margins produced as anteriorly directed lobes. Eyes absent. Antennula and antenna articulated. Barbula with 1 smooth long lobe on each side. Pereomeres distinct or weakly distinct dorsally. Oostegite 1 on convex side unknown, that on concave side with subquadrate posterior lobe approximately as large as anterior lobe. Coxal plates and dorsolateral bosses absent. 7 pereopods on both sides. Pleon of 5 pleomeres; 3 or 4 pairs of uniramous smooth lateral plates, 3 or 4 pairs of uniramous smooth pleopods; uropods present. **Male** with all pereomeres subequal in width. Eyes present or absent. Antennula and antenna articulated. Pleon without lateral indication of segmentation; uropods absent.

Subtidal, parasitising alpheid and thorid shrimps. Tropical Atlantic, Western Indo-Pacific. 2 species (An et al., 2020; Markham, 1985).

Mediophrixus Markham, 1990

Diagnosis. **Female** body linear, compact, distorted approximately 80°; head rounded, anterolateral margins produced as anteriorly directed lobes. Single eye present. Antennula and antenna absent. Barbula with 1 smooth short lobe on each side. Pereomeres weakly distinct dorsally. Oostegite 1 on convex side with triangular expanded posterior lobe, larger than anterior lobe, that on concave side unknown. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 2 pereopods on convex side. Pleon of 4 pleomeres; pleotelson absent; 4 pairs of uniramous smooth lateral plates, and 4 pairs of uniramous smooth pleopods; uropods absent. **Male** with all pereomeres subequal in width. Eyes present. Antennula and antenna articulated. Pleon with lateral indication of segmentation; uropods absent.

Intertidal, parasitising alpheid shrimps. Central Indo-Pacific. 1 species (Markham, 1990).

Mesophryxus Bruce, 1973

Diagnosis. **Female** body linear, compact, distorted approximately 55°; head elongate, anterolateral margins produced as anterolaterally directed lobes. Eyes present. Antennula papilliform; antenna articulated. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. Oostegite 1 on convex side with ovate posterior lobe, larger than anterior lobe, that on concave side without posterior lobe. Coxal plates present at base of all fully developed pereopods; dorsolateral bosses absent. 7 pereopods on concave side, 2 pereopods on convex

side. Pleon of 1 fused segment; 3 pairs of uniramous smooth lateral plates; 3 pairs of uniramous smooth pleopods; uropods absent. **Male** with pereomeres narrower posteriorly. Eyes absent. Antennula non-articulated; antenna articulated. Pleon without lateral indication of segmentation; uropods absent.

Subtidal, parasitising palaemonid shrimps. Western Indo-Pacific. 1 species (Bruce, 1973a).

Metaphrixus Nierstrasz and Brender à Brandis, 1931

Diagnosis. **Female** body linear, elongate, distorted approximately 70–90°; head rounded, anterolateral margins not produced. Eyes present or absent. Antennula articulated; antenna articulated or non-articulated. Barbula with 1 smooth slender and 1 short blunt lobe on each side or 2 smooth slender lobes. Pereomeres distinct dorsally. Oostegite 1 on convex side with subquadrate posterior lobe, as large as anterior lobe, that on concave side with small finger-like posterior lobe. Coxal plates absent; dorsolateral bosses present on concave side or absent. 7 pereopods on concave side, 2 or 3 pereopods on convex side. Pleon of 5 pleomeres; 4 pairs of uniramous smooth lateral plates; 4 pairs of uniramous smooth pleopods; uropods absent. **Male** with middle pereomeres widest. Eyes present. Antennula and antenna articulated. Pleon without lateral indication of segmentation; uropods absent.

Subtidal-Shelf, parasitising hippolytid and palaemonid shrimps. Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific. 5 species (Ribeiro et al., 2024; Shimomura et al., 2006).

Micropodiphryxus Boyko, 2012

Diagnosis. **Female** body ovate, distorted approximately 10°; head ovate, anterolateral margins not produced. Eyes present or absent. Antennula and antenna unknown. Barbula unknown. Pereomeres distinct dorsally. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 4 pereopods on convex side. Pleon of 5 pleomeres; 4 pairs of biramous smooth lateral plates; 4 pairs of biramous smooth pleopods; pleotelson bifid; uropods absent. **Male** unknown.

Subtidal, parasitising crangonid shrimps. Western Indo-Pacific. 1 species (Boyko, 2012).

Miophrixus Barnard, 1955

Diagnosis. **Female** with 7 pereopods on concave side, 2 pereopods on convex side. Pleon of 3 pleomeres; 2 pairs of uniramous smooth lateral plates; 2 pairs of uniramous smooth pleopods; uropods present. [Other characters not known.] **Male** with eyes present. Uropods absent. [Other characters not known]

Subtidal, parasitising hippolytid shrimps. Western Indo-Pacific. 1 species (Barnard, 1955).

Neophryxus Bruce, 2007

Diagnosis. **Female** body linear, distorted approximately 70°; head rounded. Eyes absent. Antennula absent; antenna non-articulated. Barbula with 2 smooth long lobes on each side. Pereomeres distinct dorsally. Oostegite 1 on convex side with large ovate posterior lobe, larger than anterior lobe, that on concave side with elongate, rounded posterior lobe larger than anterior lobe. 4 oostegites on convex side, 5 on concave side. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 1 on convex side. Pleon of 5 pleomeres; lateral plates absent, 4 pairs of uniramous smooth pleopods; uropods present. **Male** with pereomeres subequal in width. Eyes absent. Antennula articulated; antenna of 1 segment. Pleon with lateral indication of segmentation, uropods absent.

Intertidal, parasitising palaemonid shrimps. Western Indo-Pacific. 1 species (Bruce, 1973b).

Orophryxus Bruce, 1972

Diagnosis. **Female** body linear, distorted approximately 90°; head fused to pereon, indistinct. Eyes present. Antennula as articulated flattened plate; antenna as large tubular segment with additional small distal segment. Barbula unknown. Pereomeres distinct dorsally, feebly distinct on concave side. 4 oostegites on convex side of body, 3 on concave side. Coxal plate and dorsolateral boss presence/absence unclear. 2 pereopods on concave side; 4 on convex side. Pleon a small non-articulated lamina; lateral plates, pleopods, and uropods absent. **Male** unknown.

Intertidal, parasitising palaemonid shrimps. Western Indo-Pacific. 1 species (Bruce, 1972b).

Pliophrixus Caroli, 1930

Diagnosis. **Female** with 7 pereopods on concave side, 3 on convex side. [Other characters not known.] **Male** unknown.

Subtidal, parasitising processid shrimps. Temperate Northern Atlantic. 1 species (Caroli, 1930).

Quadripediphryxus Saito, 2020

Diagnosis. **Female** body linear, distorted approximately 10°; head subquadrate. Eyes present. Antenna and antennula articulated. Barbula with 2 smooth short lobes on each side. Pereomeres 1–3 fused to head, 4–7 distinct dorsally and on concave side. Oostegite 1 on concave side with minute posterior lobe, that on convex side with posterior lobe subequal in size to anterior lobe. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 4 on convex side. Pleon of 4 pleomeres; pleotelson minute; 4 pairs of uniramous oval lamellar lateral plates and 4 pairs of biramous pleopods; minute dorsally positioned lobes (uropods?) on terminal pleomere present. **Male** with pereomeres subequal in width. Eyes present. Antenna and antennula articulated. Uropods absent.

Subtidal, Temperate Northern Pacific, parasitising alpheid shrimp. 1 species (Saito, 2020).

Sigyn An, Boyko and Li, 2015

Diagnosis. **Female** body linear, distorted approximately 90°; head rounded. Eyes absent. Single pair of articulated antennae present (antennulae absent). Barbula with 7 or 8 smooth short acute lobes on each side. Pereomeres distinct dorsally. Oostegite 1 on concave side with small triangular posterior lobe, that on convex side with elongate, distally acute posterior lobe subequal in size to anterior lobe. Coxal plates and dorsolateral bosses absent. 7 pereopods on both sides, crowded together on concave

side. Pleon of 5 pleomeres, terminal pleomere (pleotelson?) as sphere covered with tubercles; 4 pairs of uniramous lamellar smooth lateral plates and 4 pairs of uniramous smooth pleopods; uropods absent. **Male** with pereomeres subequal in width. Eyes present. Antenna and antennula articulated. Pleon without lateral indications of segmentation; uropods absent.

Intertidal, parasitising alpheid shrimps. Central Indo-Pacific. 1 species (An et al., 2015).

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Subfamily Keponinae Boyko, Moss, Williams and Shields, 2013

Figures 6.14, 6.15

Species in the genera of Keponinae are all branchial ectoparasites of brachyuran crabs, with the exception of one species of *Dactylokepon*, which parasitises slipper lobsters, species of *Coxalione*, *Hemicepon* and *Procepon*, which parasitise gebiids, and both species of *Castrione*, which parasitise axiids. Bodies of mature females are generally dorsoventrally inflated with slight to moderate distortion of the head relative to the body, often have middorsal projections on one or more of the posterior pereomeres, and usually have elongate uniramous lateral plates and pleopods with digitate margins. Females of species in some genera (e.g. *Carcinione*, *Coxalione*) deviate considerably from the typical members of the subfamily. Males usually have a pleon with distinct segmentation, often have midventral tubercles on the pereon and/or pleon, and if pleopods are present they are typically sessile and uropods are absent. The sole species of *Hemicepon* was described based on a mature male and a male in the process of transitioning to a female; no additional specimens have been reported and placement in Keponinae is tentative. The key is modified from that of An et al. (2020). The subfamily Keponinae includes *Cardiocepon* Nobili, 1906, the only semiterrestrial epicaridean, parasitic on gecarcinid crabs.

Diagnosis. **Female** body ovate and/or elongate, body weakly to not distorted; head distinct from pereon, bilobed or not bilobed; frontal lamina present or absent. Eyes present or absent. Antennula and antenna articulated. Maxilliped with setose or non-setose articulated or non-articulated palp or without palp. Barbula with 2–5 short smooth or with crenulate/digitate bumps or lobes on each side. Pereomeres distinct dorsally, with middorsal projections on pereomeres 5, 6 and/or 7 or without middorsal projections. 5 pairs of oostegites. Oostegite 1 with triangular, subquadrate or ovate posterior lobe, larger, smaller or subequal to anterior lobe; internal ridge smooth or digitate/tuberculate. Marsupium closed. Coxal plates, dorsolateral bosses and tergal projections present or absent. Pleon of 6 pleomeres, narrower or not narrower than pereon; middorsal projection on pereomere 1 present or absent. 5 pleomeres with elongated uniramous smooth or tuberculate lateral plates with digitate, crenulate or smooth margins or lateral plates absent; 5 pairs of uniramous or biramous smooth or tuberculate pleopods with smooth or digitate margins; uropods uniramous or biramous, smooth or tuberculate, with smooth to digitate margins. **Male** approximately 2–7 times as long as wide, pereomeres narrower or not narrower posteriorly. Head narrower than pereon. Eyes present or absent. Antennula and antenna articulated. Pereopods subequal or anterior pairs 1–4 larger. Midventral tubercles present or absent. Pleon segmented or fused; lateral plates present or absent; pleopods present or absent; posterolateral corners of pleomere 6 rounded or produced into lobes; uropods present or absent.

Key to genera of the subfamily Keponinae

The key is based on female and male characters. *Hemicepon* is excluded (see above).

1.	Pereomere 2 of female reduced (fig. 6.14a, b)	*Onychocepon*
–	All pereomeres of female normally developed	2
2.	1 pair of lateral plates on all pleomeres of female	3
–	2 pairs of lateral plates on all pleomeres of female (fig. 6.14c)	*Cardiocepon*
3.	Female with middorsal projections on some pereomeres	4
–	Female without middorsal projections on any pereomeres	12
4.	Pleopods of female with well-developed endopods	5
–	Pleopods of female with reduced or absent endopods	8
5.	Some pleomeres of male fused (fig. 6.14d)	*Scyracepon*
–	All pleomeres of male distinct	6
6.	Female with middorsal projection on pleomere 1 (fig. 6.14e, f)	*Megacepon*
–	Female without middorsal projection on any pleomere	7
7.	Male without pleopods (fig. 6.14g, h)	*Ergyne*
–	Male with pleopods (fig. 6.14i)	*Allokepon*
8.	Pleopods of female without endopods (fig. 6.14j, k)	*Mesocepon*
–	Pleopods of female with reduced endopods	9

9. Middorsal projections on more than pereomeres 6 and 7 of female 10
– Middorsal projections only on pereomeres 6 and 7 of female 11
10. Lateral plates and pleopods of female with digitate margins (fig. 6.14l) ..... *Cancricepon*
– Lateral plates and pleopods of female with smooth margins (fig. 6.14m) ..... *Paracepon*
11. Pereomere 6 of female with more than 1 projection (fig. 6.14n) ..... *Tylokepon*
– Pereomere 6 of female with 1 projection (fig. 6.14o) ..... *Grapsicepon*
12. Pleopods of female with well-developed endopods, at least on anterior pleopods 13
– Pleopods of female all with very reduced endopods 21
13. Lateral plates and pleopods of female with smooth margins 14
– Lateral plates and pleopods of female with digitate margins 16
14. Male with lateral plates (fig. 6.14p, q) ..... *Procepon*
– Male without lateral plates 15
15. Female with wide lamellar lateral plates, male with slender uropods (fig. 6.14r, s) ..... *Coxalione*
– Female with narrow lateral plates, male with stout uropods (fig. 6.14t) ..... *Hypocepon*
16. Head of female with bilobate anterior margin 17
– Head of female with convex anterior margin 18
17. Surfaces of lateral plates and pleopods of female covered with tubercles, margins sparsely digitate (fig. 6.14u) ..... *Anacepon*
– Surfaces of lateral plates and pleopods of female medially smooth, margins densely digitate 20
18. Coxal plates smooth (fig. 6.14v) ..... *Dactylokepon*
– Coxal plates covered with tubercles 19
19. Coxal plates swollen (fig. 6.14w) ..... *Kepon*
– Coxal plates not swollen, with crenulate surfaces and small thin projections (fig. 6.14x) ..... *Rhizophoracepon*
20. Male without pleopods (fig. 6.15a, b) ..... *Metacepon*
– Male with pleopods (fig. 6.15c, d) ..... *Heterocepon*
21. Female with 5 pairs of biramous pleopods and uropods (fig. 6.15e, f) ..... *Castrione*
– Female with 5 pairs of uniramous pleopods and uropods 22
22. Lateral plates of female with smooth margins 23
– Lateral plates of female with digitate margins 24
23. Pleopods of female with exopods slightly shorter than corresponding lateral plates (fig. 6.15g) ..... *Metathelges*
– Pleopods of female with exopods much shorter than corresponding lateral plates (fig. 6.15h) ..... *Atypocepon*
24. Male with all pleomeres fused (fig. 6.15i, j) ..... *Hypercepon*
– Male with some pleomeres separated 25
25. Female with reduced frontal lamina (fig. 6.15k) ..... *Apocepon*
– Female with well-developed frontal lamina 26
26. Female with tuberculate frontal lamina (fig. 6.15l, m) ..... *Onkokepon*
– Female with smooth frontal lamina 27
27. Male with long uropods (fig. 6.15n–p) ..... *Leidya*
– Male with short uropods (fig. 6.15q, r) ..... *Trapezicepon*

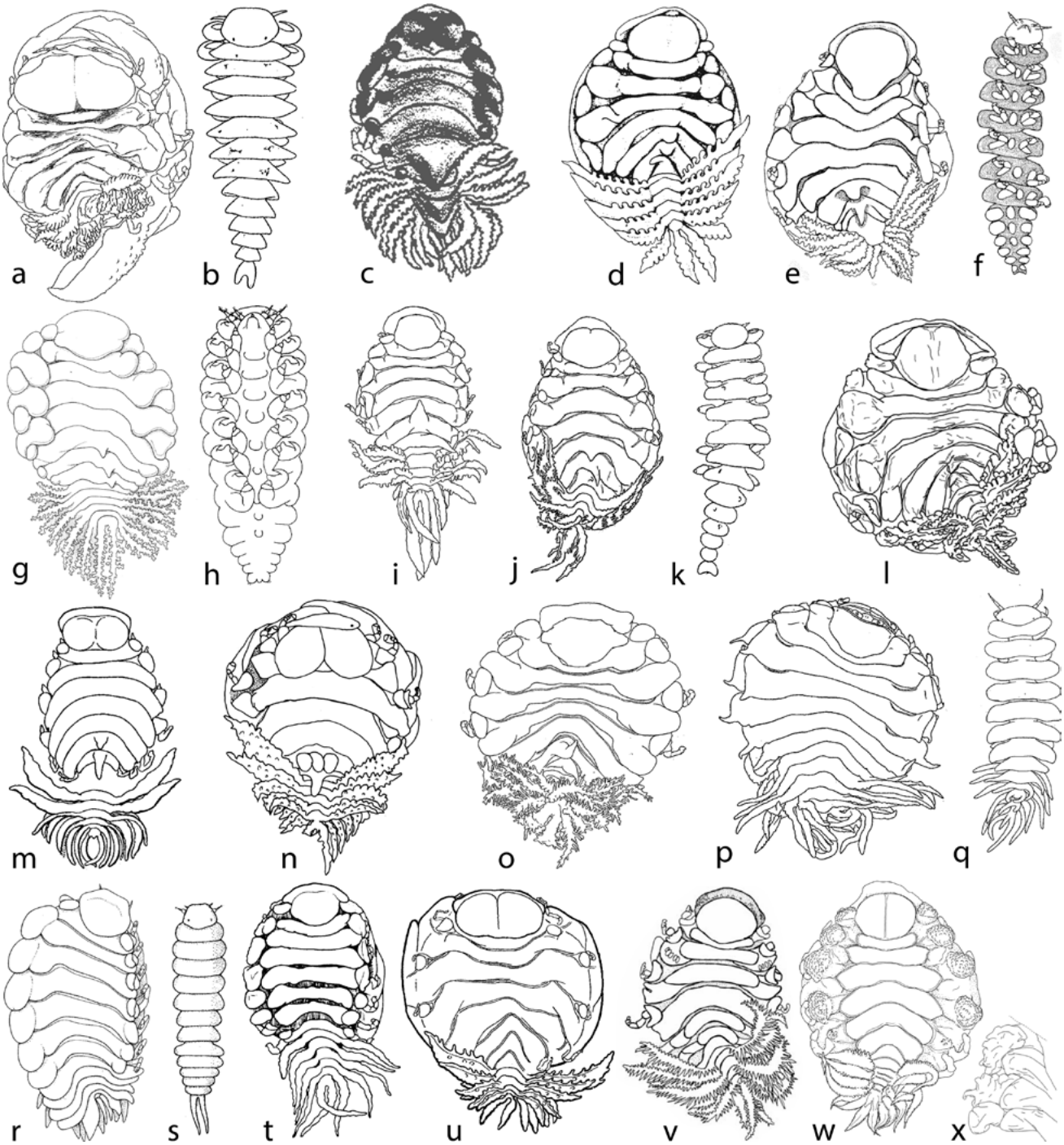


Figure 6.14. Keponinae. *Onychocepon resupinum* Shiino, 1936: a, female dorsal view; b, male dorsal view. *Cardiocepon pteroides* Nobili, 1906: c, female dorsal view. *Scyracepon tuberculosa* Tattersall, 1905: d, female dorsal view. *Megacepon sheni* An, Boyko and Li, 2012: e, female dorsal view; f, male ventral view. *Ergyne cervicornis* Risso, 1816: g, female dorsal view; h, male ventral view. *Allokepon tiariniae* (Shiino, 1937): i, female dorsal view. *Mesocepon tosizimensis* Shiino, 1951: j, female dorsal view; k, male dorsal view. *Cancricepon castroi* An, Wang, Boyko and Williams, 2019: l, female dorsal view. *Paracepon stebbingi* Nierstrasz and Brender à Brandis, 1931: m, female dorsal view. *Tylokepon bonnieri* Stebbing, 1904: n, female dorsal view. *Grapsicepon rotundum* Shiino, 1936: o, female dorsal view. *Procepon insolitum* Shiino, 1937: p, female dorsal view; q, male dorsal view. *Coxalione inaequalis* Bourdon, 1977: r, female dorsal view; s, male dorsal view. *Hypocepon enoeensis* Nierstrasz and Brender à Brandis, 1930: t, female dorsal view. *Anacepon sibogae* Nierstrasz and Brender à Brandis, 1931: u, female dorsal view. *Dactylokepon richardsonae* Stebbing, 1910: v, female dorsal view. *Kepon grapsi* (Nobili, 1905): w, female dorsal view. *Rhizophoracepon magnagibbus* Williams, Boyko and Tri, 2023: x, female coxal plates and tergal projections on pereomeres 5–7.

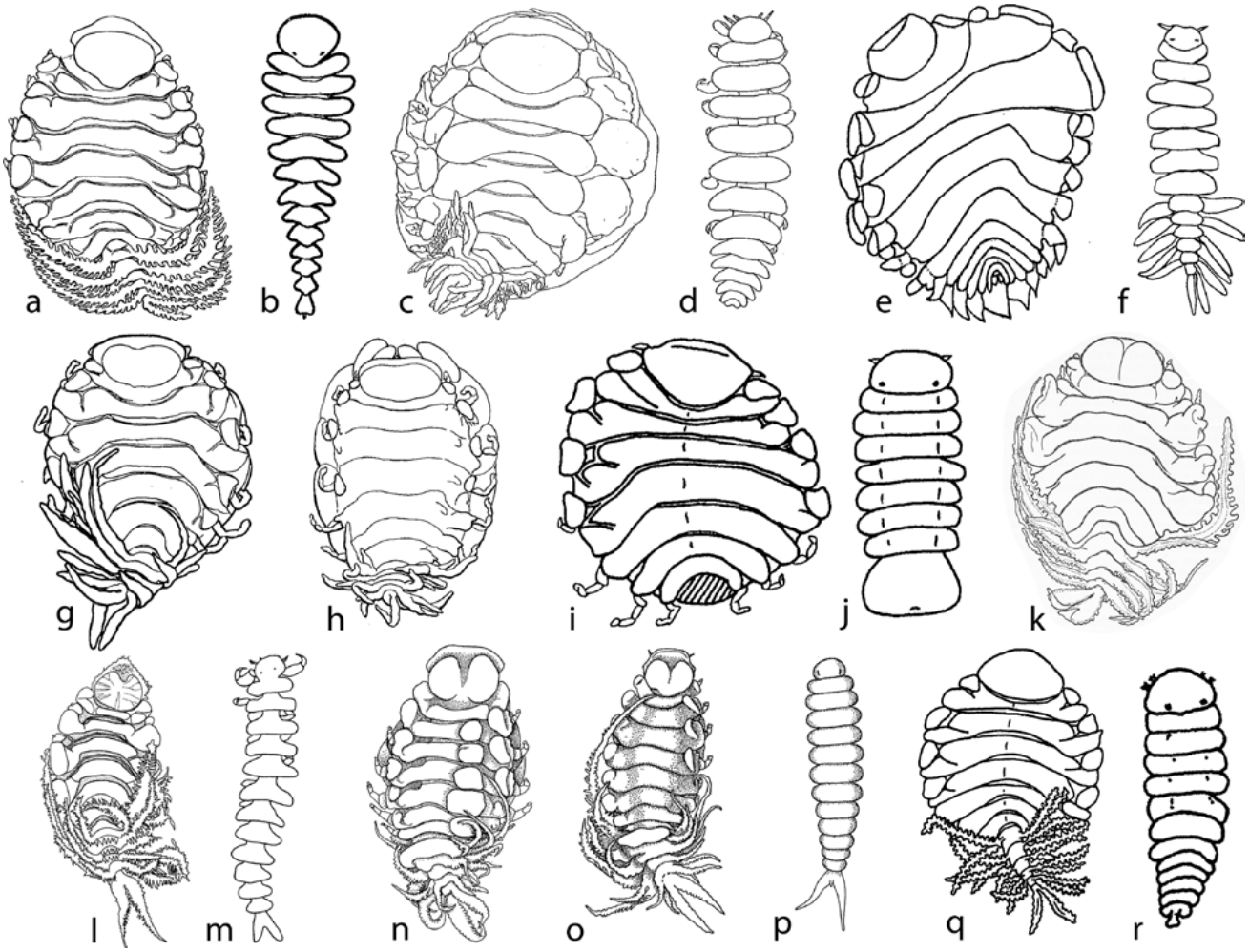


Figure 6.15. Keponinae. *Metacepon leidyi* Nierstrasz and Brender à Brandis, 1931: a, female dorsal view; b, male dorsal view. *Heterocepon marginatum* Shiino, 1936: c, female dorsal view; d, male dorsal view. *Castrione longicaudata* Brasil Lima, 1980: e, female dorsal view; f, male dorsal view. *Metathelges japonicus* (Nierstrasz and Brender à Brandis, 1931): g, female dorsal view. *Atypocepon intermedium* Nierstrasz and Brender à Brandis, 1931: h, female dorsal view. *Hypercepon guamensis* Danforth, 1972: i, female dorsal view, hatched area shows where pleopods are missing; j, male dorsal view. *Apocepon pulcher* Nierstrasz and Brender à Brandis, 1930: k, female dorsal view. *Onkokepon articulatus* An, Yu and Li, 2006: l, female dorsal view; m, male dorsal view. *Leidya distorta* (Leidy, 1855): n, female dorsal view; o, immature female dorsal view; p, male dorsal view. *Trapezicepon domeciae* Danforth, 1972: q, female dorsal view; r, male dorsal view.

Allokepon Markham, 1982

Diagnosis. **Female** ovate, body weakly to not distorted; head bilobed or not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 short smooth lobes on each side. Middorsal projections on pereomeres 6 and 7. Oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge digitate. Coxal plates present or absent; dorsolateral bosses and tergal projections absent. Pleon narrower than pereon. Lateral plates smooth, with digitation on margins; pleopods smooth, biramous, with digitate margins; uropods smooth, uniramous, with digitate margins. **Male** approximately 3–4 times as long as wide, pereomeres narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal–shelf, parasitising epialtid, inachoidid and portunid crabs. Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific. 5 species (Duan et al., 2008; Markham, 1982).

Anacepon Nierstrasz and Brender à Brandis, 1931

Diagnosis. **Female** elongate, body not distorted; head bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated or non-articulated palp. Barbula with 2 short lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with triangular posterior lobe, larger than anterior

lobe; internal ridge digitate. Dorsolateral bosses, coxal plates and tergal projections present. Pleon narrower than pereon. Lateral plates smooth, with digitate margins, first pair extremely long; pleopods smooth, biramous, exopods elongate with digitate margins, endopods rudimentary; uropods smooth, uniramous, with crenulated margins. **Male** approximately 3–4 times as long as wide, pereomeres not narrower posteriorly. Eyes absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 segments; lateral plates absent; 4 or 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 produced into lobes; uropods absent.

Shelf, parasitising parthenopid crabs. Central Indo-Pacific. 1 species (Nierstrasz and Brender à Brandis, 1931).

Apocepon Nierstrasz and Brender à Brandis, 1930

Diagnosis. **Female** elongate, body not distorted; head distinct from pereon, bilobed; frontal lamina present. Eyes absent. Antennula and antenna articulated. Maxilliped with setose articulated or non-articulated palp. Barbula with 2 short lobes on each side. Pereomeres distinct dorsally, without middorsal projections. 5 pairs of oostegites. Oostegite 1 with triangular posterior lobe, larger than anterior lobe; internal ridge digitate. Marsupium closed. Dorsolateral bosses, coxal plates and tergal projections present. Pleon narrower than pereon, 5 pleomeres with strongly elongated lateral plates smooth, with digitation on margins, first pair extremely long; 5 pairs of biramous smooth pleopods, exopods elongate with digitate margins, endopods rudimentary; uropods uniramous, smooth, broad, with crenulated margins. **Male** approximately 3–4 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes absent. Antennula and antenna articulated. Pereopods subequal. Midventral tubercles absent. Pleon segmented; pleopods as small lobes on pleomeres 1–4 or 1–5; posteroventral corners of pleomere 6 produced into lobes; uropods absent.

Shelf, parasitising leucosiid crabs. Central Indo-Pacific. 3 species (An et al., 2006b).

Atypocepon Nierstrasz and Brender à Brandis, 1931

Diagnosis. **Female** ovate, body not distorted; head not bilobed; frontal lamina present. Eyes absent. Antennula and antenna not described. Maxilliped not described. Barbula not described. Pereomeres without middorsal projections. Oostegite 1 not described. Dorsolateral bosses present; tergal projections and coxal plates absent. Pleon narrower than pereon. Lateral plates smooth, with smooth margins; pleopods smooth, biramous (exopod large, endopod rudimentary) with smooth margins; uropods smooth, uniramous, with smooth margins. **Male** unknown.

Slope, host unknown. Central Indo-Pacific. 1 species (Nierstrasz and Brender à Brandis, 1931).

Cancricepon Giard and Bonnier, 1887

Diagnosis. **Female** ovate, body weakly distorted; head bilobed or not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 short smooth lobes on each side. Large middorsal projections present on pereomeres 5–7. Oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge digitate. Dorsolateral bosses present, tergal projections present or absent, coxal plates absent. Pleon narrower than pereon. Lateral plates digitate, with digitate margins; pleopods digitate, biramous; uropods digitate, uniramous. **Male** approximately 2–3 times as long as wide, pereomeres not narrower posteriorly. Eyes present or absent. Anterior 3 or 4 pairs of pereopods larger than posterior pairs. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 slightly produced into lobes or rounded; uropods absent.

Intertidal–shelf, parasitising dacryopilumnid, domeciid, eriphiid, panopeid, pilumnid, pseudothombiliid, scalopidid, trapeziid and xanthid crabs. Temperate Northern Atlantic, Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific. 11 species (An et al., 2019).

Cardiocepon Nobili, 1906

Diagnosis. **Female** elongate, body not distorted; head bilobed; frontal lamina present. Eyes absent. Maxilliped with non-setose, non-articulated palp. Barbula not described. Middorsal projections present on pereomeres 6 and 7. Oostegite 1 with ovate posterior lobe, much larger than anterior lobe; internal ridge with few small lobes. Coxal plates present; tergal projections and dorsolateral bosses absent. Pleon narrower than pereon. Lateral plates tuberculate, with digitate margins. Pleopods tuberculate, biramous, with digitate margins; uropods tuberculate, uniramous, with digitate margins. **Male** unknown.

Semiterrestrial, parasitising gecarcinid crabs. Central Indo-Pacific. 1 species (Boyko, 2003).

Castrione Brasil Lima, 1980

Diagnosis. **Female** ovate, body weakly to not distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose, non-articulated palp. Barbula with 2 smooth short lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with ovate posterior lobe, larger than anterior lobe; internal ridge with few small lobes. Coxal plates and tergal projections present; dorsolateral bosses absent. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods smooth, uniramous, with digitate margins; uropods smooth, uniramous, with digitate margins. **Male** approximately 2–3 times as long as wide, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 segments; lateral plates absent; 5 pairs of elongate uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods uniramous.

Subtidal–shelf, parasitising micheleid shrimps. Tropical Atlantic, Central Indo-Pacific. 2 species (Markham, 1995).

Coxalione Bourdon, 1977

Diagnosis. **Female** elongate, body weakly distorted; head not bilobed; frontal lamina indistinct. Eyes absent. Maxilliped without palp. Barbula with 2 short lobes on each side, outer

lobe smooth, inner lobe crenulate. Pereomeres without middorsal projections. Oostegite 1 with ovate posterior lobe with distal triangular projection, smaller than anterior lobe; internal ridge tuberculate. Coxal plates and dorsolateral bosses present; tergal projections absent. Pleon not narrower than pereon. Lateral plates smooth, with smooth margins; pleopods smooth, biramous, with smooth margins; uropods smooth, uniramous, with smooth margins. **Male** approximately 3–4 times as long as wide, pereomeres narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleonite 6 rounded; uropods uniramous, elongate.

Subtidal, parasitising laomediid shrimps. Central Indo-Pacific. 1 species (Bourdon, 1977).

Dactylokepon Stebbing, 1910

Diagnosis. **Female** elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with non-setose non-articulated palp. Barbula with 2 digitate short lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with ovate posterior lobe bearing distal triangular extension, subequal to anterior lobe; internal ridge digitate. Dorsolateral bosses and tergal projections present, coxal plates absent. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods digitate, biramous; uropods smooth, uniramous with digitate margins. **Male** approximately 3–4 times as long as wide, pereomeres narrower posteriorly. Eyes present. Pereopods 1 and 2 larger than others. Midventral tubercles absent. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 produced into lobes or rounded; uropods absent.

Shelf, parasitising leucosiid, pilumnid, pinnotherid, portunid, tetraliid, trapeziid and xanthid crabs, and scyllarid lobsters. Temperate Northern Atlantic, Tropical Atlantic, Western and Central Indo-Pacific. 11 species (An et al., 2007).

Ergyne Risso, 1816

Diagnosis. **Female** elongate, body not distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with non-setose non-articulated palp. Barbula with 2 smooth bumps or short lobes on each side. Middorsal projections present on pereomeres 5–7. Oostegite 1 with ovate posterior lobe bearing distal triangular extension, smaller than anterior lobe; internal ridge with few low bumps, not digitate. Dorsolateral bosses and coxal plates present, tergal projections absent. Pleon not narrower than pereon. Lateral plates smooth, with digitate margins; pleopods digitate, biramous; uropods smooth, uniramous, with digitate margins. **Male** approximately 2–3 times as long as wide, pereomeres not narrower posteriorly. Eyes absent. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; pleopods absent; posterolateral corners of pleomere 6 produced into short lobes; uropods absent.

Subtidal, parasitising portunid crabs. Temperate Northern Atlantic. 1 species (Bourdon, 1968).

Grapsicepon Giard and Bonnier, 1887

Diagnosis. **Female** ovate, body not or weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Antennula and antenna not described. Maxilliped with setose articulated palp. Barbula with 2 pairs of smooth lobes on each side. Middorsal projections present on pereomeres 6 and 7. Oostegite 1 with ovate posterior lobe bearing triangular distal process, smaller than anterior lobe; internal ridge digitate. Dorsolateral bosses and coxal plates present; tergal projections absent. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods digitate, biramous; uropods smooth, uniramous, with digitate margins. **Male** approximately 3–4 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal, parasitising grapsid, majid, mithracid, tetraliid, and xanthid crabs. Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific. 6 species (Markham, 1988).

Hemicepon Lemos de Castro and Brasil-Lima, 1980

Diagnosis. **Transitional male to female** elongate, body not distorted; head not bilobed; frontal lamina absent. Eyes present. Maxilliped with distally bifurcated articulated palp. Barbula not described. Pereomeres without middorsal projections. No oostegites (not mature). Dorsolateral bosses, tergal projections and coxal plates absent. Pleon not narrower than pereon. Lateral plates smooth, with smooth margins; pleopods smooth, biramous, with smooth margins; uropods smooth, uniramous, with smooth margins. **Male** approximately 6–7 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 weakly produced; uropods absent.

Intertidal, parasitising upogebiid shrimps. Tropical Atlantic. 1 species (Lemos de Castro and Brasil-Lima, 1980).

Heterocepon Shiino, 1936

Diagnosis. **Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 pairs of smooth lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge digitate. Dorsolateral bosses and tergal projections absent; coxal plates present. Pleon narrower than pereon. Lateral plates smooth, with crenulated margins; pleopods smooth, biramous, with digitate margins; uropods smooth, uniramous, with weakly crenulate margins. **Male** approximately 3–4 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal, parasitising pinnotherid crabs. Temperate Northern Pacific, Central Indo-Pacific. 2 species (Boyko and Williams, 2024; Janssen and Brandt, 1994; Shiino, 1936a).

Hypercepon Danforth, 1972

Diagnosis. **Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Antennula and antenna present. Maxilliped not described. Barbula not described. Pereomeres without middorsal projections. Oostegite 1 not described. Dorsolateral bosses and tergal projections present; coxal plates absent. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods smooth, uniramous, with digitate margins; uropods smooth, uniramous, with smooth margins. **Male** approximately 2–3 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods not described in detail. Midventral tubercles absent. Pleon fused; lateral plates absent; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal, parasitising trapeziid crabs. Eastern Indo-Pacific. 1 species (Danforth, 1972).

Hypocepon Nierstrasz and Brender à Brandis, 1930

Diagnosis. **Female** ovate, body not distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated palp. Barbula with 2 pairs of smooth lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with ovate posterior lobe bearing small triangular projection, subequal in size to anterior lobe; internal ridge digitate. Coxal plates present; tergal projections and dorsolateral bosses absent. Pleon narrower than pereon. Lateral plates smooth, with slightly crenulate margins; pleopods smooth, biramous, finger-like, with smooth margins; uropods smooth, biramous, with crenulate margins. **Male** approximately 3–4 times as long as wide, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal, parasitising pinnotherid crabs. Central Indo-Pacific. 1 species (Boyko and Williams, 2024; Markham, 1992).

Kepon Duvernoy, 1840

Diagnosis. **Female** ovate, body weakly distorted; head bilobed; frontal lamina present. Eyes absent. Maxilliped with non-setose non-articulated palp. Barbula with 2 pairs of digitate lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with triangular posterior lobe, subequal in size or larger than anterior lobe; internal ridge digitate. Coxal plates present, covered in tubercles; tergal projections and dorsolateral bosses absent. Pleon narrower than pereon. Lateral plates tuberculate, with digitate margins; pleopods tuberculate, biramous, with digitate margins; uropods tuberculate, uniramous, with digitate margins. **Male** approximately 3–4 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 strongly produced; uropods absent.

Intertidal–shelf, parasitizing grapsid, majid and varunid crabs. Western and Central Indo-Pacific. 4 species (Uyeno and Boyko, 2020).

Leidya Cornalia and Panceri, 1861

Diagnosis. **Female** elongate, body weakly distorted; head bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 pairs of smooth elongate lobes on each side. Middorsal projections present or absent. Oostegite 1 with elongate ovate posterior lobe, larger than anterior lobe; internal ridge digitate. Coxal plates present; tergal projections and dorsolateral bosses absent. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods smooth, biramous, with digitate margins; uropods smooth, uniramous, with digitate margins. **Male** approximately 4–5 times as long as wide, pereomeres narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods long, filamentous, uniramous.

Intertidal, parasitising grapsid and ocypodid crabs. Temperate Northern and Tropical Atlantic, Temperate Northern Pacific. 4 species (Markham, 2002).

Megacepon George, 1947

Diagnosis. **Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with non-setose, non-articulated palp. Barbula with 2 smooth long lobes on each side. Middorsal projection on pereomere 6. Oostegite 1 with elongate posterior lobe, much larger than anterior lobe; internal ridge digitate. Dorsolateral bosses and tergal projections present; coxal plates absent. Pleon narrower than pereon; middorsal projection on pleomere 1. Lateral plates smooth, with digitate margins; pleopods digitate, biramous, with digitate margins; uropods smooth, uniramous, with digitate margins. **Male** approximately 4–5 times as long as wide, pereomeres not narrower posteriorly. Eyes absent. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 weakly produced; uropods as sessile, ventrally displaced discs or absent.

Intertidal–subtidal, parasitising sesarmid and varunid crabs. Western and Central Indo-Pacific, Temperate Northern Pacific. 6 species (An et al., 2012).

Mesocepon Shiino, 1951

Diagnosis. **Female** elongate, body weakly distorted; head bilobed; frontal lamina present. Eyes absent. Maxilliped with setose, non-articulated palp. Barbula not described. Middorsal projections on pereomeres 5–7. Oostegite 1 with subquadrate posterior lobe bearing distal rounded lobe, subequal to anterior lobe; internal ridge digitate. Dorsolateral bosses and tergal projections present; coxal plates absent. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods smooth, uniramous, with digitate margins; uropods smooth, uniramous, with digitate margins. **Male** approximately 4 times as long as wide, pereomeres not narrower posteriorly. Eyes absent. Pereopod 1 larger than others. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; pleopods absent; posterolateral corners of pleomere 6 weakly produced; uropods absent.

Subtidal, parasitising leucosiid crabs. Temperate Northern Pacific. 1 species (Shiino, 1951).

Metacepon Nierstrasz and Brender à Brandis, 1931

Diagnosis. **Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped with non-setose, non-articulated palp. Barbula with 2 smooth short lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with triangular posterior lobe, subequal to or smaller than anterior lobe; internal ridge slightly tuberculate. Dorsolateral bosses and coxal plates present; tergal projections absent. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods smooth, uniramous, with digitate margins; uropods smooth, uniramous, with digitate margins. **Male** approximately 3 times as long as wide, pereomeres narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile pleopods; posterolateral corners of pleomere 6 weakly to moderately produced; uropods absent.

Subtidal–shelf, parasitising matutid and pilumnid crabs. Central Indo-Pacific. 2 species (Bourdon and Stock, 1979; Markham, 1992).

Metathelges Nierstrasz & Brender à Brandis, 1923

Diagnosis. **Female** ovate/elongate, body not distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped with setose non-articulated palp. Barbula with 2 smooth bumps or short lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with ovate posterior lobe bearing distal triangular extension, smaller than anterior lobe; internal ridge smooth. Dorsolateral bosses, coxal plates and tergal projections present. Pleon narrower or not narrower than pereon. Lateral plates smooth, with smooth margins; pleopods smooth, biramous, with smooth margins; uropods smooth, uniramous, with smooth margins. **Male** approximately 3–4 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods 1 and 2 larger than others. Midventral tubercles absent. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 produced into lobes; uropods absent.

Shelf–slope, parasitising cyclodorippid crabs. Central Indo-Pacific, Temperate Northern Pacific. 4 species (Boyko, 2024, 2025; Boyko and Williams, 2021).

Onkokepon An, Yu and Li, 2006

Diagnosis. **Female** elongate, body not distorted; head bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 pairs of digitate lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with subquadrate posterior lobe bearing triangular projection, subequal to anterior lobe; internal ridge digitate. Coxal plates absent; tergal projections and dorsolateral bosses present. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods smooth, biramous, with digitate margins; uropods smooth, uniramous, with digitate margins. **Male** approximately 4–5 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods 1 and 2 larger than posterior pairs. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 produced into lobes; uropods absent.

Shelf, parasitising leucosiid crabs. Central Indo-Pacific. 2 species (An et al., 2006a).

Onychocepon Pérez, 1921

Diagnosis. **Female** ovate, body not distorted to strongly distorted; head bilobed; frontal lamina present. Eyes absent. Maxilliped without palp. Barbula with 2 digitate short lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with subquadrate posterior lobe, subequal to anterior lobe; internal ridge with few small lobes. Coxal plates present; tergal projections and dorsolateral bosses absent. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods smooth, biramous, with digitate margins; uropods smooth, uniramous, with digitate margins. **Male** approximately 2–3 times as long as wide, pereomeres narrower posteriorly. Eyes present. Pereopods 1 and 2 larger than posterior pairs. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 produced into short lobes; uropods absent.

Subtidal, parasitising pinnotherid crabs. Central Indo-Pacific, Temperate Northern Pacific. 3 species (Shiino, 1936b).

Paracepon Nierstrasz and Brender à Brandis, 1931

Diagnosis. **Female** elongate, body not distorted; head bilobed; frontal lamina present. Eyes absent. Antennula and antenna not described. Maxilliped not described. Barbula not described. Middorsal projections on pereomeres 6 and 7. Oostegite 1 not described. Coxal plates and tergal projections absent; dorsolateral bosses present. Pleon narrower than pereon. Lateral plates tuberculate, with undulating (not digitate) margins; pleopods smooth, biramous, with undulating (not digitate) margins; uropods smooth, uniramous, with undulating (not digitate) margins. **Male** elongate, approximately 3–4 times as long as wide, pereomeres not narrower posteriorly. Antennula and antenna not described. Eyes absent. Pereopods not described. Midventral tubercles not described. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 produced into short lobes; uropods absent.

Slope, parasitising inachid crabs. Western and Central Indo-Pacific. 2 species (Nierstrasz and Brender à Brandis, 1931; Pillai, 1954).

Procepon Shiino, 1937

Diagnosis. **Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes present. Maxilliped without palp or with setose non-articulating palp. Barbula with 2–5 crenulate short lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with ovate posterior lobe bearing triangular lobe, smaller or larger than anterior lobe; internal ridge with few tubercles or highly digitate. Dorsolateral bosses

absent; coxal plates and tergal projections present. Pleon not narrower than pereon. Lateral plates smooth, with smooth margins; pleopods smooth, biramous, with smooth margins; uropods smooth, uniramous, with smooth margins. **Male** approximately 2–3 times as long as wide, pereomeres narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments; lateral plates present; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods uniramous.

Subtidal, parasitising upogebiid shrimps. Western and Central Indo-Pacific, Temperate Northern Pacific. 3 species (An et al., 2009).

Rhizophoracepon Williams, Boyko and Tri, 2023

Diagnosis. **Female.** Head subovate, frontal lamina thin, extending to lateral margin of head. Eyes absent. Barbula with 2 slender subequal falcate pointed lateral projections on each side, middle region smooth. Maxilliped with large non-setose palp. Coxal plates on pereomeres 1–7 rounded with crenulate surface and small thin projections; dorsolateral bosses and tergal projections absent. Pereomeres without middorsal projections. Oostegite 1 with subcircular anterior article, subequal in size to posterior article, internal ridge digitate, posterior article rounded with distolateral triangular projection. Pereopods subequal in structure, posterior pairs slightly longer than anterior. Pleomeres 1–5 each bearing a pair of biramous digitate pleopods and uniramous digitate lateral plates, surfaces crenulate. Endopods, exopods, and lateral plates subequal in size. Uropods uniramous, surface smooth, margins slightly crenulate. **Male.** Pereomeres not narrower posteriorly. Head ovate, distinctly separated from pereomere 1. Eyes present. Pleon without midventral tubercles. Pereopods subequal in size and structure except anterior three pairs with longer dactyli. Pleomeres 1–5 each with low, rounded pleopods bearing nipple-like extension, pleomeres 1–4 with midventral tubercles; pleomere 6 posterolaterally extended into 2 flat, broad, smooth rami separated by large triangular median indentation; uropods absent.

Intertidal, parasitising pinnotherid crabs. Central Indo-Pacific. 1 species (Williams et al., 2023).

Scyracepon Tattersall, 1905

Diagnosis. **Female** ovate, body weakly to moderately distorted; head bilobed or not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 or 3 pairs of smooth lobes on each side. Pereomeres with or without middorsal projections. Oostegite 1 with triangular or subrectangular posterior lobe, subequal to anterior lobe; internal ridge digitate. Coxal plates absent; tergal projections and dorsolateral bosses present. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods digitate, biramous; uropods smooth, uniramous, with digitate margins. **Male** approximately 2–3 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments, distinct ventrally but fused dorsally; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Intertidal–slope, parasitising corystid, epialtid, eriphiid, geryonid, goneplacid, macrophthalmid, majid, portunid and xanthid crabs. Temperate Northern Atlantic, Temperate Southern Africa, Indo West-Pacific, Temperate Northern Pacific. 11 species (An et al., 2020).

Trapezicepon Bonnier, 1900

Diagnosis. **Female** ovate, body weakly to moderately distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 pairs of smooth lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge digitate. Coxal plates absent; tergal projections and dorsolateral bosses present. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods smooth, biramous, with digitate margins; uropods smooth, uniramous, with digitate margins. **Male** approximately 3–4 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal, parasitising domeciid and trapeziid crabs. Western and Eastern Indo-Pacific. 2 species (An et al., 2019).

Tylokepon Stebbing, 1904

Diagnosis. **Female** ovate, body weakly distorted; head bilobed; frontal lamina present. Eyes absent. Maxilliped with non-setose non-articulated palp. Barbula with 2 or 3 pairs of smooth lobes on each side. Pereomeres 6 and 7 with middorsal projections. Oostegite 1 with ovate or triangular posterior lobe, subequal to anterior lobe; internal ridge smooth. Coxal plates and tergal projections absent; dorsolateral bosses present. Pleon narrower than pereon. Lateral plates tuberculate or smooth, with smooth margins; pleopods smooth, biramous, with smooth to slightly undulating margins; uropods smooth, uniramous, with smooth margins. **Male** approximately 4 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 slightly produced; uropods ventrally displaced, uniramous.

Subtidal–shelf, parasitising epialtid, majid and parthenopid crabs. Central Indo-Pacific, Temperate Northern Pacific. 5 species (An et al., 2018).

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Subfamily Orbioninae Codreanu, 1967

Figure 6.16

Genera in Orbioninae can be distinguished from those of other bopyrid subfamilies in that females have little to no distortion of the head and pleon relative to the pereon but the coxal plates and often the dorsolateral bosses are much larger on one side of the body; the frontal lamina is also well developed. Species in Orbioninae are the only known bopyrid ectoparasites in the branchial chambers of penaeoid shrimp; some species are also found on aristeid, solenocerid, and sicyoniid shrimp hosts. An et al. (2022) questioned the monophyly of *Orbione*. The key is modified from An et al. (2022). Males of representative genera are figured.

Diagnosis. **Female** body ovate; all pereomeres distinct or with median regions of some fused; head ovate, not bilobed; frontal lamina large. Eyes present or absent. Antennula and antenna articulated. Barbula with 2 digitate lobes on each side. Maxilliped with articulated or non-articulated palp. Marsupium open or closed. Oostegite 1 internal ridge digitate or smooth. Coxal plates present, larger on one side of pereon. Dorsolateral bosses present. 5 pairs of subequal pereopods or posterior pereopods larger or smaller than anterior pairs. Pleon of 5 or 6 segments, not distorted or distorted up to 30°. 5 pairs of tuberculate biramous pleopods; 5 pairs of smooth or tuberculate lateral plates or lateral plates absent; uropods uniramous or biramous, smooth or tuberculate. **Male** pereomeres subequal in width or with 3–5 broader, head wider than long. Eyes present or absent. Antennula and antenna articulated. Midventral tubercles present or absent. 7 pairs of subequal pereopods or anterior pairs larger or posterior pairs larger. Pleomeres fused into single segment, sometimes with traces of segmentation, pleopods and uropods present or absent.

Key to females of genera of Orbioninae

1.	5 pleomeres	2
–	6 pleomeres	3
2.	Pleomeres 2–4 with rudimentary lateral plates; pereomeres medially fused (fig. 6.16a, b)	*Anisorbione*
–	All pleomeres with well-developed lateral plates; pereomeres distinct (fig. 6.16c, d)	*Epipenaeon*
3.	Body asymmetrical	4
–	Body symmetrical	5
4.	Uropods uniramous (fig. 6.16e)	*Asymmetrorbione*
–	Uropods biramous (fig. 6.16f, g)	*Parasymmetrorbione*
5.	Coxal plates and lateral plates reduced; short side of body with coxal plates only on pereomere 1 (fig. 6.16h)	*Minicopenaeon*
–	Coxal plates and lateral plates well developed; short side of body without coxal plates on pereomere	6
6.	Body ovate; pleomere 6 with lateral plates (fig. 6.16i, j)	*Orbione*
–	Body oblong; pleomere 6 without lateral plates	7
7.	All pereomeres of both sides with subequal coxal plates (fig. 6.16k, l)	*Parapenaeonella*
–	Only first two pereomeres with subequal coxal plates	8
8.	Lateral plates of pleomeres well developed, lamellar, margins serrated (fig. 6.16m, n)	*Aparapenaeon*
–	Lateral plates of pleomeres reduced to narrow strips, margins not serrated (fig. 6.16o, p)	*Parapenaeon*

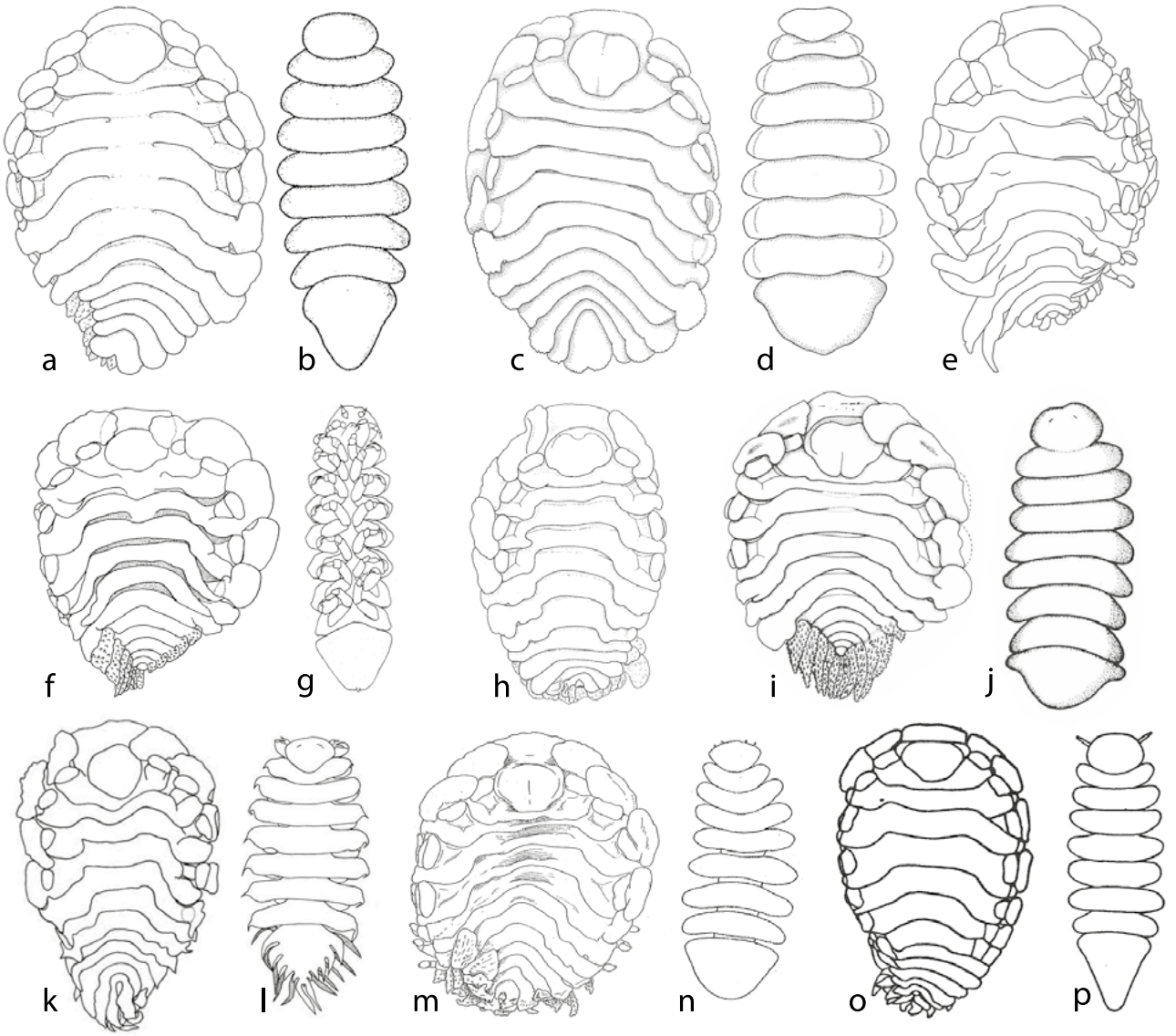


Figure 6.16. Orbioninae. *Anisorbione curva* Bourdon, 1981: a, female dorsal view; b, male dorsal view. *Epipenaeon ingens* Nobili, 1906: c, female dorsal view; d, male dorsal view. *Asymmetrorbione drepanopleon* Boyko, 2003: e, female dorsal view. *Parasymmetrorbione bicaudata* An, Boyko and Li, 2013: f, female dorsal view; g, male ventral view. *Minicopenaeon crosnieri* (Bourdon, 1979): h, female dorsal view. *Orbione digitata* Bourdon, 1982: i, female dorsal view; j, male dorsal view. *Parapenaeonella distincta* Shiino, 1949: k, female dorsal view; l, male dorsal view. *Aparapenaeon japonica* (Thielemann, 1910): m, female dorsal view; n, male dorsal view. *Parapenaeon consolidata* Richardson, 1904: o, female dorsal view; p, male dorsal view.

Anisorbione Bourdon, 1981

Diagnosis. **Female** with pereomeres fused medially; head not distorted. Eyes absent. Maxilliped with non-articulated palp. Marsupium closed. Oostegite 1 internal ridge slightly digitate. 5 pairs of subequal pereopods. Pleon of 5 pleomeres, distorted 30°. Lateral plates absent; uropods biramous, tuberculate. **Male** with pereomeres subequal in width. Eyes absent. Midventral tubercles absent. 7 pairs of subequal pereopods. Pleomeres fused into single segment, pleopods and uropods absent.

Shelf, parasitising penaeid shrimps. Central Indo-Pacific. 1 species (Bourdon, 1981).

Aparapenaeon An, Yin, Chen, Boyko and Liu, 2022

Diagnosis. **Female** with all pereomeres distinct or with median regions of some fused. Eyes absent. Maxilliped with non-articulated palp. Marsupium open or closed. Oostegite 1 internal ridge digitate. Pereomeres 1–4 with dorsolateral bosses and large coxal plates on long side of body, but only pereomeres

1 and 2 with large coxal plates on short side of body, coxal plates on pereomeres 3 and 4 small or absent. 5 pairs of pereopods, posterior pereopods larger or smaller than anterior pairs. Pleon of 6 segments, not distorted or distorted up to 30°; pleomeres 1–5 with lamellar lateral plates, margins serrated, sometimes covered with small tubercules. 5 pairs of tuberculate biramous pleopods. Uropods biramous. **Male** with pereomeres subequal in width or with 3–5 broader. Eyes absent. Midventral tubercles absent. 7 pairs of subequal pereopods or anterior pairs larger. Pleopods and uropods absent.

Shelf, parasitising penaeid shrimps. Western and Central Indo-Pacific, Temperate Northern Pacific. 4 species (An et al., 2022).

Asymmetrorbione Boyko, 2003

Diagnosis. **Female** with all pereomeres distinct; one side of pereon and pleon distinctly longer than other, head weakly distorted. Eyes present or absent. Maxilliped with non-articulated palp. Marsupium open. Oostegite 1 internal ridge smooth. 5 pairs of pereopods, posterior pairs larger. Pleon of 6 segments, not distorted. 5 pairs of smooth uniramous lateral plates, larger on longer side; uropods uniramous, smooth. **Male** with pereomeres 3–5 broadest. Eyes absent. Midventral tubercles absent. 7 pairs of subequal pereopods. Pleomeres fused into single segment, pleopods and uropods absent.

Subtidal–slope, parasitising sicyoniid shrimps, Western and Central Indo-Pacific. 2 species (Boyko, 2003).

Epipenaeon Nobili, 1906

Diagnosis. **Female** with all pereomeres distinct; head not distorted. Eyes present or absent. Maxilliped with non-articulated palp. Marsupium open. Oostegite 1 internal ridge digitate. 5 pairs of pereopods, posterior pairs larger. Pleon of 5 segments, weakly distorted. 5 pairs of smooth uniramous lateral plates, larger on one side of pleon; uropods biramous, tuberculate. **Male** with pereomeres subequal in width. Eyes present or absent. Midventral tubercles absent. 7 pairs of pereopods, posterior pairs larger. Pleomeres fused into single segment, sometimes with traces of segmentation, pleopods and uropods absent.

Shelf, parasitising penaeid shrimps. Temperate Northern Atlantic (Mediterranean, introduced), Temperate Southern Africa, Western and Central Indo-Pacific. 7 species (An et al., 2022).

Minicopenaeon Bourdon, 1981

Diagnosis. **Female** with all pereomeres distinct; head not distorted. Eyes absent. Maxilliped with non-articulated palp. Marsupium open or closed. Oostegite 1 internal ridge digitate. 5 pairs of pereopods, posterior pairs smaller. Pleon of 6 segments, not distorted. 5 pairs of smooth uniramous lateral plates, larger on one side of pleon; uropods biramous, tuberculate. **Male** with pereomeres subequal in width. Eyes absent. Midventral tubercles absent. 7 pairs of subequal pereopods. Pleomeres fused into single segment, sometimes with traces of segmentation, pleopods and uropods absent.

Shelf–slope, parasitising penaeid shrimps. Western and Central Indo-Pacific. 4 species (An et al., 2013b).

Orbione Bonnier, 1900

Diagnosis. **Female** with all pereomeres distinct; head not distorted. Eyes absent. Maxilliped with non-articulated palp. Marsupium open or closed. Oostegite 1 internal ridge digitate. 5 pairs of pereopods, posterior pairs larger. Pleon of 6 segments, not distorted. 5 pairs of tuberculate uniramous lateral plates; uropods uniramous, tuberculate. **Male** with pereomeres subequal in width. Eyes present. Midventral tubercles absent. 7 pairs of pereopods, posterior pairs larger. Pleomeres fused into single segment, sometimes with traces of segmentation, pleopods and uropods absent.

Shelf, parasitising aristeid, penaeid and solenocerid shrimps. Western and Central Indo-Pacific, Temperate Northern Pacific. 8 species (Boyko et al., 2025).

Parapenaeon Richardson, 1904

Diagnosis. **Female** body with all pereomeres distinct; head not distorted. Eyes absent. Maxilliped with non-articulated palp. Marsupium open or closed. Oostegite 1 internal ridge digitate. Pereomeres 1–4 with dorsolateral bosses and large coxal plates on long side of body, pereomeres 1 and 2 with large coxal plates on short side of body. 5 pairs of pereopods, poster pairs larger. Pleon of 6 segments, not distorted or weakly distorted. 5 pairs of smooth uniramous lateral plates, larger on one side of pleon; uropods biramous, tuberculate. **Male** with pereomeres subequal in width. Eyes present or absent. Midventral tubercles absent. 7 pairs of pereopods, anterior pairs larger. Pleomeres fused into single segment, sometimes with traces of segmentation, pleopods and uropods absent.

Shelf, parasitising penaeid shrimps. Western and Central Indo-Pacific, Temperate Northern Pacific. 6 species (An et al., 2022).

Parapenaeonella Shiino, 1949

Diagnosis. **Female** body with all pereomeres distinct; head not distorted. Eyes absent. Maxilliped with non-articulated palp. Marsupium open or closed. Oostegite 1 internal ridge digitate. 5 pairs of pereopods, posterior pairs larger. Pleon of 6 segments, not distorted. 5 pairs of tuberculate or smooth uniramous lateral plates; uropods uniramous, tuberculate. **Male** with pereomeres subequal in width. Eyes present. Midventral tubercles present or absent. 7 pairs of subequal pereopods. Pleomeres fused into single segment with lateral indications of segments, broad anteriorly, tapering distally, pleopods and uropods uniramous.

Shelf–slope, parasitising penaeid shrimps. Western and Central Indo-Pacific, Temperate Northern Pacific. 6 species (An et al., 2022).

Parasymmetrorbione An, Boyko and Li, 2013

Diagnosis. **Female** body with all pereomeres distinct except 1 and 2; one side of pereon and pleon distinctly longer than other; head weakly distorted. Eyes absent. Maxilliped with articulated

palp. Marsupium open. Oostegite 1 internal ridge digitate. 5 pairs of pereopods, posterior pairs larger. Pleon of 6 segments, not distorted. 5 pairs of tuberculate uniramous lateral plates, larger on longer side; uropods biramous, tuberculate. **Male** with pereomeres subequal in width. Eyes absent. Midventral tubercles absent. 7 pairs of subequal pereopods. Pleomeres fused into single segment, pleopods and uropods absent.

Shelf, parasitising solenocerid shrimps. Central Indo-Pacific. 1 species (An et al., 2013a).

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Subfamily Phyllodurinae Markham, 1977

Figure 6.17

The sole genus and species in Phyllodurinae is an ectoparasite on the abdomens of upogebiids. It can be distinguished from other epicarideans in that the females have a linear, non-distorted body, smooth (outer) and tuberculate (inner) barbula lobes, ischia of posterior pairs of pereopods extremely elongate, first pleomere bearing papillose processes, and a triangular pleon bearing 5 pairs of uniramous falcate lateral plates and pleopods. Males have the posterior 5 pleomeres with posterolaterally extended tapered lateral lobes and 5 pairs of uniramous sac-like pleopods.

Phyllodurus abdominalis Stimpson, 1857 is known with certainty only from the Pacific coast of North America, from southern British Columbia to Baja California (Markham, 1977, 2005). There are reports of a "*Phyllodurus* sp." from Japan (e.g. Itani, 2004) and another is known from southeastern Australia but these specimens have neither been described nor illustrated, their identity is unclear, and the genus is at present monotypic.

Diagnosis. **Female** (fig. 6.17a, b) body subtriangular; pereomeres distinct; head longer than wide, triangular, not bilobed, not distorted. Frontal lamina present. Eyes absent. Barbula with 1 smooth tapered outer lobe and 1 tuberculate tapered inner lobe on each side. Antennula and antenna articulated. Maxilliped without articulated palp. Marsupium closed. 5 pairs of oostegites; oostegite 1 with extended triangular posterior lobe; internal ridge smooth. Coxal plates present. Dorsolateral bosses present. Middorsal projections absent. 7 pairs of pereopods, dactyli and propodi subequal in size, ischia progressively longer in posterior pairs. Pleon of 6 segments, triangular, narrower than pereon; pleomere 1 with dorsal papillose process on each side of anterior margin; 5 pairs of uniramous smooth falcate lateral plates. 5 pairs of uniramous smooth pleopods as elongate, falcate lobes. Uropods uniramous, smooth, falcate on sharply pointed pleotelson. **Male** (fig. 6.17c) pereomeres subequal in width, head wider than long. Eyes present. Antennula and antenna articulated. Midventral tubercles absent. 6 pairs of pereopods, dactyli and propodi subequal. Pleon of 6 pleomeres, posterior 5 with posterolaterally extended tapered lateral lobes, 5 pairs of uniramous sac-like pleopods, uropods absent. Abdominal parasites.

Phyllodurus Stimpson, 1857

Diagnosis. As for family.

Intertidal, parasitising upogebiid shrimps. Temperate Northern Pacific. 1 species (Markham, 1977).

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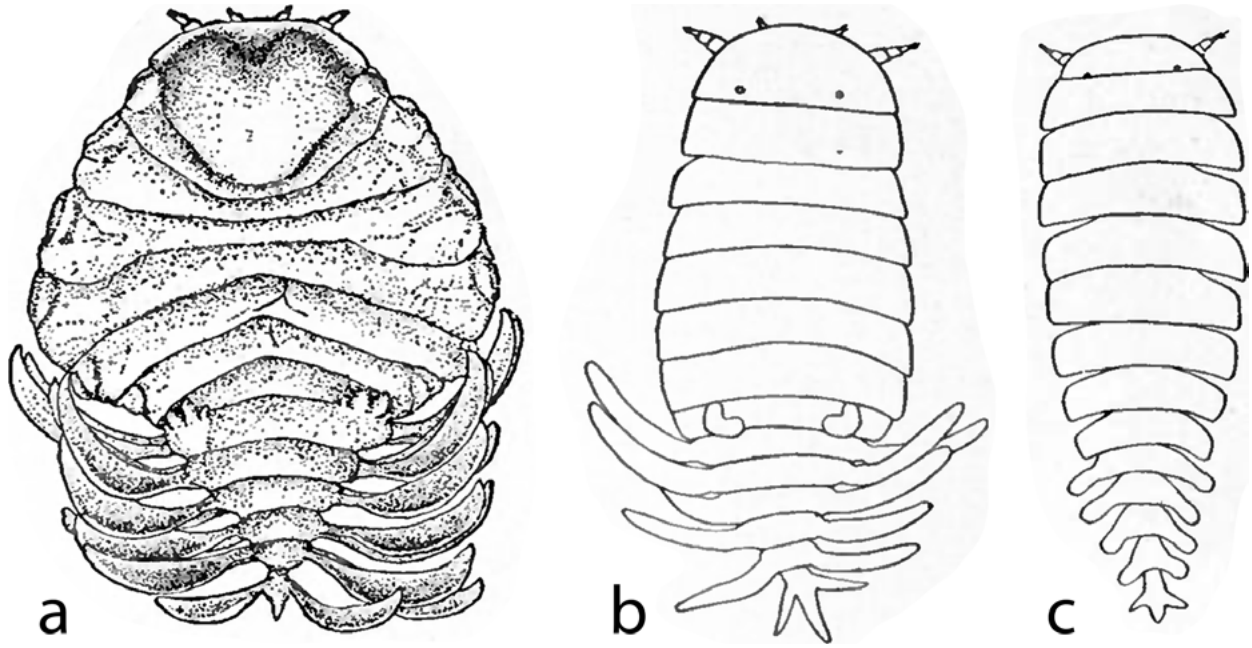


Fig. 6.17. Phyllodurinae. *Phyllodurus abdominalis* Stimpson, 1857: a, female dorsal view. b, juvenile female dorsal view. c, male dorsal view.

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Subfamily Pleurocryptellinae Williams and Boyko *in* Williams, Boyko and Stewart, 2024

Figure 6.18

Members of Pleurocryptellinae are branchial ectoparasites of chirostylid, munidid, and munidopsid squat lobsters. The genera in Pleurocryptellinae can be distinguished from all other bopyrid genera in that the epicaridium larvae have teardrop-shaped bodies with a large yolk sac extending between the uropods. Females of species in *Pleurocryptella* and *Pagurocryptella* have 7 pairs of oostegites; the only other genera that contain species with this character are *Septembopyrina* An, Boyko and Li, 2015 and *Bopyrinella* Nierstrasz and Brender à Brandis, 1925 (Bopyrinae); females of species in *Paragigantione*, *Parapleurocryptella*, and *Pleurocryptina* have the typical 5 pairs of oostegites. Males of all species in Pleurocryptellinae have segmented maxillipeds and those in *Pleurocryptella*, *Paragigantione* and *Pleurocryptina* have articulated uropods.

Diagnosis. **Female** body elongate or ovate, weakly distorted to distorted; head bilobed or not bilobed; frontal lamina present. Eyes present or absent. Maxilliped with setose articulated and segmented palp, setose non-articulated palp, or without palp. Barbula with 1 or 2 long smooth lobes or 1 long lobe and 1 small nub on each side or 1 short smooth lobe on each side, median region smooth. 5 or 7 pairs of oostegites; oostegite 1 with ovate posterior lobe, smaller, subequal to or larger than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections present or absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower or not narrower than pereon. Lateral plates absent or reduced; 4 or 5 pairs of smooth biramous pleopods or 4 pairs of smooth biramous pleopods and 1 pair of smooth uniramous pleopods or 3 pairs of biramous and 2 pairs of smooth uniramous pleopods, pleopods of 1 or 2 segments; uropods uniramous, smooth, distally bilobed or entire. **Male** approximately 2–4 times as long as wide, head narrower or as wide as pereon, pereomeres narrower or not narrower posteriorly. Eyes present or absent. Maxillipeds segmented, distally setose (in some species the maxilliped segmentation may be indistinct). Pereopods 1 and 2 larger than other pairs or all pereopods subequal. Midventral tubercles present or absent. Pleon of 6 pleomeres; 5 pairs of pleopods; posterolateral corners of pleomere 6 rounded or indented; uropods present, articulated or non-articulated. **Epicaridium larva** body teardrop shape with large yolk sac, extending between uropods.

Key to females of genera of Pleurocryptellinae

1.	7 pairs of oostegites	2
–	5 pairs of oostegites	3
2.	5 pairs of biramous pleopods (fig. 6.18j–o)	*Pleurocryptella*
–	3 or 4 pairs of biramous pleopods (fig. 6.18p–s)	*Pagurocryptella*
3.	Uropods distally bilobed (fig. 6.18a–i)	*Paragigantione*
–	Uropods not distally bilobed	4
4.	5 pairs of biramous pleopods (fig. 6.18t, u)	*Parapleurocryptella*
–	4 pairs of biramous pleopods (fig. 6.18v)	*Pleurocryptina*

Pagurocryptella Boyko and Williams, 2010

Diagnosis. **Female** elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp or with setose non-articulated palp. Barbula with 1 long smooth lobe and 1 small nub on each side, median region smooth. 7 pairs of oostegites; oostegite 1 with ovate posterior lobe, larger than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 4 pairs of smooth biramous pleopods or 3 pairs of biramous and 2 pairs of uniramous smooth pleopods; uropods uniramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres narrower posteriorly. Eyes absent. Pereopods subequal. Midventral tubercles absent. Pleon of 5 or 6 pleomeres; pleopods, posterolateral corners of pleomere 6 and uropods unknown.

Shelf–bathyal, parasitising pagurid and parapagurid hermit crabs. Temperate Northern Atlantic, Central Indo-Pacific. 2 species (Boyko and Williams, 2010; Kato et al., 2018; Kokasko et al., 2025).

Paragigantione Barnard, 1920

Diagnosis. **Female** ovate-elongate, body weakly distorted to distorted; head not bilobed. Maxilliped without palp. Barbula with 1 long smooth lobe on each side. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, larger than anterior lobe. Lateral plates reduced; 5 pairs of smooth biramous pleopods; uropods uniramous, distally bilobed. **Male** approximately 2–3 times as long as wide, head narrower than pereon. Pereopods subequal. Posterolateral corners of pleomere 6 rounded.

Slope, parasitising munidid squat lobsters. Temperate Northern Atlantic, Tropical Atlantic, Temperate Southern Africa, Central Indo-Pacific, Temperate Australasia. 5 species (Bourdon, 1981; Boyko et al., 2024).

Parapleurocryptella Bourdon, 1972

Diagnosis. **Female** ovate or elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated and segmented palp. Barbula with 1 short smooth lobe on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, smaller or larger than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower or not narrower than pereon. Lateral plates absent; 5 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** approximately 2 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes absent. Maxilliped segmented. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of sessile pleopods; posterolateral corners of pleomere 6 rounded; uropods present.

Slope, parasitising chirostylid and munidopsid squat lobsters. Tropical Atlantic, Central Indo-Pacific, Temperate Australasia. 3 species (Bourdon, 1972; Kokasko et al., 2025).

Pleurocryptella Bonnier, 1900

Diagnosis. **Female** elongate or ovate, body weakly distorted; head bilobed or not bilobed. Maxilliped with setose articulated and segmented palp. Barbula with 2 long smooth lobes or 1 long lobe and 1 small nub on each side. 7 pairs of oostegites; oostegite 1 with ovate posterior lobe, smaller or subequal to anterior lobe. Lateral plates absent or reduced; 5 pairs of smooth biramous pleopods or 4 pairs of smooth biramous pleopods and 1 pair of smooth uniramous pleopods, pleopods of 1 or 2 segments; uropods uniramous, smooth, distally not bilobed. **Male** approximately 3–4 times as long as wide, head as wide as pereon. Pereopods 1 and 2 larger than other pairs. Posterolateral corners of pleomere 6 rounded or indented.

Shelf–abyssal, parasitising chirostylid, munidid, and munidopsid squat lobsters. Temperate Northern Atlantic, Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific, Tropical Eastern Pacific. 11 species and 1 subspecies (Williams et al., 2020, 2024).

Pleurocryptina Nierstrasz and Brender à Brandis, 1929

Diagnosis. **Female** ovate, body weakly distorted; head bilobed; frontal lamina present. Eyes present. Maxilliped with setose non-articulated palp. Barbula with 1 long smooth lobe and 1 nub on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, larger than anterior lobe;

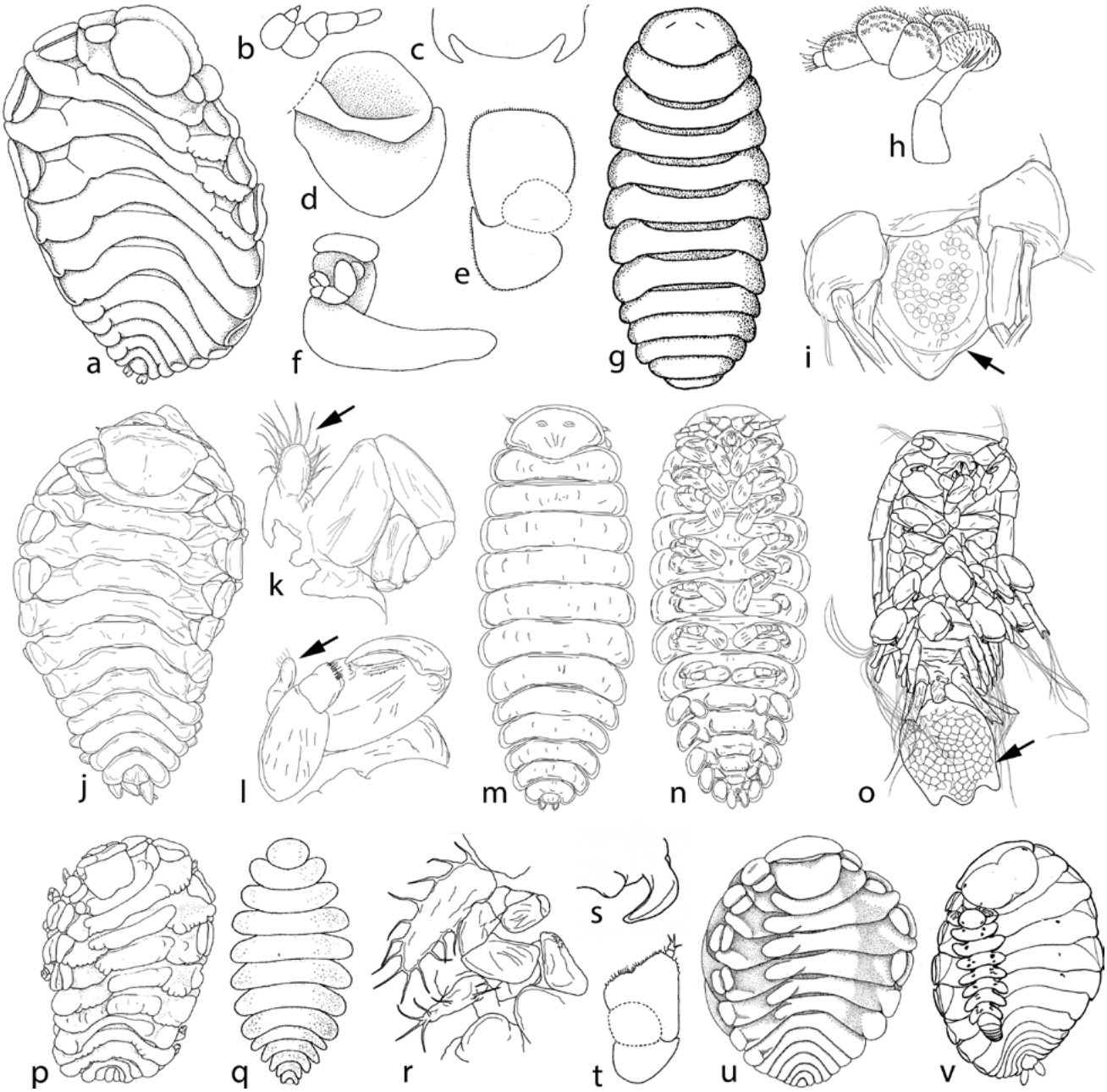


Fig. 6.18. Pleurocryptellinae. *Paragigantione europaea* Boyko et al., 2024: a, female dorsal view; b, female left antennae; c, female barbula; d, female left oostegite 1, inner view; e, female left maxilliped; f, female right oostegite 5 and pereopod 5; g, male dorsal view; h, male right antenna, antennula and maxilliped. *Paragigantione americana* (Markham, 1974): i, epicaridium larvae, ventral view of uropods and yolk sac (arrow). *Pleurocryptella poseidon* Williams and Boyko *in* Williams, Boyko and Stewart, 2024: j, female dorsal view; k, female left pereopod 7 with oostegite (arrow); l, female left pereopod 1 and maxilliped (arrow); m, male dorsal view; n, male ventral view; o, epicaridium larva with yolk sac (arrow). *Pagurocryptella paguri* (Bourdon, 1979): p, female dorsal view; q, male dorsal view. *Pagurocryptella holthuisi* Boyko and Williams, 2010: r, left pereopod 7 and oostegites 6 and 7; s, left side of barbula. *Parapleurocryptella minuta* Bourdon, 1972: t, female maxilliped; u, female dorsal view. *Pleurocryptina indica* Nierstrasz and Brender à Brandis, 1929: v, female dorsal view, with male attached.

internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates small; 4 pairs of smooth biramous pleopods and 1 pair of smooth uniramous pleopods; uropods uniramous, smooth. **Male** approximately 3–4 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Segmented maxillipeds present. Pereopods 1 and 2 larger than other pairs. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of pleopods; posterolateral corners of pleomere 6 rounded; uropods present.

Shelf, parasitising galatheid squat lobsters. Central Indo-Pacific. 1 species (Bourdon and Stock, 1979; Kokasko et al., 2025).

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Subfamily Pseudioninae Codreanu, 1967

Figures 6.19–6.22

Pseudioninae was considered the ancestral taxon within Bopyridae (Markham, 1986; Shiino, 1965) but that was based on the inclusion of *Pleurocryptella* in the subfamily; that genus is now placed in Pleurocryptellinae. As can be seen from the diagnosis below, nearly every character is variable within Pseudioninae and no synapomorphies can be identified. Species in Pseudioninae are also found parasitising the widest range of definitive hosts of any epicaridean group, being found as ectoparasites on species in Achelata, Anomura, Astacidea, Axiidea, Brachyura, Caridea and Gebiidea. The subfamily and several included genera are doubtfully monophyletic and in need of revision. Boyko et al. (2017) defined *Pseudione sensu stricto* to contain only eight species (with one subsequently described), and the diagnosis below reflects this, as well as the recent removal of 13 species to the genus *Cryptione* Hansen, 1897. The remaining species parasitising galatheoids and unknown hosts are considered *Pseudione sensu lato* and are also in need of revision; they will not key out to *Pseudione*.

Diagnosis. **Female** body ovate to elongate, not distorted to highly distorted (c. 120°); head bilobed or not bilobed; frontal lamina present or absent, expanded or not expanded laterally. Eyes present or absent. Maxilliped with setose or non-setose, articulated or non-articulated, segmented or non-segmented palp or palp absent. Barbula with 1–4 long or short smooth, digitate or tuberculate lobes on each side or without lobes, median region smooth or digitate. Oostegite 1 with triangular, oblong, ovate or subquadrate posterior lobe or ovate posterior lobe bearing triangular, recurved or finger-like distal projection, larger, subequal or smaller than anterior lobe; internal ridge smooth or digitate. Coxal plates, dorsolateral bosses and tergal projections present or absent. Mediodorsal lobes present or absent. Pereopods elongate or not elongate, with or without propodal sockets. Pleon abruptly narrower or not narrower than pereon. Lateral plates slender, tubular or broad, large or reduced, or absent; 3–5 pairs of smooth or tuberculate uniramous or biramous pleopods, 1 or 2-segmented, with smooth or crenulate margins; uropods smooth or tuberculate, uniramous, biramous, or uniramous and bifid distally, smooth or crenulate margins, or absent. **Male** approximately 1–5 times as long as wide, head narrower than pereon or as wide as pereon, pereomeres narrower or not narrower posteriorly. Eyes present or absent. Segmented

maxillipeds present or absent. Pereopods subequal or some pairs larger. Midventral tubercles present or absent. Pleon of 1–6 pleomeres; lateral plates present or absent; 3–5 pairs of uniramous or biramous pleopods or pleopods absent; posterolateral corners of pleomere 6 rounded or extended; uropods articulated, rounded or bifid, or absent.

Key to genera of the subfamily Pseudioninae

(Based on female and male characters; modified from Williams et al., 2019.)

1.	Abdominal parasites	2
–	Branchial parasites	4
2.	Under folded abdomen of pinnotherid or cryptochirid hosts, pleopods biramous	3
–	Under abdomen of caridean shrimps, pleopods uniramous (fig. 6.19a)	*Pleonobopyrus*
3.	Head of female rounded, oostegite 1 with sharp point on posterior margin, coxal plates well developed, pereopods isomorphic, uropods posteriorly extended and foliaceous (fig. 6.19b, c)	*Rhopalione*
–	Head of female subquadrate, oostegite 1 with rounded posterior margin, coxal plates small, pereopod 1 approximately half as large as pereopod 7, uropods short, rounded lateral lobes (fig. 6.19d, e)	*Spathione*
4.	Body of female fully enclosed within branchial chamber of host	5
–	Body of female partly within branchial chamber and extending onto abdomen of host (fig. 6.19f, g)	*Bopyrophryxus*
5.	Females parasitising hermit crabs or king crabs	6
–	Females parasitising other hosts	14
6.	Females greatly distorted, typically 90° or more and/or with propodal sockets on pereopods	7
–	Females less distorted (generally <70°) or nearly symmetrical, lacking propodal sockets on pereopods	8
7.	Females with propodal sockets on pereopods (fig. 6.19h, i)	*Asymmetrione*
–	Females without propodal sockets on pereopods, body strongly distorted (fig. 6.19j)	*Parasymmetrione*
8.	Females with biramous uropods	9
–	Females with uniramous uropods or uropods absent	10
9.	Females with 6 pairs of pleonal lateral plates (fig. 6.19k)	*Pagurion*
–	Females with 5 pairs of pleonal lateral plates (fig. 6.19l)	*Parapagurion*
10.	Females with pleomere 6 ventrally displaced, not visible in dorsal view	11
–	Females with pleomere 6 not ventrally displaced, visible in dorsal view	12
11.	Males with uniramous pleopods (fig. 6.19m, n)	*Bopyrissa*
–	Males with biramous pleopods (fig. 6.19o)	*Propseudione*
12.	Females with 5 pairs of biramous pleopods	13
–	Females with some pleopods uniramous (fig. 6.19p, q)	*Pseudionella*
13.	Males with uniramous pleopods (fig. 6.20a)	*Eremitione*
–	Males without pleopods (fig. 6.20b, c)	*Paguristione*
14.	Females with long, extended, blunt ended anterolateral projections on head, coxal plates completely covering both sides of each pereomere, parasitising sand crabs (Hippoidea) (fig. 6.20d, e)	*Albunione*
–	Females lacking anterolateral projections on head	15
15.	Females parasitising caridean shrimps	16
–	Females parasitising other hosts	20

16. Females with 5 pleomeres (fig. 6.20f) ..... *Nikione*

– Females with 6 pleomeres 17

17. Females with 5 pairs of uniramous pleopods (fig. 6.20g) ..... *Pontobopyrus*

– Females with some pleopods biramous 18

18. Females with 5 pairs of biramous pleopods 19

– Females with pleopods 1 and 2 biramous, others uniramous (fig. 6.20h) ..... *Shiinoella*

19. Uropods biramous (fig. 6.20i) ..... *Paranikione*

– Uropods uniramous (fig. 6.20j) ..... *Cryptione*

20. Females parasitising axiideans, gebiideans, or brachyurans 21

– Females parasitising other hosts 34

21. Pleon of female highly compressed, parasitising axiideans (fig. 6.20k) ..... *Ionella*

– Pleon of female elongate 22

22. Females with lateral plates 23

– Females without lateral plates 31

23. Females with distinct constrictions along length of lateral plates and pleopods, parasitising axiideans and gebiideans (fig. 6.20l) ..... *Acrobelione*

– Females without distinct constrictions along length of lateral plates and pleopods (may have crenulate edges and tubercles) 24

24. Pleomeres of male widely separate, distolateral margins extended, parasitising axiideans (fig. 6.20m, n) ..... *Robinione*

– Pleomeres of male not widely separate, distolateral margins not extended 25

25. Females with small coxal plates on pereomeres 1–4 26

– Females with elongate, sickle-shaped coxal plates on pereomeres 1–4, parasitising axiideans and brachyurans (fig. 6.20o) ..... *Gigantione*

26. Females parasitising brachyurans (fig. 6.20p) ..... *Carcinione*

– Females parasitising other hosts 27

27. Males with articulated uropods 28

– Males without articulated uropods 29

28. Maxilliped with palp, oostegite 1 internal ridge margin and barbula digitate, parasitising axiideans and gebideans (fig. 6.20q) ..... *Progebiophilus*

– Maxilliped without palp, oostegite 1 internal ridge margin and barbula smooth, parasitising gebideans (fig. 6.20r) ..... *Orthione*

29. Body of male with pleon wider than pereon, parasitising gebideans (fig. 6.20s, t) ..... *Upogebione*

– Body of male with pleon narrower than pereon 30

30. Females with irregular protuberances on dorsolateral margins of pleomeres 1–6 (fig. 6.20u), parasitising axiideans ..... *Zeaione*

– Females without irregular protuberances, parasitising axiideans and astacideans (fig. 6.20v) ..... *Pseudione sensu stricto*

31. Females with elongate pleopods and uropods, visible in dorsal view 32

– Females with short elongate pleopods and uropods, not visible in dorsal view 33

32. Females with posterior margin of head not reaching posterior margin of pereomere 1, head triangular with

eyespots, parasitising gebideans (fig. 6.20w) ..... *Aporobopyroides*

– Females with posterior margin of head reaching posterior margin of pereomere 1, head subquadrate, eyespots absent, parasitising gebideans (fig. 6.21a) ..... *Upogebiophilus*

33. Females with 6 distinct pleomeres, uropods absent, parasitising gebideans (fig. 6.21b, c) ..... *Gyge*

– Females with fusion, fewer than 6 pleomeres, uropods present, parasitising gebideans (fig. 6.21d, e) ..... *Pauperella*

34. Females with 5 pleomeres 35

– Females with 6 pleomeres 38

35. Females without uropods, parasitising porcellanids (fig. 6.21f) ..... *Kolourione*

– Females with uniramous or biramous uropods 36

36. Males with 5 pleomeres, parasitising porcellanids (fig. 6.21g, h) ..... *Allorbimorphus*

– Males with fewer than 5 pleomeres 37

37. Females with uniramous uropods, parasitising munidid squat lobsters (fig. 6.21i, j) ..... *Balanopleon*

– Females with biramous uropods, parasitising porcellanids (fig. 6.21k) ..... *Orbimorphus*

38. Barbula of female with 1 elongate lateral projection on each side 39

– Barbula of female with 2 or more elongate lateral projections on each side 41

39. Females without uropods, parasitising porcellanids (fig. 6.21l) ..... *Discomorphus*

– Females with uropods 40

40. Females with enlarged lateral plates, parasitising munidid and munidopsid squat lobsters (fig. 6.22b) ..... *Bathione*

– Females without enlarged lateral plates, parasitising munidid squat lobsters (fig. 6.21m) ..... *Galathocrypta*

41. Females with bilobed head 42

– Females without bilobed head 43

42. Females with oostegite 1 posterior lobe subquadrate, internal ridge smooth, pleopodal endopod and exopod slender, parasitising munidid squat lobsters (fig. 6.21n) ..... *Goleathopseudione*

– Females with oostegite 1 posterior lobe ovate with triangular extension, internal ridge digitate, pleopodal endopod and exopod lamellar, parasitising porcellanids, eumunidid and munidid squat lobsters (fig. 6.22a) ..... *Parionella*

43. Females with well-developed lateral plates 44

– Females without well-developed lateral plates 46

44. Males with midventral tubercles, parasitising porcellanids and munidid squat lobsters (fig. 6.22c, d) ..... *Aporobopyrina*

– Males without midventral tubercles 45

45. Females with well-developed uniramous or biramous uropods, parasitising porcellanids, galatheids and munidid squat lobsters (fig. 6.22e, f) ..... *Pleurocrypta*

– Females with minute uniramous uropods or without uropods, parasitising porcellanids, galatheids and munidid squat lobsters (fig. 6.22g, h) ..... *Anuropodione*

46. Females with biramous uropods, parasitising munidid squat lobsters (fig. 6.22i, j) ..... *Munidion*

– Females with uniramous uropods or without uropods 47

47. Females without uropods, body of males broad, squat (width >1/2 of length), parasitising munidid squat lobsters (fig. 6.22k, l) ..... *Ovoionella*

– Females with uniramous uropods, body of males elongate (width ~1/3 of length) 48

48. Females without coxal plates, parasitising porcellanids (fig. 6.22m, n) ..... *Astalione*
– Females with coxal plates 49
49. Females with small coxal plates 50
– Females with well-developed coxal plates 51
50. Females with small lateral plates, males with 5 pleomeres, parasitising porcellanids and munidid squat lobsters (fig. 6.22o) ..... *Parione*
– Females with moderately developed lateral plates, pyriform body, males with 6 pleomeres, parasitising porcellanids (fig. 6.22p) ..... *Aporobopyrus*
51. Males with pleopods, parasitising porcellanids (fig. 6.22q) ..... *Parioninella*
– Males without pleopods, parasitising galatheids (fig. 6.22r) ..... *Parionina*

Acrobelione Bourdon, 1981

Diagnosis. **Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated or non-articulated palp. Barbula with 2 long digitate lobes on each side, median region digitate. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distal projection, smaller than anterior lobe; internal ridge digitate. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present, slender; 5 pairs of crenulate biramous pleopods; uropods uniramous, crenulate. **Male** approximately 3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 5 or 6 pleomeres; uniramous pleopods or pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal–shelf, parasitising callianassid and upogebiid shrimps. Temperate North Atlantic, Tropical Atlantic, Central Indo-Pacific. 4 species (Boyko et al., 2017).

Albunione Markham and Boyko, 1999

Diagnosis. **Female** elongate, body not distorted; head not bilobed; frontal lamina present, expanded laterally into large flaps. Eyes absent. Maxilliped with setose articulated or non-articulated palp. Barbula with 2 long smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distal projection, subequal to or smaller than anterior lobe; internal ridge digitate. Coxal plates and tergal projections present, dorsolateral bosses absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present, slender; 5 pairs of crenulate biramous pleopods; uropods uniramous, crenulate. **Male** approximately 3–4 times as long as wide, head as wide as pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present or absent. Pleon of 6 pleomeres; lateral plates elongate; pleopods uniramous; posterolateral corners of pleomere 6 extended; uropods absent.

Shelf, parasitising albuneid sand crabs. Tropical Atlantic, Central Indo-Pacific. 3 species (Markham and Boyko, 2003).

Allorbimorphus Bourdon, 1976

Diagnosis. **Female** elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp or with setose non-articulated palp. Barbula with 2 long smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distal projection, smaller than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates reduced; 4 or 5 pairs of smooth biramous pleopods; uropods uniramous or biramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes absent. First 3 pairs of pereopods larger. Midventral tubercles absent. Pleon of 3–6 pleomeres; pleopods uniramous or absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal–shelf, parasitising porcellanid crabs. Western and Central Indo-Pacific, Temperate Australasia. 5 species (An et al., 2012; Bourdon, 1976).

Anuropodione Bourdon, 1967

Diagnosis. **Female** elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp. Barbula with 2 long smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distal projection, smaller than anterior lobe; internal ridge digitate. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present; 5 pairs of smooth biramous pleopods; uropods absent. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes absent. Pereopods subequal. Midventral tubercles absent. Pleon of 1–6 pleomeres; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Shelf–slope, parasitising munidid squat lobsters. Temperate Northern Atlantic, Tropical Atlantic. 5 species (Alves-Júnior et al., 2019; Boyko et al., 2018).

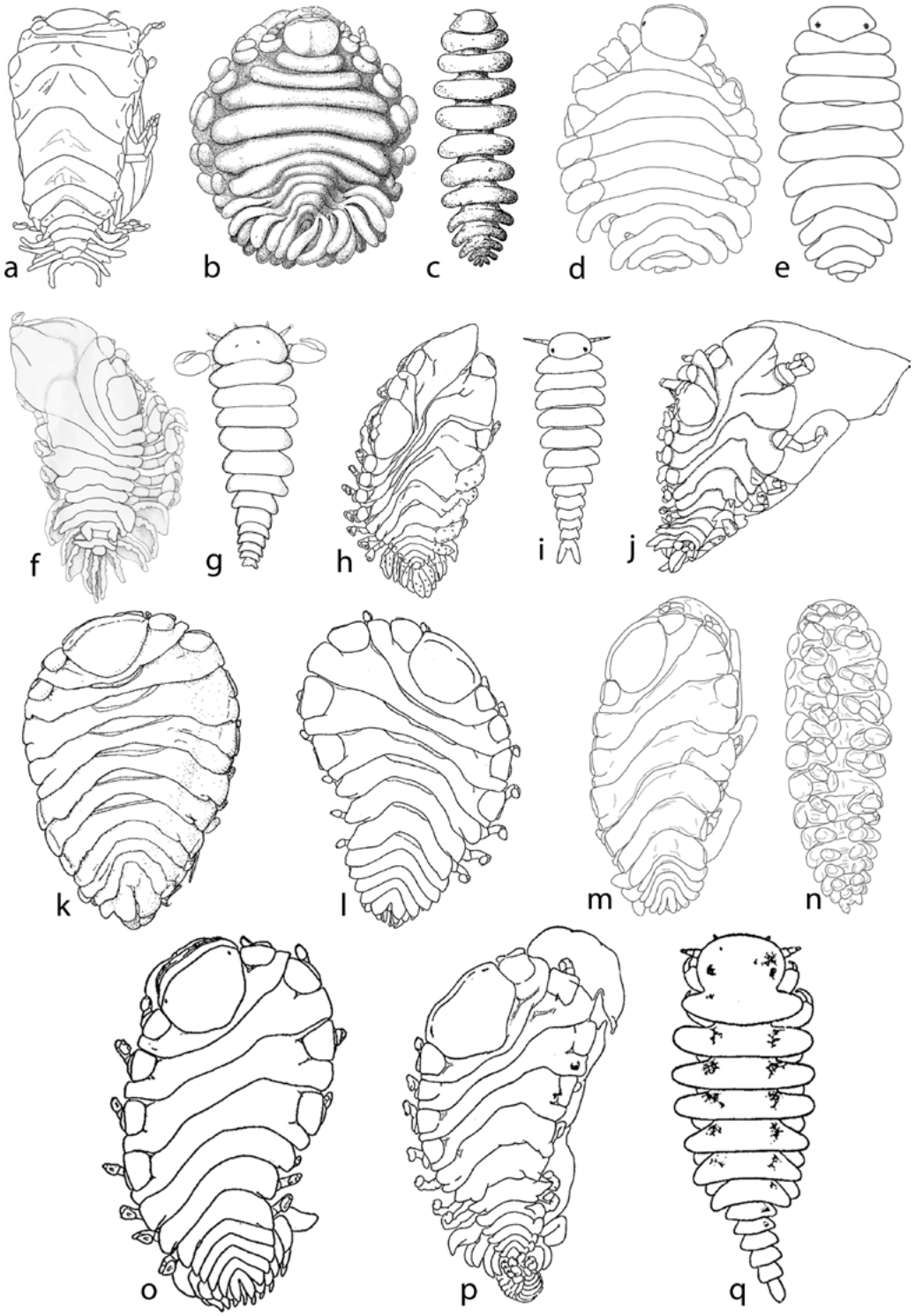


Figure 6.19. Pseudioninae. *Pleonobopyrus kumanonadensis* Saito and Moritaki, 2020: a, female dorsal view. *Rhopalione uromyzon* Pérez, 1920: b, female dorsal view; c, male dorsal view. *Spathione aprosdovrima* Boyko and van der Meij, 2018: d, female dorsal view; e, male dorsal view. *Bopyrophryxus branchiabdominalis* Codreanu, 1965: f, female dorsal view; g, male dorsal view. *Asymmetrione asymmetrica* (Shiino, 1933): h, female dorsal view; i, male dorsal view. *Parasymmetrione tuberculineata* An, Markham and Yu, 2010: j, female dorsal view. *Pagurion tuberculata* Shiino, 1933: k, female dorsal view. *Parapagurion calcinicola* Shiino, 1933: l, female dorsal view. *Bopyrissa magellanica* Nierstrasz and Brender à Brandis, 1931: m, female dorsal view; n, male ventral view. *Propseudione rhombicosoma* Shiino, 1933: o, female dorsal view. *Pseudionella attenuata* Shiino, 1949: p, female dorsal view, with male attached to pleopods; q, male dorsal view.

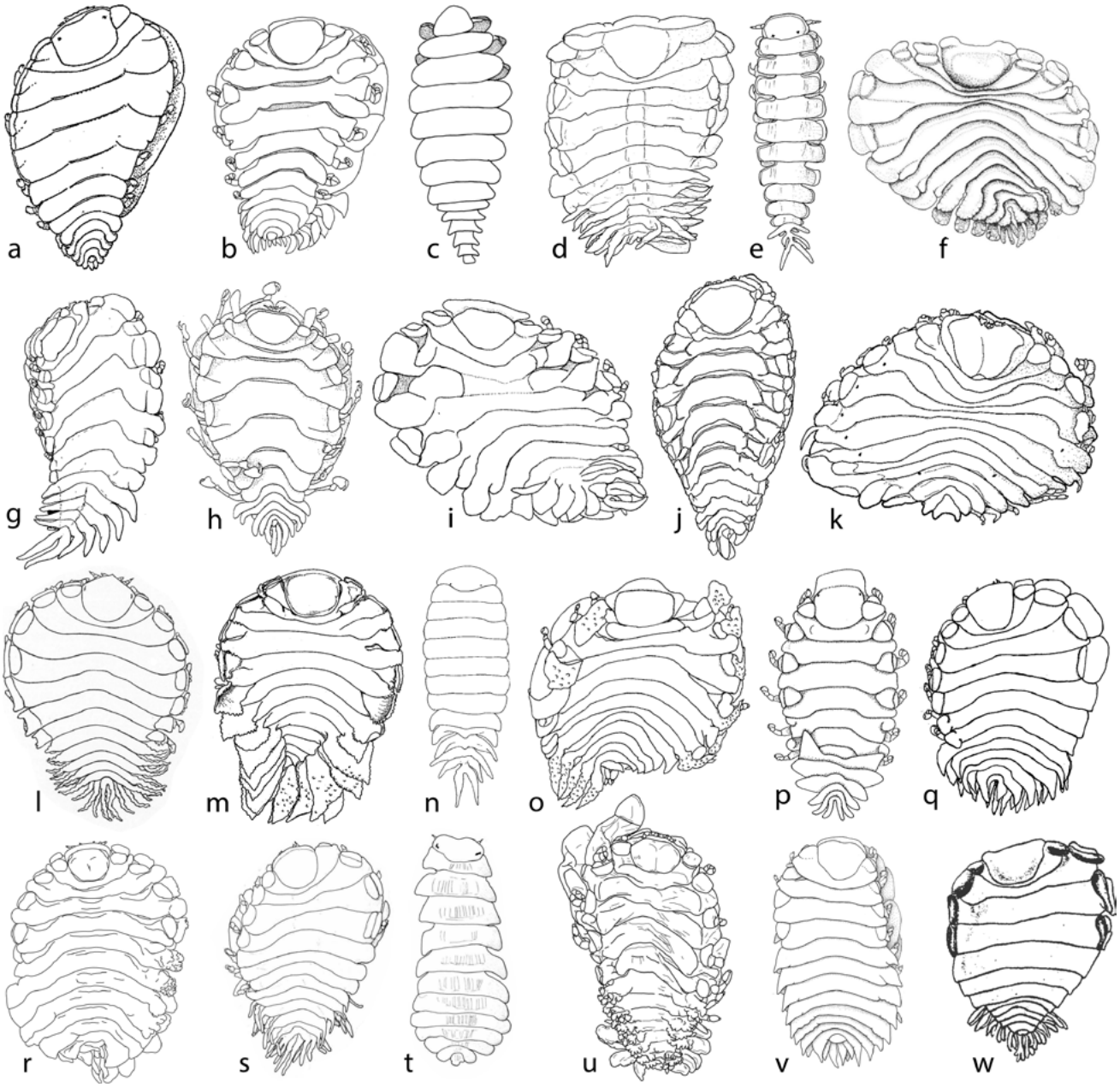


Figure 6.20. Pseudioninae. *Eremitione hyndmanni* (Bate and Westwood, 1867): a, female dorsal view. *Paguristione uniuropodus* An, Zhao and Markham, 2016: b, female dorsal view; c, male dorsal view. *Albunione indecora* (Markham, 1988): d, female dorsal view; e, male dorsal view. *Nikione natalensis* Kensley, 1974: f, female dorsal view. *Pontobopyrus abyssorum* Markham, 1979; g, female dorsal view. *Shiinoella gracilipes* Bourdon, 1972: h, female dorsal view. *Paranikione sibogae* An, Boyko and Li, 2015: i, female dorsal view. *Cryptione elongata* Hansen, 1897: j, female dorsal view. *Ionella maculata* Markham, 1994: k, female dorsal view. *Acrobelione langi* (Van Name, 1920): l, female dorsal view. *Robinione overstreerti* (Adkison and Heard, 1995): m, female dorsal view; n, male dorsal view. *Gigantione tuberculata* An, Williams and Jiang, 2016: o, female dorsal view. *Carcinione platypleura* Bourdon, 1983: p, female dorsal view. *Progebiophilus sinicus* Markham, 1982: q, female dorsal view. *Orthione griffenis* Markham, 2004: r, female dorsal view. *Upogebione phuketensis* Markham, 1985: s, female dorsal view; t, male dorsal view. *Zeaione everta* Boyko and Williams *in* Andrade et al., 2025: u, female dorsal view. *Pseudione callianassae* Kossmann, 1881: v, female dorsal view. *Aporobopyroides upogebiae* Nobili, 1906, w, female dorsal view.

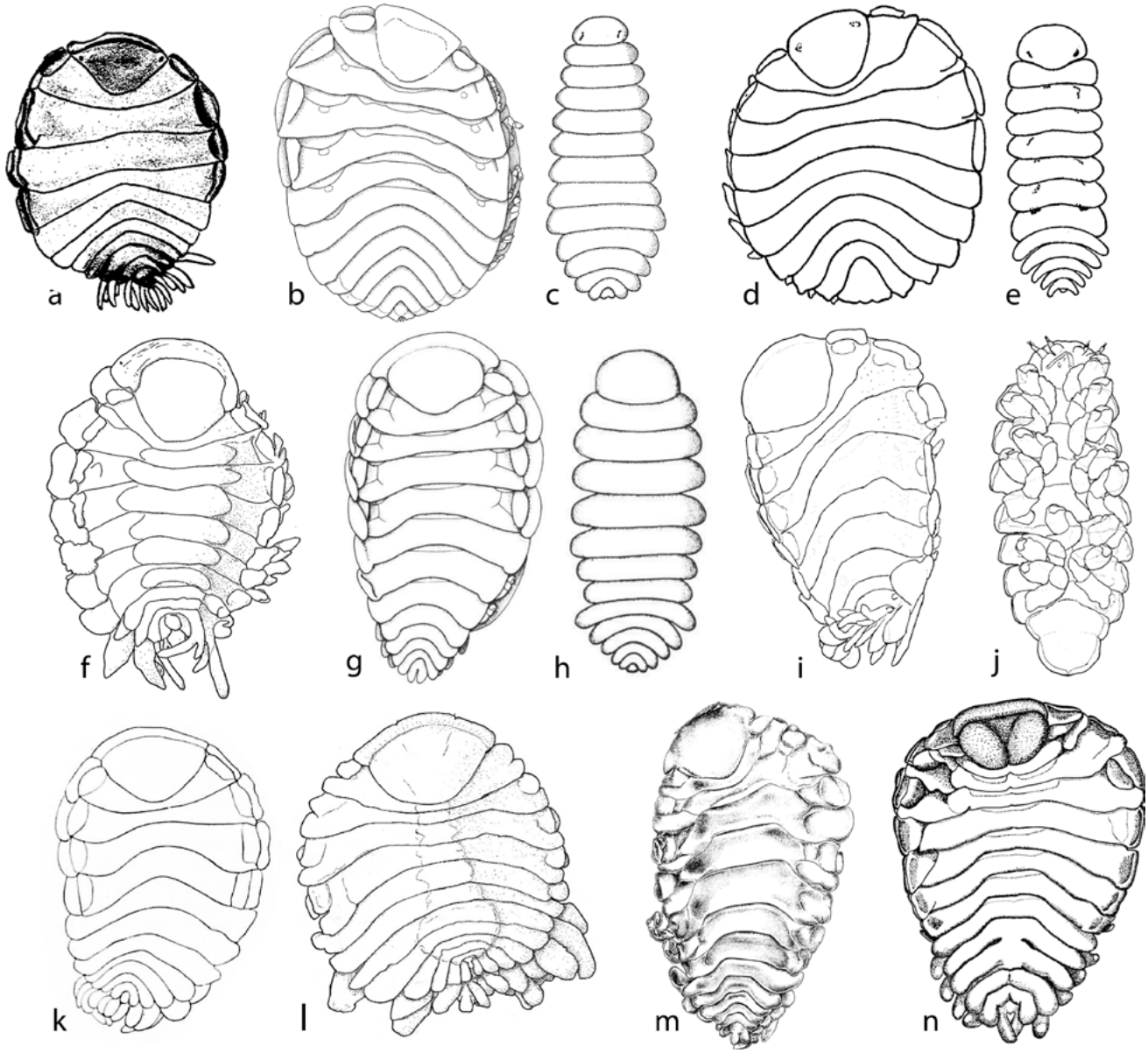


Figure 6.21. Pseudioninae. *Upogebiophilus rhadames* Nobili, 1906: a, female dorsal view. *Gyge branchialis* Cornalia and Panceri, 1861: b, female dorsal view; c, male dorsal view. *Pauperella rotunda* Nierstrasz and Brender à Brandis, 1929: d, female dorsal view; e, male dorsal view. *Kolourione premordica* Markham, 1978: f, female dorsal view. *Allorbimorphus lamellosus* (Nierstrasz and Brender à Brandis, 1923): g, female dorsal view; h, male dorsal view. *Balanopleon tortuganus* Markham, 1974: i, female dorsal view; j, male ventral view. *Orbimorphus constrictus* Richardson, 1910: k, female dorsal view. *Discomorphus magnifoliatus* Markham, 2008: l, female dorsal view. *Galathocrypta acaudata* Román-Contreras and Soto, 2002: m, female dorsal view. *Goleathopseudione bilobatus* Román-Contreras, 2008: n, female dorsal view.

Aporobopyrina Shiino, 1934

Diagnosis. **Female** elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose, non-articulated palp. Barbula with 2 long smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distal projection, smaller than anterior lobe; internal ridge smooth or with weak digitations. Coxal plates, dorsolateral bosses, and tergal projections present. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present, small; 5 pairs of smooth biramous pleopods; uropods biramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles present. Pleon of 4–6 pleomeres; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

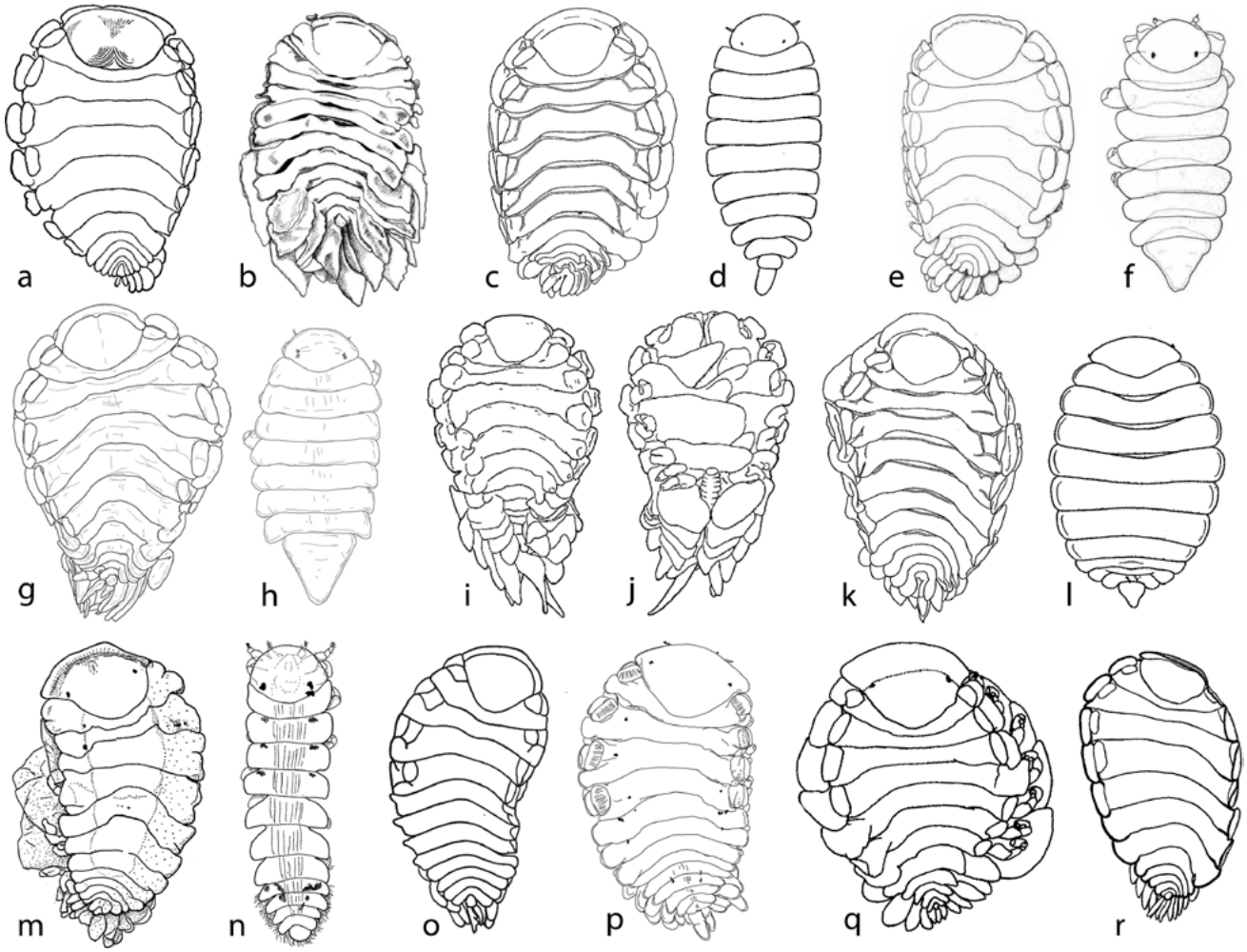


Figure 6.22. Pseudioninae. *Parionella richardsonae* Nierstrasz and Brender à Brandis, 1923: a, female dorsal view. *Bathione magnafolia* Román-Contreras and Boyko, 2007: b, female dorsal view. *Aporobopyrina lamellata* Shiino, 1934: c, female dorsal view; d, male dorsal view. *Pleurocrypta petrolisthis* Markham, 1988: e, female dorsal view; f, male dorsal view. *Anuropodione amphiandra* (Codreanu, Codreanu and Pike, 1966): g, female dorsal view; h, male dorsal view. *Munidion princeps* Hansen, 1897: i, female dorsal view; j, female ventral view, with male positioned among pleopods. *Ovoionella obovata* (Shiino, 1958): k, female dorsal view; l, male dorsal view. *Astalione cruciaria* Markham, 1975: m, female dorsal view; n, male dorsal view. *Parione paucisecta* (Richardson, 1904): o, female dorsal view. *Aporobopyrus galleonus* Williams and Madad, 2010: p, female dorsal view. *Parioninella astridae* Nierstrasz and Brender à Brandis, 1930: q, female dorsal view. *Parionina pacifica* Nierstrasz and Brender à Brandis, 1929: r, female dorsal view.

Intertidal–slope, parasitising munidid squat lobsters and porcellanid crabs. Tropical Atlantic, Western and Central Indo-Pacific. 4 species (Bourdon, 1983).

Aporobopyroides Nobili, 1906

Diagnosis. **Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with non-articulated palp. Barbula not described. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing recurved distal projection, smaller than anterior lobe; internal ridge smooth. Coxal plates present; dorsolateral bosses and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates absent; 5 pairs of biramous pleopods with crenulate margins; biramous uropods with crenulated margins. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 5 pleomeres; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal, parasitising upogebiid shrimps. Temperate Northern Atlantic. 1 species (Nobili, 1906).

Aporobopyrus Nobili, 1906

Diagnosis. **Female** ovate to elongate, body weakly to moderately distorted; head not bilobed; frontal lamina present

or absent. Eyes present or absent. Maxilliped with setose non-articulating palp or without palp. Barbula with 1–3 tuberculate or smooth lobes on each side, median region smooth or digitate. 5 pairs of oostegites; oostegite 1 ovate with triangular distal projection posterior lobe, subequal to anterior lobe; internal ridge smooth or digitate. Coxal plates present, dorsolateral bosses present or absent, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 5 pairs of smooth or tuberculate biramous pleopods with smooth or crenulate margins; uniramous uropods smooth or tuberculate with smooth or crenulate margins. **Male** approximately 3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal or first 2 pairs larger. Midventral tubercles present or absent. Pleon of 5 pleomeres; 5 pairs of uniramous ovate pleopods; posterolateral corners of pleomere 6 rounded or slightly extended; uropods absent.

Intertidal–slope, parasitising porcellanid crabs and galatheid and munidid squat lobsters. Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific, Tropical Eastern Pacific. 21 species (An et al., 2026; Bourdon, 1976; Williams and Madad, 2010).

Astalione Markham, 1975

Diagnosis. **Female** elongate, body distorted ca. 40°; head not bilobed; frontal lamina present. Eyes present. Maxilliped without palp. Barbula with 2 short smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge smooth. Coxal plates, dorsolateral bosses and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates absent; 5 pairs of smooth biramous pleopods with smooth margins; smooth uniramous uropods with smooth margins. **Male** approximately 3–4 times as long as wide, head as wide as pereon, pereomeres not narrower posteriorly. Eyes present. First pair of pereopods larger than others. Midventral tubercles absent. Pleon of 5 pleomeres, fringed with setae; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Intertidal, parasitising porcellanid crabs. Tropical Atlantic. 1 species (Markham, 1975a).

Asymmetrione Codreanu, Codreanu and Pike, 1965

Diagnosis. **Female** elongate, body not distorted to strongly distorted up to c. 90°; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped without palp. Barbula with 1 or 2 short smooth or digitate lobes on each side, median region smooth or digitate. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular or fingerlike distal projection, smaller than or subequal to anterior lobe; internal ridge smooth or digitate. Coxal plates present, dorsolateral bosses and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; with propodal sockets. Pleon not narrower than pereon. Pleomeres 1–4 with flattened lateral plates and rounded lateral plates on pleomere 5 or 5 pairs of flattened lateral plates; 5 pairs of smooth or tuberculate biramous pleopods; uniramous or biramous smooth or tubercular uropods. **Male** approximately 3–4 times as long as wide, head narrower than pereon, pereomeres narrower or not narrower posteriorly. Eyes present or absent. Pereopods subequal but propodi and dactyli of first two pairs proportionately larger than others. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of round pleopods; posterolateral corners of pleomere 6 rounded or extended; uropods present or absent.

Intertidal–shelf, parasitising calcinid, diogenid and pagurid hermit crabs. Temperate North Atlantic, Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific, Temperate South America. 12 species (Williams et al., 2019).

Balanopleon Markham, 1974

Diagnosis. **Female** elongate, body distorted c. 30°; head not bilobed; frontal lamina present. Eyes absent. Maxilliped not described. Barbula with 1 short smooth lobe and 1 stub on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distal projection, smaller than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates small; 5 pairs of smooth biramous pleopods with smooth margins; smooth uniramous uropods with smooth margins. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 2 pleomeres, distinct dorsally, fused ventrally; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Shelf, parasitising porcellanid crabs. Tropical Atlantic. 1 species (Markham, 1974).

Bathione Román-Contreras and Boyko, 2007

Diagnosis. **Female** ovate to elongate, body weakly distorted or not distorted; head not bilobed, fused medially with pereomere 1; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 1 long smooth lobe on each side, median region digitate. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing small distolateral slender lobe, smaller than anterior lobe; internal ridge digitate. Coxal plates present, dorsolateral bosses and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates greatly enlarged, edges crenulate; 5 pairs of large smooth or tuberculate biramous pleopods with crenulate margins; uniramous uropods large, smooth. **Male** approximately 3–4 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of sessile pleopods; posterolateral corners of pleomere 6 slightly extended; uropods absent.

Slope, parasitising munidid and munidopsid squat lobsters. Temperate Northern Pacific, Temperate South America. 2 species (Román-Contreras and Boyko, 2007).

Bopyrissa Nierstrasz and Brender à Brandis, 1931

Diagnosis. **Female** elongate, body weakly to strongly distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped without palp or with setose articulated or non-articulated palp. Barbula with 1 long tuberculate lobe and 1 short tuberculate lobe on each side or 1 long smooth or tuberculate lobe on each side, median region smooth or tuberculate. 5 pairs of oostegites; oostegite 1 ovate with triangular projection, posterior lobe larger, smaller than or subequal to anterior lobe; internal ridge digitate or smooth. Coxal plates absent, dorsolateral bosses present or absent, tergal projections present or absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 5 pairs of smooth or tuberculate biramous pleopods or 4 pairs biramous and 1 pair uniramous; uropods uniramous, smooth or tuberculate. **Male** approximately 2–4 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present or absent. Pleon of 6 pleomeres; 4 or 5 pairs of round or sessile pleopods; posterolateral corners of pleomere 6 rounded or weakly or strongly extended; uropods absent.

Intertidal–subtidal, parasitising calcinid and diogenid hermit crabs. Temperate Northern Atlantic, Tropical Atlantic, Central and Eastern Indo-Pacific, Temperate Northern Pacific, Tropical Eastern Pacific. 14 species (Williams et al., 2019).

Bopyrophryxus Codreanu, 1965

Diagnosis. **Female** elongate, body distorted c. 80°; head not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp. Barbula with 1 short smooth lobe on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, larger than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates large; 5 pairs of tuberculate uniramous pleopods with tuberculate margins; uniramous uropods tuberculate with tuberculate margins. **Male** approximately 2–3 times as long as wide, head as wide as pereon, pereomeres not narrower posteriorly. Eyes present. Pereopod 1 much larger than posterior pereopods. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of ovoid pleopods; posterolateral corners of pleomere 6 extended; uropods absent.

Intertidal–slope, parasitising parapagurid and pagurid hermit crabs. Central Indo-Pacific. 1 species (Bourdon and Boyko, 2005).

Carcinione Bourdon, 1983

Diagnosis. **Female** elongate, body not distorted; head not bilobed; frontal lamina present. Eyes present. Maxilliped without palp. Barbula without lobes, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, smaller than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates well developed with crenulate edges; 1 pair of biramous pleopods and 4 pairs of uniramous pleopods with crenulate edges; uropods uniramous with crenulate edges. **Male** approximately 3 times as long as wide, head narrower than pereon, pereomeres narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal, parasitising cryptochirid crabs. Central Indo-Pacific. 1 species (Boyko and van der Meij, 2018).

Cryptione Hansen, 1897

Diagnosis. **Female** elongate, body nearly straight to distorted (<55°); head not bilobed; frontal lamina present, narrow to wide. Maxilliped with setose palp, some species with setose region below palp. Barbula with 1 or 2 lobes on each side. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distolateral projection, smaller than anterior lobe; internal ridge smooth or digitate. Pereopods increasing in size posteriorly; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 5 pairs of biramous pleopods decreasing in size posteriorly, endopods smaller than exopods; uropods uniramous or reduced. **Male** approximately 4–7 times as long as wide, head subobvate, as wide as pereon, pereomeres not narrower posteriorly. Eyes present or absent. Maxillipeds absent. Pereopods subequal. Pleon of six pleomeres; 5 pairs of uniramous pleopods; posterolateral corners of pleomere 6 extended; uropods absent.

Subtidal–bathyal, parasitising caridean shrimps. Temperate Northern Atlantic, Tropical Atlantic, Temperate South America, Central Indo-Pacific, Temperate Northern Pacific, Tropical Eastern Pacific, Temperate Australasia. 11 species (Williams et al., 2024).

Discomorphus Markham, 2008

Diagnosis. **Female** ovate, body not distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated palp. Barbula with 1 minute nub on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge digitate. Coxal plates reduced, tergal projections present, dorsolateral bosses absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 5 pairs of smooth biramous pleopods; uropods absent. **Male** unknown.

Intertidal, parasitising porcellanid crabs. Temperate Northern Pacific. 1 species (Markham, 2008).

Eremitione Williams, Boyko and Madad, 2019

Diagnosis. **Female** elongate, body weakly to strongly distorted or not distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped with setose non-articulated or articulated palp or palp absent. Barbula with 1 long smooth lobe and 1 short smooth or tuberculate lobe on each side or

short lobe absent, median region smooth or tuberculate. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular or distal recurved projection or lobe triangular, subequal to or larger than anterior lobe; internal ridge digitate. Coxal plates present or absent, dorsolateral bosses present or absent, tergal projections present or absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 5 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres narrower posteriorly. Eyes present or absent. Pereopods subequal or pereopod 1 smaller. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of sessile or raised pleopods; posterolateral corners of pleomere 6 rounded or weakly or strongly extended; uropods absent.

Subtidal–slope, parasitising calcinid, diogenid, pagurid and pylochelid hermit crabs and lithodid king crabs. Temperate Northern Atlantic, Tropical Atlantic, Temperate South America, Central Indo-Pacific, Temperate Northern Pacific. 11 species (Golovan et al., 2024; Williams et al., 2019).

Galathocrypta Román-Contreras and Soto, 2002

Diagnosis. **Female** elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 1 long smooth lobe on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with oblong posterior lobe, smaller than anterior lobe; internal ridge smooth. Coxal plates, dorsolateral bosses and tergal projections present. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates reduced; 5 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** approximately 2 times as long as wide, head narrower than pereon, pereomeres narrower posteriorly. Eyes absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of sessile pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Slope, parasitising munidopsid squat lobsters. Tropical Atlantic. 1 species (Román-Contreras and Soto, 2002).

Gigantione Kossmann, 1881

Diagnosis. **Female** ovate, body slightly distorted, symmetrical or asymmetrical; head bilobed or not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp. Barbula with 1 smooth lobe on each side, median region smooth or digitate. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, smaller than or subequal to anterior lobe; internal ridge smooth or digitate. Coxal plates present, narrow and extended, dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates slender and tapering; 5 pairs of smooth or digitate biramous pleopods with smooth or digitate margins; uropods smooth, biramous or uniramous but distally bifid, with smooth margins. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres narrower or not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of uniramous or biramous pleopods; posterolateral corners of pleomere 6 rounded; uropods distally rounded or weakly bifid.

Intertidal–slope, parasitising carpiliid, dromiid, euryplacid, goneplacid, pilumnid and xanthid crabs and axiid shrimps. Temperate Northern Atlantic, Central and Eastern Indo-Pacific, Temperate Australasia, Temperate Northern Pacific. 18 species (An et al., 2016a).

Goleathopseudione Román-Contreras, 2008

Diagnosis. **Female** elongate, body slightly distorted; head bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated palp. Barbula with 3 smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with subquadrate posterior lobe, larger than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 5 pairs of smooth biramous slender pleopods with smooth margins; uropods smooth, uniramous, slender with smooth margins. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes absent. Pereopods subequal. Midventral tubercles present. Pleon of 6 pleomeres; 5 pairs of sessile pleopods; posterolateral corners of pleomere 6 extended; uropods absent.

Abyssal, parasitising munidopsid squat lobsters. Temperate Northern Pacific. 1 species (Román-Contreras, 2008).

Gyge Cornalia and Panceri, 1861

Diagnosis. **Female** ovate to subquadrate, body slightly distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped without palp. Barbula with 2 short digitate lobes on each side, median region digitate. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, larger than anterior lobe; internal ridge digitate. Coxal plates present, dorsolateral bosses and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates absent; 3 or 4 pairs of smooth uniramous or biramous pleopods with tuberculate margins; uniramous uropods smooth with smooth margins. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of sessile pleopods or pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Intertidal–subtidal, parasitising upogebiid shrimps. Temperate Northern Atlantic, Western and Central Indo-Pacific, Temperate Australasia, Temperate Northern Pacific. 6 species (An et al., 2009; Boyko and Williams, 2025; Markham, 2004).

Ionella Bonnier, 1900

Diagnosis. **Female** ovate, body weakly distorted; head weakly bilobed or not bilobed; frontal lamina absent. Eyes present or absent. Maxilliped without palp, densely lined on margin by short setae. Barbula with 2 short, notched lobes on each side,

median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, smaller than anterior lobe; internal ridge digitate. Coxal plates present, dorsolateral bosses and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates absent; 5 pairs of digitate biramous pleopods; uropods uniramous, slender, smooth. **Male** approximately 3–4 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; pleopods uniramous, biramous or mixed; posterolateral corners of pleomere 6 rounded; uropods uniramous.

Intertidal–shelf, parasitising callianassid shrimps. Central and Eastern Indo-Pacific, Temperate Northern Pacific, Temperate South America. 5 species (Markham, 1994; Romero-Rodríquez and Álvarez, 2025).

Kolourione Markham, 1978

Diagnosis. **Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 very short smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, smaller than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes present. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Pleomeres 1 and 2 with lateral plates; 4 pairs of smooth biramous pleopods; uropods absent. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes absent. Pereopods subequal. Midventral tubercles absent. Pleomeres fused; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal–shelf, parasitising porcellanid crabs. Tropical Atlantic. 1 species (Markham, 1978a).

Munidion Hansen, 1897

Diagnosis. **Female** elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp. Barbula with 2 long smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing acute triangular projection, smaller than anterior lobe; internal ridge digitate. Coxal plates, dorsolateral bosses, and tergal projections present. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates tuberculate; 5 pairs of smooth biramous pleopods; uropods biramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles present. Pleomeres fused, often with lateral indications of segmentation; pleopods absent; posterolateral corners of pleomere slightly rounded; uropods absent.

Shelf–slope, parasitising munidid squat lobsters. Tropical Atlantic, Central Indo-Pacific, Tropical Eastern Pacific, Temperate Australasia, Temperate Northern Pacific. 9 species (Katsuragawa et al., 2025; Markham, 1975b ; Williams et al., 2026).

Nikione Kensley, 1974

Diagnosis. **Female** ovate, body distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp. Barbula with 3 long smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge smooth. Coxal plates, dorsolateral bosses, and tergal projections present. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates tuberculate; 5 pairs of tuberculate biramous pleopods; uropods biramous, tuberculate. **Male** approximately 3–4 times as long as wide, head as wide as pereon, pereomeres not narrower posteriorly. Eyes absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; pleopods absent; posterolateral corners of pleomere 6 slightly extended; uropods absent.

Shelf, parasitising processid shrimps. Temperate Southern Africa. 1 species (Kensley, 1974).

Orbimorphus Richardson, 1910

Diagnosis. **Female** elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 long smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distal projection, subequal to anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates small; 4 pairs of smooth biramous pleopods; uropods biramous, smooth. **Male** approximately 3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 1 pleomere with lateral indication of segmentation; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Intertidal, parasitising porcellanid crabs. Tropical Eastern Pacific. 1 species (Bourdon, 1976).

Orthione Markham, 1988

Diagnosis. **Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp. Barbula with 1 long smooth lobe on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, subequal to anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 5 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of uniramous sessile pleopods; posterolateral corners of pleomere 6 rounded; uropods uniramous.

Intertidal, parasitising upogebiid shrimps. Temperate

Northern Atlantic, Temperate Northern Pacific, Temperate South America. 3 species (Markham, 2004).

Ovoionella Boyko, 2004

Diagnosis. **Female** elongate-ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with non-articulated palp. Barbula with 2 short smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distal projection, smaller than anterior lobe; internal ridge digitate. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present; 5 pairs of smooth biramous pleopods; uropods absent. **Male** approximately 1–2 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles present or absent. Pleon of 4 pleomeres; 3 pairs of uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Shelf, parasitising munidid squat lobsters. Central Indo-Pacific, Temperate Northern Pacific. 1 species (Boyko, 2004).

Pagurion Shiino, 1933

Diagnosis. **Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated palp. Barbula with 1 long tuberculate lobe on each side, median region tuberculate. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, smaller than anterior lobe; internal ridge digitate. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 5 pairs of tuberculate biramous pleopods; uropods biramous, tuberculate. **Male** approximately 3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 6 pleomeres; 5 pairs of sessile or elongate pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Intertidal–slope, parasitising calcinid hermit crabs. Central Indo-Pacific, Temperate Northern Pacific. 1 species (Williams et al., 2019).

Paguristione An, Zhao and Markham, 2016

Diagnosis. **Female** elongate, body not distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated palp. Barbula with 2 long smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge digitate. Coxal plates present, dorsolateral bosses and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Pleomeres 1–3 with lateral plates; 5 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres narrower posteriorly. Eyes absent. Pereopods 3–5 larger than other pairs. Midventral tubercles absent. Pleon of 6 pleomeres; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Shelf, parasitising diogenid hermit crabs. Temperate Northern Pacific. 1 species (An et al., 2016b).

Paranikione An, Boyko and Li, 2015

Diagnosis. **Female** elongate-ovate, body distorted; head bilobed or not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 short smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, larger than anterior lobe; internal ridge smooth. Coxal plates, dorsolateral bosses, and tergal projections present. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present; 5 pairs of tuberculate biramous pleopods; uropods biramous, tuberculate. **Male** approximately 3–4 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of tubercular pleopods; posterolateral corners of pleomere 6 extended into lobes; uropods absent.

Shelf, parasitising processid shrimps. Central Indo-Pacific, Temperate Northern Pacific. 2 species (An et al., 2015).

Parapagurion Shiino, 1933

Diagnosis. **Female** elongate, body weakly or strongly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp or without palp. Barbula with 1 short or long smooth lobe on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing distal triangular projection, subequal to anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present; 5 pairs of smooth biramous pleopods; uropods uniramous or biramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of sessile pleopods; posterolateral corners of pleomere 6 rounded or weakly extended; uropods absent.

Subtidal–slope, parasitising calcined, diogenid, and parapagurid hermit crabs. Tropical Atlantic, Temperate Northern Pacific. 2 species (Markham 1978b).

Parasymmetrione An, Markham and Yu, 2010

Diagnosis. **Female** elongate, body extremely distorted (~120°); head not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp. Barbula with 2 smooth lobes and 1 nub on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with rounded posterior lobe bearing triangular distal projection, smaller than or subequal to anterior lobe; internal ridge digitate. Coxal plates and tergal projections

present, dorsolateral bosses absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present; pleopods, 5 pairs tuberculate pleopods, 4 pairs biramous and 1 pair uniramous; uropods tuberculate, uniramous. **Male** approximately 3–4 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopod 1 larger than others. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of flap-like pleopods; posterolateral corners of pleomere 6 rounded; uropods present.

Intertidal, parasitising diogenid hermit crabs. Central Indo-Pacific. 1 species (An et al., 2010).

Parione Richardson, 1910

Diagnosis. **Female** elongate, body slightly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with non-articulated palp. Barbula with 1 smooth lobe on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with rounded posterior lobe bearing triangular distal projection or triangular lobe, smaller than or subequal to anterior lobe; internal ridge smooth. Coxal plates present, dorsolateral bosses present or absent, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates short; 5 pairs of smooth biramous slender pleopods with smooth margins; uropods smooth, uniramous, slender with smooth margins. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles present. Pleon of 5 or 6 pleomeres; 4 or 5 pairs of sessile pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal–slope, parasitising munidid squat lobsters and porcellanid crabs. Temperate South America, Central Indo-Pacific, Temperate Australasia, Temperate Northern Pacific. 5 species (Bourdon, 1976).

Parionella Nierstrasz and Brender à Brandis, 1923

Diagnosis. **Female** elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp. Barbula with 2 short smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, smaller than anterior lobe; internal ridge smooth. Coxal plates present, dorsolateral bosses present or absent, tergal projections present or absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates short; 4 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes absent. Pereopods 1–3 larger than others. Midventral tubercles present. Pleon of 5 pleomeres, medially separated or fused; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal–slope, parasitising eumunidid and munidid squat lobsters and porcellanid crabs. Central Indo-Pacific, Temperate Northern Pacific. 4 species (Bourdon, 1972b).

Parionina Nierstrasz and Brender à Brandis, 1929

Diagnosis. **Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped not described. Barbula not described. Oostegites not described. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present or absent; 5 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes absent. Pereopods not described. Midventral tubercles not described. Pleon of 4 pleomeres; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Slope, parasitising galatheid squat lobsters. Central Indo-Pacific, Temperate Northern Pacific. 2 species (Nierstrasz and Brender à Brandis, 1931).

Parioninella Nierstrasz and Brender à Brandis, 1930

Diagnosis. **Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped without palp. Barbula with 1 tubercle on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, smaller than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates reduced; 5 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** approximately 2 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of uniramous pleopods; posterolateral corners of pleomere 6 rounded or slightly extended; uropods absent.

Intertidal–subtidal, parasitising porcellanid crabs. Central Indo-Pacific. 3 species (An et al., 2020).

Pauperella Nierstrasz and Brender à Brandis, 1929

Diagnosis. **Female** ovate, body weakly distorted; head not bilobed; frontal lamina absent. Eyes present. Maxilliped not described. Barbula not described. Oostegites not described. Coxal plates present, dorsolateral bosses and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon, first 2 pleomeres distinct, others fused with pleotelson. Pleomeres 1 and 2 with lateral plates; 3 pairs of smooth biramous pleopods; uropods absent. **Male** approximately 3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods not described. Midventral tubercles not described. Pleon of 6 pleomeres; pleopods not described; posterolateral corners of pleomere 6 rounded; uropods absent.

Intertidal, parasitising upogebiid shrimps. Central Indo-Pacific. 1 species (Nierstrasz and Brender à Brandis, 1929).

***Pleonobopyrus* Saito and Moritaki, 2020**

Diagnosis. **Female** elongate, body not distorted; head not bilobed; frontal lamina absent. Eyes absent. Maxilliped without palp. Barbula with 2 short smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, smaller than anterior lobe; internal ridge smooth. Dorsolateral bosses present, coxal plates and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present; 4 pairs of smooth uniramous pleopods; uropods uniramous, smooth. **Male** unknown.

Slope, parasitising crangonid shrimps. Temperate Northern Pacific. 1 species (Saito and Moritaki, 2020).

***Pleurocrypta* Hesse, 1865**

Diagnosis. **Female** elongate or ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped with setose non-articulated palp or palp absent. Barbula with 2 long or short smooth or tuberculate lobes on each side, median region smooth or tuberculate. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular projection, subequal to anterior lobe; internal ridge tuberculate. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates small or large; 5 pairs of smooth or tuberculate biramous pleopods; uropods uniramous or biramous, smooth or tuberculate. **Male** approximately 2–4 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods 1–3 larger than others. Midventral tubercles absent. Pleon of 1–6 partly to entirely fused pleomeres (often appearing as single pleomeres with lateral undulations); pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Intertidal–shelf, parasitising galatheid and munidid squat lobsters and porcellanid crabs. Temperate Northern Atlantic, Tropical Atlantic, Central Indo-Pacific. 12 species (Markham, 1988).

***Pontobopyrus* Markham, 1979**

Diagnosis. **Female** elongate, body distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated palp. Barbula with 2 short smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge smooth. Coxal plates and tergal projections present, dorsolateral bosses absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 5 pairs of smooth uniramous pleopods; uropods uniramous, smooth. **Male** unknown.

Abyssal, parasitising crangonid shrimps. Temperate Northern Atlantic. 1 species (Markham, 1979).

***Progebiophilus* Codreanu and Codreanu, 1963**

Diagnosis. **Female** ovate or elongate, body not distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped with setose articulated or non-articulated palp or palp absent. Barbula with 1–3 smooth or digitate lobes on each side, median region smooth or digitate. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distolateral projection, subequal to anterior lobe; internal ridge digitate. Coxal plates present, dorsolateral bosses present or absent, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present or absent; 5 pairs of smooth or tuberculate biramous pleopods; uropods uniramous or biramous, smooth or tuberculate. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles present or absent. Pleon of 6 pleomeres; 5 pairs of tubercular uniramous pleopods present; posterolateral corners of pleomere 6 rounded or extended; uropods present or absent.

Intertidal–subtidal, parasitising upogebiid shrimps. Temperate Northern Atlantic, Tropical Atlantic, Temperate Southern Africa, Western and Central Indo-Pacific, Temperate Australasia, Temperate Northern Pacific. 13 species (An et al., 2009; Markham, 2005).

***Propseudione* Shiino, 1933**

Diagnosis. **Female** elongate, body distorted; head not bilobed; frontal lamina present. Eyes present. Maxilliped with setose non-articulated palp. Barbula with 1 digitate lobe and 1 smooth lobe on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distolateral projection, larger than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present but not well developed; 5 pairs of large smooth biramous pleopods with smooth margins; uropods small, smooth, uniramous with smooth margins. **Male** approximately 3–4 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of tubercular biramous pleopods; posterolateral corners of pleomere 6 slightly extended; uropods absent.

Subtidal, parasitising calcinid hermit crabs. Temperate Northern Pacific. 1 species (Shiino, 1933).

Pseudione* Kossmann, 1881 *sensu stricto

Diagnosis. **Female** elongate, body not distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated or non-articulated palp adjacent to setose lobe. Barbula with 1 smooth lobe and 1 smooth nub present or absent on each side, median region smooth or digitate. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distolateral projection, smaller than anterior lobe; internal ridge smooth or digitate. Coxal plates, dorsolateral bosses and tergal projections present. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present, large; 5 pairs of

large smooth or tuberculate biramous pleopods with smooth or crenulate margins; uropods smooth or tuberculate, uniramous or biramous, with smooth margins. **Male** approximately 2–5 times as long as wide, head as wide as pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of sessile uniramous pleopods present or absent; posterolateral corners of pleomere 6 slightly extended; uropods absent.

Intertidal–slope, parasitising axiid and callianassid shrimps and nephropid lobsters. Temperate Northern Atlantic, Tropical Atlantic, Central Indo-Pacific, Temperate Australasia, Temperate Northern Pacific. 9 species (Boyko et al., 2017).

Pseudione Kossmann, 1881 *sensu lato*

Diagnosis. **Female** elongate, body weakly to moderately distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped with setose articulated or non-articulated palp or palp absent. Barbula with 2 smooth or digitate lobes on each side, median region smooth or digitate. 5 pairs of oostegites; oostegite 1 posterior lobe ovate or ovate with triangular posterior distal projection, subequal to or smaller than anterior lobe; internal ridge digitate. Coxal plates present or absent, dorsolateral bosses present, tergal projections present or absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present, small or large, smooth or tuberculate; 5 pairs of smooth or tuberculate pleopods with smooth or crenulate margins; uropods uniramous, smooth or tuberculate, with smooth or crenulate margins. **Male** approximately 3–4 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles present or absent. Pleon of 6 pleomeres; 4 or 5 pairs of sessile or raised uniramous pleopods; posterolateral corners of pleomere 6 rounded or slightly to moderately extended; uropods absent.

Subtidal–slope, parasitising galatheid, munidid and munidopsid squat lobsters. Temperate Northern Atlantic, Tropical Atlantic, Temperate Southern Africa, Western and Central Indo-Pacific, Temperate Australasia, Temperate Northern Pacific, Temperate South America. 18 species (Boyko et al., 2017 ; Williams et al., 2026).

Pseudionella Shiino, 1949

Diagnosis. **Female** elongate, body distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped with setose non-articulated palp. Barbula with 2 short digitate lobes and 1 short smooth lobe on each side, median region digitate. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates not well developed; 5 pairs of smooth pleopods with smooth margins, 2 biramous and 3 uniramous; uropods smooth, uniramous, with smooth margins. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres narrower posteriorly. Eyes present. Pereopods subequal or pereopods 1–3 larger. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of tubercular or flap-like uniramous pleopods; posterolateral corners of pleomere 6 slightly extended; uropods absent.

Intertidal–shelf, parasitising calcinid and pagurid hermit crabs. Temperate Northern Atlantic, Tropical Atlantic, Western, Eastern and Central Indo-Pacific, Temperate Northern Pacific, Temperate Southern Africa. 6 species (An et al., 2013; Boyko and Williams, 2001; Brandt et al., 2024).

Rhopalione Pérez, 1920

Diagnosis. **Female** ovate, body not distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with non-setose non-articulated palp or without palp. Barbula with 1 long and 1 short smooth lobe or 1 long lobe on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing small triangular distal projection, subequal to anterior lobe; internal ridge with few small digitations. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates smooth, tubular; 5 pairs of smooth tubular biramous pleopods; uropods uniramous, smooth, tubular. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; uniramous sessile pleopods; posterolateral corners of pleomere 6 rounded or extended; uropods absent.

Intertidal–subtidal, parasitising pinnotherid crabs. Western and Central Indo-Pacific, Temperate Australasia. 7 species (Ahyong and Boyko, 2019; Boyko and Williams, 2024).

Robinione Boyko, Williams and Shields, 2017

Diagnosis. **Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated palp. Barbula with 2 smooth or digitate lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular projection, smaller than anterior lobe; internal ridge digitate. Coxal plates and tergal projections present, dorsolateral bosses absent. Pereopods elongate; without propodal sockets. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates greatly enlarged, tuberculate; 5 pairs of tuberculate biramous pleopods; uropods uniramous, tuberculate. **Male** approximately 3–4 times as long as wide, head narrower than or as wide as pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 5 or 6 pleomeres; 5 pairs of uniramous pleopods; posterolateral corners of pleomere 6 extended; uropods absent.

Intertidal, parasitising callianassid and callichirid shrimps. Temperate Northern Atlantic, Temperate South America. 2 species (Boyko et al., 2017).

Shiinoella Bourdon, 1972

Diagnosis. **Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with

setose non-articulated palp. Barbula with 1 long and 1 short digitate lobe on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, smaller than anterior lobe; internal ridge with few small tubercles. Coxal plates and dorsolateral bosses present, tergal projections absent. Pereopods elongate; without propodal sockets. Mediodorsal lobes absent. Pleon narrower than pereon. Lateral plates smooth; 2 pairs of smooth biramous pleopods, 3 pairs of smooth uniramous pleopods; uropods uniramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes absent. Pereopods subequal, elongate. Midventral tubercles absent. Pleon of 6 pleomeres with posterior 3 nearly fused; pleopods absent; posterolateral corners of pleomere 6 slightly extended; uropods absent.

Slope, parasitising alpheid shrimps. Western Indo-Pacific. 1 species (Bourdon, 1972a).

Spathione Boyko and van der Meij, 2018

Diagnosis. **Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes present. Maxilliped without palp. Barbula with 3 short smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, smaller than anterior lobe; internal ridge smooth. Coxal plates and tergal projections present, dorsolateral bosses absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates smooth; 4 pairs of smooth tubular biramous pleopods, 1 pair of smooth uniramous pleopods; uropods uniramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 5 pleomeres; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal, parasitising cryptochirid crabs. Central Indo-Pacific. 1 species (Boyko and van der Meij, 2018).

Upogebione Markham, 1985

Diagnosis. **Female** ovate, body moderately distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with articulated palp. Barbula with 2 short smooth lobes on each side, median region digitate. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge digitate. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present; 5 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present or absent. Pleon of 5 pleomeres; 4 pairs of uniramous sessile pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal, parasitising upogebiid shrimps. Tropical Atlantic, Central Indo-Pacific. 4 species (An et al., 2009).

Upogebiophilus Nobili, 1906

Diagnosis. **Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes present. Maxilliped without palp. Barbula with 3 or 4 short smooth lobes on each side, median region not described. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing small triangular distal projection, subequal to anterior lobe; internal ridge smooth. Coxal plates present, dorsolateral bosses and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates absent; 5 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** size not described, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 5 pleomeres; 4 pairs of uniramous sessile pleopods; posterolateral corners of pleomere 6 rounded; uropods uniramous.

Subtidal, parasitising upogebiid shrimps. Western Indo-Pacific. 1 species (Nobili, 1906).

Zeaione Boyko and Williams *in* Andrade et al., 2025

Diagnosis. **Female** elongate, body weakly distorted; head weakly bilobed; frontal lamina present. Eyes absent. Maxilliped with articulated non-segmented palp. Barbula with 3 short smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, smaller than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not markedly narrower than pereon; dorsolateral margins of pleomeres 1–6 with numerous, irregular, mostly semi-spherical protuberances. Lateral plates broad, lamellar, with scalloped posterior margins; 5 pairs of smooth biramous pleopods with bilobed endopods; uropods biramous, smooth. **Male** approximately 3 times as long as wide, head narrower than pereon, pereomeres slightly narrower posteriorly. Eyes present. Maxillipeds segmented. Pereopods subequal. Midventral tubercles absent. Pleon of six pleomeres; 5 pairs of uniramous sessile pleopods; posterolateral corners of pleomere 6 extended; uropods absent.

Subtidal, parasitising eucalliacid shrimps. Temperate Australasia. 1 species (Andrade et al., 2025).

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Family Entoniscidae Kossmann, 1881

Figure 6.23

Entoniscidae is a relatively small group (45 species) of endoparasites that reside in the visceral cavities of anomuran, brachyuran and shrimp hosts. Characters of females, males, epicaridium larvae and cryptoniscus larvae are included in the diagnoses when known, because all these life history stages exhibit informative traits. Entoniscid females are highly modified, with bulbous heads positioned in the host's gonad or hepatopancreas, reduced or absent pereopods, and a variable number of oostegites that form the brood chamber. Presently, three subfamilies are recognised: Diogenioninae (2 species), Entoniscinae (8 species) and Entioninae (35 species), differing in morphology of the female marsupium, oostegites, and pleural lamellae and the pereopod structure of males. Most mature entoniscid females exhibit one or more projections containing ovarian tissue on the pereomeres called ovarian processes; these are located on five possible positions of the pereon: anterior dorsolateral, dorsal, lateral, posterolateral and ventral. Dorsal ovarian processes are found only in *Entione* and *Cancrion* (Adkison, 1990). However, dorsal ovarian processes could easily be confused with anterior dorsolateral ovarian processes, especially considering that it is likely that all ovarian processes vary in size and/or shape according to the development of the female. In contrast, the presence of unpaired ventral ovarian processes appears to be a more consistent feature. Males exhibit a less modified isopod body plan with distinct segmentation, but those of all species lack pereopods on pereomere 7 or have them highly reduced. Some males possess medioventral spines (= hyposphenians or midventral hooks) on posterior pereomeres or anterior pleomeres.

Epicaridium larvae of entoniscids exhibit a modified pereopod 6; in some genera this includes an elongate pereopod 6 with unique propodal extensions. The life cycle has not been completely worked out for any entoniscid, but a copepod host is assumed to be involved in most cases (see life cycle in McDermott et al., 2019). One entoniscid species (*Entionella fluviatilis* Miyashita, 1941) is known to bypass the copepod intermediate host; females of this species brood their larvae until they reach the cryptoniscus stage, which are then released and find new definitive hosts (Miyashita, 1941). This the only documented case of such an abbreviated life cycle in epicarideans. Cryptoniscus larvae typically have antennae with seven segments (four peduncular and three flagellar) but in at least one case the flagellar segments are reduced (Boyko and Williams, 2015). Much investigation remains to be done on the diversity of the group, with multiple undescribed species and cryptic species likely in all subfamilies (e.g. Adkison, 1990; DeTorre et al., 2023). Note that the diagnosis of *Entionella* is based only on the type species (*E. fluviatilis*), because the other species in this genus differ markedly in the morphology of pereopod 6 of the epicaridium larvae. The key is based on male and female characters (modified from DeTorre et al., 2023).

Diagnosis (modified from Adkison, 1990). **Female** body symmetrical, body regions distinct, segments often indistinct. Head bulbous, rounded, with or without dorsal groove; antennae reduced to 2 unsegmented ridges on anterior margin of head. Maxilliped not lamellar, development variable, in mature specimens well-developed with 3 lobes present, exopod largest, other lobes reduced. Oral cone present, reduced in size. Eyes absent. Pereopods with reduced segmentation or absent. Ovarian processes often present in anterior dorsolateral, dorsal, lateral, posterolateral and ventral locations. Brood pouch formed by up to 7 oostegites or by oostegites and host-derived sheath. Oostegite 1 often greatly developed with up to 3 lobes (ascendant, transverse and recurrent). Pleon of 6 segments. Pleural lamellae (= lamina) development variable from absent to simple lobes to complexly folded. Pleopods uniramous, up to 5 pairs. Uropods present or absent. **Male** head often fused with pereomere 1. Antennula and antenna present or reduced to pair of antennula in form of unsegmented lobes with tuft of setae. Pereopods of 6 pairs, with or without distinct segments. Pereomere 7 pereopods reduced to small protuberances or

absent. Medioventral spine present or absent on medioventral surface of posterior pereomeres or anterior pleomeres. Pleon with 6 segments, without pleopods. Posterior margin of pleomere 6 entire or bifid. **Epicaridium larva** (fig. 6.23k, n) with pereopod 6 similar in size (e.g., fig. 6.23l) to preceding pereopods or dissimilar in size (some greatly elongate, e.g., fig. 6.23o, p) and form (carpus and propodus typically fused, reduced dactylus, sometimes with processes). Pleopods of 5 uniramous or biramous pairs. Uropods biramous, peduncle shorter than rami. **Cryptoniscus larva** antenna typically of 7 segments – 4 peduncular and 3 flagellar (rarely 1 flagellar segment). Pereopod 7 longer, more slender than anterior pereopods. Pleopods of 5 pairs; 1–4 uniramous, 5 uniramous or biramous.

Key to genera of Entoniscidae

1. Marsupium of female formed by close adhesion of oostegites to host membrane; males with segmented pereopods (fig. 6.23f) 2
– Oostegites free, not adhering to host membrane (fig. 6.23a), pleural lamellae absent, females without pereopods, males with unsegmented pereopods (fig. 6.23b) ..... Entoniscinae ... 3
2. Parasitic in hermit crabs; females without pleural lamellae, female with heart in pleomere 1 (fig. 6.23e) ..... Diogenioninae ... 18
– Parasitic in other decapods; females with well-developed pleural lamellae, female with heart in pleomere 3 (fig. 6.23g) ..... Entioninae ... 6
3. Parasitic in hermit crabs; oostegite 1 of female largest with ascendant and recurrent lobes, oostegites 2–5 at posterior end of pereon (fig. 6.23c); male with antennae not projecting beyond margin of head (fig. 6.23d) ..... *Paguritherium*
– Parasitic in other decapods 4
4. Female without maxilliped (fig. 6.23a); terminal segment of male bifurcated (fig. 6.23b) ..... *Entoniscoides*
– Female with maxilliped (fig. 6.23h); pleotelson of male undivided 5
5. Female with more than 2 pairs of oostegites; unpaired dorsal ovarian processes ..... *Entoniscus*
– Female with oostegite 1 absent; only 2 pairs of oostegites forming brood pouch ..... *Synalpheion*
6. Males with 5 pairs of pereopods (fig. 6.23j); pereon of female with pairs of lateral ovarian processes and without unpaired ventral or dorsal processes (fig. 6.23g–i) ..... *Allocancrion*
– Males with 6 pairs of pereopods (fig. 6.23m) 7
7. Pereon of female without ovarian processes 8
– Pereon of female with at least 1 ovarian process 9
8. Female with 2 transverse lobes on oostegite 1 and fused oostegites 2–5; males with pair of lateral expansions on each of first 2 pleomeres (fig. 6.23m) ..... *Pinnixion*
– Female with 1 transverse lobe on oostegite 1 and separate oostegites 2–5; males with pair of expansions only on pleomere 1 ..... *Entionella*
9. Mature female with dorsal ovarian processes of variable number, rarely absent 10
– Mature female without dorsal ovarian processes 12
10. Mature female with 2 ventral ovarian processes ..... *Entione*
– Mature female without ventral ovarian processes 11
11. Epicaridium larvae with elongate pereopod 6 (long merus and carpus) (fig. 6.23p) ..... *Cancrion*
– Epicaridium larvae with short pereopod 6 (short merus and carpus) (compare to fig. 6.23l) ..... *Cryptocancrion*
12. Female with dorsolateral ovarian processes 13
– Female without dorsolateral ovarian processes 15

13. Pereon of female with 1 unpaired dorsolateral ovarian process ..... *Micippion*
– Pereon of female with paired dorsolateral ovarian processes 14
14. Female with 1 pair of dorsolateral ovarian processes ..... *Portunion*
– Female with 2 pairs of dorsolateral ovarian processes ..... *Priapion*
15. Female with 1 unpaired ventral ovarian process ..... *Xanthion*
– Female with 2 unpaired ventral ovarian processes 16
16. Oostegite 1 of female without transverse lamellae (compare to fig. 6.23i) ..... *Pinnotherion*
– Oostegite 1 of female with transverse lamellae 17
17. Posterior oostegites of female reduced, not enclosing recurrent lamella of oostegite 1 (compare to fig. 6.23i) ..... *Tiarinion*
– Posterior oostegites of female enclosing recurrent lamella of oostegite 1 ..... *Achelion*
18. Female with marsupium formed by oostegites 1–4, pleopods absent ..... *Diogenion*
– Female with marsupium formed by oostegites 1–7, pleopods present ..... *Paradiogenion*

Subfamily Diogenioninae DeTorre, Williams and Boyko, 2023

Diogenion Codreanu, Codreanu and Pike, 1960

Diagnosis. **Female** head with dorsal groove; antennula broad, antenna reduced; maxilliped small. Oostegites 1–7 present; oostegite 1 without ascendant lobe, with strongly developed recurrent lobe lined with pleat-like folds; brood pouch formed by overlapping of oostegites 1–4, oostegites 5–7 reduced. Pereopods 1–7 present. Pleon slender, heart in pleomere 1; pleural lamellae, pleopods and uropods absent. **Male** with antennula and antenna, antennula projecting beyond margin of head; head not fused with pereomere 1. Pereopods 1–6 present, multisegmented; pereopod 7 absent or greatly reduced. Pleon of 5 pleomeres plus pleotelson, medioventral spines absent, pleotelson bifurcated, uropods absent. **Epicaridium larva** with pereopods 1–6 isomorphic; pereopod 7 absent; pereopod 6 subequal in length to pereopod 5. Pleon with 5 pairs of biramous pleopods. Telson tapering to point. Uropods with endopod slightly longer than exopod. **Cryptoniscus larva** unknown.

Subtidal, parasitising diogenid hermit crabs Western Indo-Pacific. 1 species (Codreanu et al., 1960; DeTorre et al., 2023).

Paradiogenion Shinoda and Shimomura *in* Shinoda, Takiyama, Fujita, Nakano and Shimomura, 2026

Diagnosis. Female head with dorsal groove; antennula broad, antenna reduced; maxilliped small. Oostegites 1–7 present; oostegite 1 without ascendant lobe, with strongly developed recurrent lobe lined with pleat-like folds; brood pouch formed by overlapping of oostegites 1–7. Pereopods 1–7 present. Pleon slender, heart in pleomere 1; 4 uniramous pleopods, pleural lamellae and uropods absent. **Male** with antennula and antenna, antennula projecting beyond margin of head; head not fused with pereomere 1. Pereopods 1–6 present, multisegmented; pereopod 7 absent. Pleon of 5 pleomeres plus pleotelson, medioventral spines absent, pleotelson distally bifurcated, uropods absent. **Epicaridium larva** with pereopods 1–6 isomorphic; pereopod 7 absent; pereopod 6 subequal in length to pereopod 5. Pleon with 5 pairs of biramous pleopods. Telson tapering to point. Uropods with endopod slightly longer than exopod. **Cryptoniscus larva** unknown.

Subtidal, parasitising diogenid hermit crabs Temperate Northern Pacific. 1 species (Shinoda et al., 2026).

Subfamily Entoniscinae Kossmann, 1881

Entoniscoides Miyashita, 1940

Diagnosis. **Female** head with dorsal groove; maxilliped present. Pereon without ovarian processes; pereopods absent; brood pouch formed by 5 pairs of oostegites, oostegites deeply divided or notched; oostegite 1 forming part of brood pouch. Heart in pleomere 1; 5 pairs of uniramous pleopods; posterior margin of pleomere 6 entire; uropods absent. **Male** head fused with pereomere 1; antenna elongate, projecting well beyond margin of head; pereopods unsegmented; medioventral spines and pleopods absent; posterior margin of pleomere 6 deeply notched, uropods present. **Epicaridium larva** not present as free-swimming stage; larvae released from brood chamber as cryptoniscus larva; pereopod 6 subequal in length to pereopod 5. **Cryptoniscus larva** with eyes present; antennula with basal segment not enlarged into plate, without teeth; antenna of 5 segments: 4 peduncular and 1 flagellar. Pereonal coxal plates without teeth. Pleon with 5 pairs of uniramous pleopods; uropods biramous.

Intertidal–subtidal, parasitising xanthid crabs. Temperate Northern Pacific. 1 species (Miyashita, 1940).

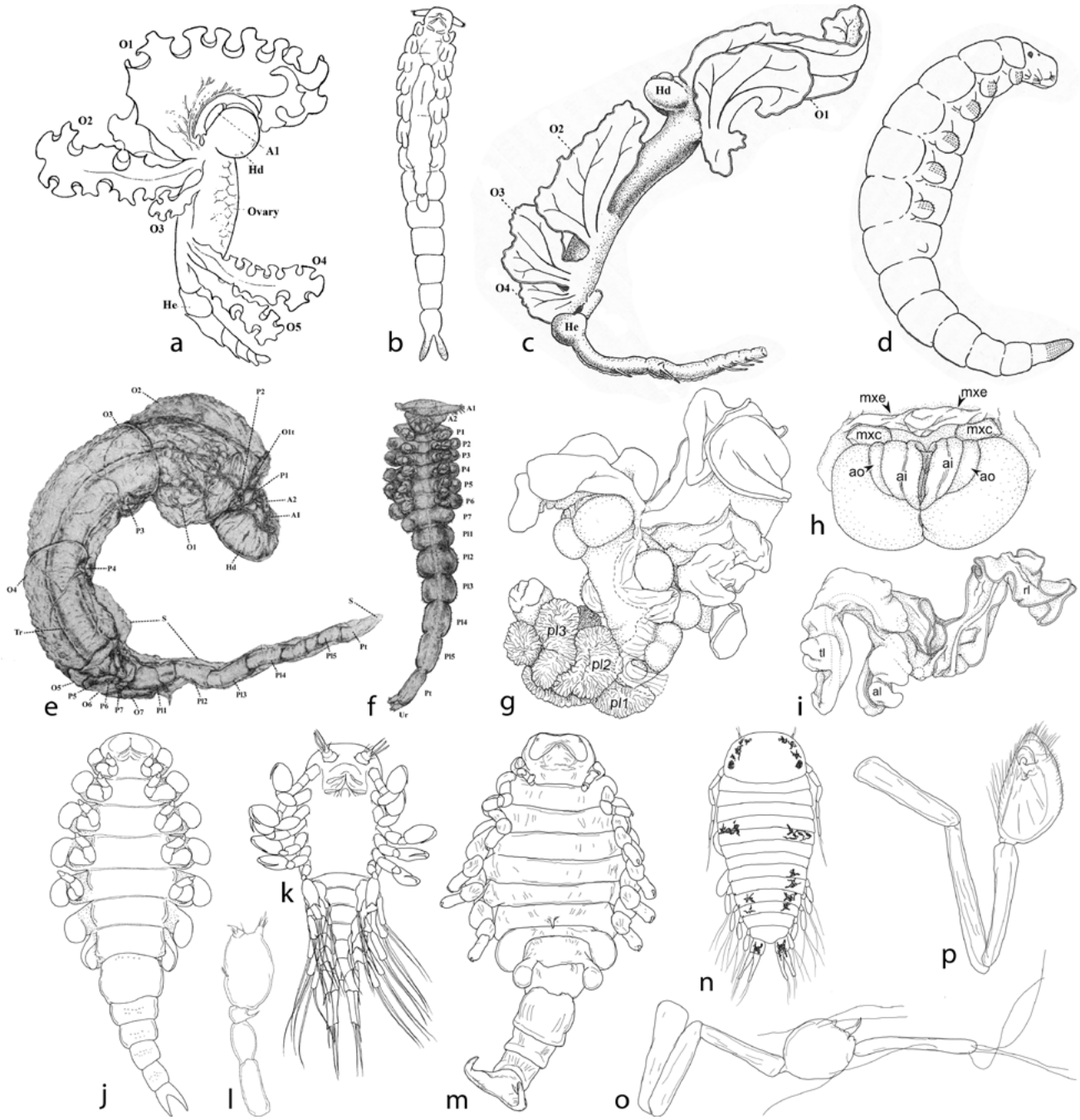


Figure 6.23. Entoniscidae (a–d, Entoniscinae; e, f, Diogenioninae; g–p, Entioninae). *Entoniscoides okadai* Miyashita, 1940: a, female lateral view; b, male ventral view. *Paguritherium alatum* Reinhard, 1945: c, female lateral view; d, male lateral view. *Diogenion vermifactus* Codreanu, Codreanu and Pike, 1960: e, female lateral view; f, male ventral view. *Allocancrion yunnu* Uyeno and Boyko, 2020: g, female lateral view; h, head; i, oostegite 1; j, male ventral view; k, epicaridium larva ventral view; l, pereopod 6 of epicaridium larva. *Pinnixion sexdecennia* McDermott, Williams and Boyko, 2019: m, male ventral view; n, epicaridium larva dorsal view; o, pereopod 6 of epicaridium larva. *Cancrion carolinus* Pearse and Walker, 1939: p, pereopod 6 of epicaridium larva. Abbreviations: al, ascendant lobe; A1, antennula; A2, antenna; Hd, head; He, heart; mxc, maxilliped coxopod; mxe, maxilliped exopod; O1–O7, oostegites 1–7; O1t, transverse plate of oostegite 1; P1–P7, pereopods 1–7; Pl1–5, pleopods 1–5; Pt, pleotelson; rl, recurrent lobe; S, host sheath; tl, transverse lobe; Tr, ovarian thoracic trunk; Ur, uropods.

Entoniscus Müller, 1862

Diagnosis. **Female** head with strong dorsal groove; maxilliped absent; pereopods present; number of oostegites variable; ovarian processes unpaired, dorsal, number variable; heart in pleomere 1; number of pleopods variable; posterior margin of pleomere 6 variable; uropods absent. **Male** antenna projecting beyond margin of head; pereopods unsegmented; medioventral spines and pleopods absent; posterior margin of pleomere 6 variable; uropods absent. **Epicaridium larva** with pereopod 6 subequal in length to pereopod 5, dactylus reduced. Pleopods 1–4 with medial angle of peduncle bearing 1 seta, exopod bearing 3 long setae; pleopod 5 smaller than pleopod 4, medial angle peduncle bearing 1 rudimentary seta, exopod bearing 3 rudimentary setae. **Cryptoniscus larva** unknown.

Intertidal–subtidal, parasitising porcellanid crabs. Temperate Northern Atlantic, Temperate South America, Temperate Northern Pacific. 4 species (Shiino, 1942).

Paguritherium Reinhard, 1945

Diagnosis. **Female** head with dorsal groove; antennula and antenna present as fused pads; maxilliped present. Pereon without ovarian processes; oostegites 1–5 present, oostegite 1 largest, ascendant and recurrent lobes present; other oostegites on posterior of pereon, multilobed, directed dorsally; oostegite 5 reduced. Heart in pleomere 1; 5 pairs of pleopods; posterior margin of pleomere 6 entire; uropods absent. **Male** antenna projecting beyond margin of head; pereopods unsegmented; medioventral spines and pleopods absent; posterior margin of pleomere 6 entire. **Epicaridium larva** with pereopod 6 subequal in length to pereopod 5, dactylus reduced; pleopods 1–3 each with medial angle of peduncle bearing 1 long seta, exopod bearing 3 long setae; pleopod 4 with medial angle of peduncle bearing 1 short seta, exopod bearing 3 long setae; pleopod 5 reduced, setae absent. **Cryptoniscus larva** unknown.

Intertidal–shelf, parasitising pagurid hermit crabs. Temperate Northern Atlantic. 2 species (DeTorre et al. 2023; Reinhard, 1945).

Synalpheion Coutière, 1908

Diagnosis. **Female** head without dorsal groove; maxilliped absent. Pereon with 2 pairs of posterolateral ovarian processes; brood pouch formed by 2 pairs of oostegites; 1 oostegite on each ovarian process; oostegites multilobed, folded; oostegite 1 absent. Heart in pleomere 1; 5 pairs of uniramous pleopods; posterior margin of pleomere 6 entire; uropods absent. **Male** antenna slightly projecting beyond margin of head; pereopods unsegmented; pereomeres without lateral projections; medioventral spines and pleopods absent; posterior margin of pleomere 6 entire; uropods absent. **Epicaridium larva** with pereopod 6 subequal in length to pereopod 5, carpo-propodus with 2 processes; pleopods 1–4 each with medial angle of peduncle bearing 1 long seta, exopod bearing 3 long setae; pleopod 5 with medial angle of peduncle bearing 1 seta, exopod bearing 3 long setae. **Cryptoniscus larva** unknown.

Subtidal, parasitising alpheid shrimps. Tropical Atlantic. 1 species (Coutière, 1908).

Subfamily Entioninae Codreanu, Codreanu and Pike, 1960

Achelion Hartnoll, 1966

Diagnosis. **Female** oostegite 1 with well-developed ascendant, transverse and recurrent lobes, oostegites 2–5 delicate, fused. Thorax with 2 large midventral ovarian processes, dorsal ovarian processes absent. Heart in pleomere 3. Pleural lamellae 1–4 convoluted, 5 simple. **Male** head fused with pereomere 1. Pereomeres with flattened lateral expansions. Medioventral spines on pleomeres 1 and 2. Pleomere 6 bifid. **Epicaridium larva** with pereopod 6 much longer than others, carpo-propodus with well-developed terminal process, dactylus reduced. **Cryptoniscus larva** unknown.

Subtidal, parasitising mithracid crabs. Tropical Atlantic. 1 species (Hartnoll, 1966).

Allocancrion Uyeno and Boyko, 2020

Diagnosis. **Female** with body U-shaped. Head oval with 2 bulbous cephalic lobes; 2 pairs of antennal lobes. Maxillipeds paired, uniramous. Pereon with 4 pairs of ventrolateral ovarian processes, without ventral processes; pereopods absent. Oostegite 1 well developed, composed of ascendant lobe, elongate transverse lobes, and large recurrent lobe. Oostegites 2–5 fused into single large membranous flap covering oostegite 1. Pleon not distinctly segmented, bulbous heart in pleomere 3, 5 pairs of uniramous pleopods; pleomeres 1–3 with pair of pleural lamellae; pleopods 1–4 with oval lobes; pleopod 5 as small lobe. Terminal pleomere with 2 pairs of tapered projections. **Male** with ovoid head, incompletely fused to pereomere 1. Eyes present. Antennula as bulbous lobe with cluster of setae. Antenna absent. Maxilliped a conical projection with apical element. Pereon with 7 pereomeres, 1–5 each with pair of pereopods. Pereopods increasing in size posteriorly, all segments distinct. Pereomere 7 with pair of lateral gonopores. Pleon with 5 pleomeres plus pleotelson; pleopods absent; pleotelson with pair of tapering lateral lobes, uropods absent. **Epicaridium larva** antennula with 3 articles. Antenna elongate, with 6 articles. Mandible 2 segmented. Maxilla slender with apical long seta. Maxilliped with 2 apical setae. Pereon with 6 pairs of pereopods. Pereopods 1–6 subequal in size with all articles distinctly separated except carpus fused to propodus. Pereopod 6 with small dactylus incompletely fused to carpo-propodus. Pleon with 6 pleomeres and pleotelson. 5 pairs of uniramous pleopods. Terminal pleomere with biramous uropods; exopod and endopod subequal in length with 2 setae each and sharp processes on distal tip. **Cryptoniscus larva** unknown.

Intertidal, parasitising plagusiid crabs. Central Indo-Pacific. 1 species (Uyeno and Boyko, 2020).

Cancrion Giard and Bonnier, 1887

Diagnosis. **Female** with dorsal ovarian processes, ventral processes absent; oostegite 2 covering basal part of oostegite 1. Pleural lamellae of pleomeres 1 and 2 complex, pleomeres 3 and 4 complex or simple. **Male** without ventromedial spines on pleon. **Epicaridium larva** with pereopod 6 much longer than pereopod 5, distodorsal margin of carpo-propodus with well-developed flange-like process. **Cryptoniscus larva** with 7 pairs of isomorphic pereopods.

Intertidal-subtidal, parasitising panopeid, pilumnid, portunid, and xanthid crabs. Temperate Northern and Tropical Atlantic, Temperate South America, Temperate Northern Pacific, Central Indo-Pacific, Temperate Australasia. 8 species (Oanh and Boyko, 2020).

Cryptocancrion Williams, Boyko, Tepolt and Blakeslee, 2023

Diagnosis. **Female** with sheath secreted by host surrounding parasite except for perforation at posterior end. Head as 2 bulbous lobes, bearing 2 pairs of antennae, 1 pair of minute maxillipeds. Pereon compact, with variable (0–4) numbers of dorsal ovarian processes; pereopods absent. 5 pairs of oostegites forming brood pouch; oostegite 1 with ascendant lobe projecting anteriorly and dorsally, 2 simple transverse lobes, 1 recurrent lobe extending entire length of pereon; oostegites 2–5 fused in mature females. Pleon composed of 5 segments with overlapping uniramous pairs of pleopods, terminal pair expanded laterally. 2 pairs of complex pleural lamellae on pleomeres 1 and 2; bulbous heart in pleomere 3. Distal end of pleon with 2 finger-like projections. **Male** head fused with pereomere 1, pereomeres 2–7 distinct dorsally. Head with pair of large eyes. Antennulae as large, separate ovate lobes, with short setae; antennae absent. Maxillipeds absent. Pereopods 1–6 with propodus and carpus fused; pereopod 7 reduced to rounded nub. Pleon of 5 segments plus pleotelson; pleomeres distinctly narrower posteriorly, pleopods absent. Pleotelson with 2 short, distally rounded, lobes; uropods absent. **Epicaridium larva** with antennula of 3 articles; antenna elongated, approximately half length of body, of 6 articles. Oral cone with sucker-shaped structure at terminus. Pereopod 6 subequal in length to other pereopods, propodus bearing long digitiform process tipped with long terminal setae and small pointed dactylus. **Cryptoniscus larva** unknown.

Intertidal, parasitising panopeid crabs. Temperate Northern Atlantic. 1 species (Williams et al., 2023).

Entione Kossmann, 1881

Diagnosis. **Female** with 2 large unpaired ventral ovarian processes, posterior process slightly longer than anterior; 2 pairs of large dorsolateral ovarian processes surrounding 2 pairs of small tubercles. Oostegite 1 with ascendant and recurrent lobes. Pleural lamellae well developed (2 or 3 pairs), pleopods reduced, lamellar. **Male** with jointed pereopods. Terminal pereonal segment and pleomeres 1 and 2 with medioventral spines. **Epicaridium larva** pereopod 6 subequal in length to pereopod 5. **Cryptoniscus larva** unknown.

Subtidal, parasitising inachid and grapsid crabs. Temperate South America, Temperate Northern Atlantic. 2 species (Giard and Bonnier, 1887).

Entionella Miyashita, 1941

Diagnosis. **Female**, first oostegite with well-developed ascendant, lateral and recurrent lobes. Thorax without ovarian processes. Heart in pleomere 3. **Male** with jointed pereopods. Pereomeres expanded laterally as flat plates. Pleomeres 1–4 with medioventral spines. **Epicaridium larva** with pereopod 6 subequal in size to others, dactylus reduced (note: above is for the type species, others with pereopod 6 longer than 5). **Cryptoniscus larva** body elongate, fusiform. Antennula of 3 segments, basal joint not toothed; antenna of 5 segments, reaching to pereomere 3. Coxal plates narrow, without teeth. 7 pairs of pereopods present, anterior 4 pairs with stout propodi, last 3 pairs more elongate with slender propodi and elongated dactyli. Pleon of 5 segments, each with pair of pleopods. Uropodal inner ramus longer than outer ramus; each ramus with 1 long and 1 short seta.

Intertidal–subtidal, freshwater and marine, parasitising eriphiid, majid, sesarmid and varunid crabs. Temperate Northern Atlantic, Temperate Northern Pacific. 4 species (Demassieux and Veillet, 1980).

Micippion Shiino, 1942

Diagnosis. **Female** with 2 ventral ovarian processes and one dorsal ovarian process. Marsupium complete, oostegite 1 enclosed by oostegite 2, which is completely fused with oostegite 3; oostegites 4 and 5 separate. Pleural lamellae of pleomeres 1–4 folded. **Male**, head fused with pereomere 1; pleomere 1 with medioventral spines. **Epicaridium larva** with pereopod 6 well developed, propodus bearing terminal process. **Cryptoniscus larva** unknown.

Subtidal, parasitising majid crabs. Temperate Northern Pacific. 1 species (Shiino, 1942).

Pinnixion McDermott, Williams and Boyko, 2019

Diagnosis. **Female** with sheath secreted by host surrounding entire parasite except for perforation at posterior end. Head rounded, dorsally distinctly divided into 2 bulbous lobes, bearing 2 pairs of antennae. Maxilliped with subquadrate curved coxopod, lamellar exopod. Pereon without ovarian processes, pereopods absent. 5 pairs of oostegites forming brood pouch, margins entire. Oostegite 1 with 1 ascendant lobe, 2 transverse lobes, 1 recurrent lobe; oostegites 2–5 fused in mature females, covering oostegite 1. Pleomeres 1–3 each with distinct uniramous flattened pair of pleopods overlaying one another; pleomeres 4, 5 with reduced pleopods. 2 pairs of complex pleural lamellae positioned medially on pleon. Bulbous heart in pleomere 3. Terminal pleomere with pair of anteroventral lobes, 2 long, tapered lateral projections, 4 distal finger-like projections. **Male** with pereomere 1 ventrally fused with trapezoidal head. Head with pair of mediolateral cephalic slits, eyes present. Antennulae as large ovate lobes fused medially; antenna absent. Pair of mitten-shaped maxillipeds at base of

oral cone. Pereomere 7 with small, setose medioventral spine. 6 pairs of pereopods with dactylus; propodus, carpus fused into 1 cylindrical segment. Pleomeres 1, 2 with large lateral hemispherical lobes, lobes on pleomere 1 more than twice as large as those on pleomere 2. Pleotelson with 2 elongated tapered posterolateral lobes. **Epicaridium larva** with antennula of 2 rounded articles, antenna elongated, approximately half length of body, of 6 articles. Pereopod 6 greatly elongated with long, cylindrical process, articulated with propodus/carpus dorsal to dactylus. **Cryptoniscus larva** unknown.

Subtidal, parasitising pinnotherid crabs. Temperate Northern and Tropical Atlantic. 1 species (McDermott et al., 2019).

Pinnotherion Giard and Bonnier, 1889

Diagnosis. **Female** with 2 ventral ovarian processes, dorsal processes absent. Marsupium closed, oostegite 1 without transverse lamella, enclosed by other pairs. Pleural lamellae folded in pleomeres 1–4. **Male** head fused with pereomere 1; pleomeres with ventromedial processes. **Epicaridium larva** with pereopod 6 not prehensile or longer than others, rudimentary dactylus present. **Cryptoniscus larva** body elongate, fusiform; 7 pairs of pereopods, 1–6 each with short dactyli, pereopod 7 with elongate dactylus.

Subtidal, parasitising inachid and pinnotherid crabs. Temperate Northern Atlantic, Temperate Northern Pacific. 2 species (Shiino, 1942).

Portunion Giard and Bonnier, 1886

Diagnosis. **Female** with 2 ventral and 1 pair of anterodorsal ovarian processes. Marsupium complete; ascendant lamellae of oostegite 1 entirely covered by oostegite 2. Pleomeres 1–4 with folded pleural lamellae. **Male** head fused or distinct from pereomere 1; pleon with medioventral spines. **Epicaridium larva** with pereopod 6 not prehensile or longer than others; propodus with simple process at tip and rudimentary dactylus. **Cryptoniscus larva** body elongate, fusiform; 7 pairs of pereopods, 1–6 each with short dactyli, pereopod 7 with elongate dactylus.

Subtidal, parasitising carcinid, epialtid, grapsid, polybiid and varunid crabs. Temperate Northern Atlantic (including Mediterranean Sea), Indo-West Pacific, Temperate Northern Pacific. 10 species (Chaix and Veillet, 1981; Huang et al., 2025; Oanh and Boyko, 2026).

Priapion Giard and Bonnier, 1888

Diagnosis. **Female** with anterior pair of dorsolateral ovarian processes, 2 unpaired ventral ovarian processes; last pereomere with 2 large, rounded bulges. Pleural lamellae of pleon and pleopods highly developed on lateral edges of pleon, terminal segment with 2 symmetrical, quadrangular parts, joined to each other along almost entire length. **Male** head not fused with pereomere 1; pleomere 1 with elongate penis. **Epicaridium larva** unknown. **Cryptoniscus larva** unknown.

Subtidal, parasitising polybiid crabs. Temperate Northern Atlantic. 1 species (Giard and Bonnier, 1888).

Tiarinion Shiino, 1942

Diagnosis. **Female** with 2 ventral processes, dorsal processes absent. Oostegite 1 with well-developed ascendant lamella, smaller transverse and recurrent lamellae that may be fused. Oostegite 1 largely uncovered by oostegite 2; oostegites 3–5 small, rudimentary; oostegite 6, 7 present or absent. Pleural lamellae folded on pleomeres 1, 2, simple on pleomeres 3, 4. **Male** head fused with pereomere 1; pleomeres 1, 2 with medioventral spines or spines absent. **Epicaridium larva** with pereopod 6 much longer than others, strongly prehensile, propodus bearing well-developed terminal process. **Cryptoniscus larva** antennula of 6 segments. Maxilliped present. Merus of first pereopod with 1 spine on outer side and 1 seta on inner side. Pleon with shallow median notch on posterior margin.

Subtidal, parasitising epialtid crabs. Temperate Northern Pacific, Central Indo-Pacific. 2 species (Shields and Ward, 1998).

Xanthion Shiino, 1942

Diagnosis. **Female** with single ventral process. Marsupium incompletely closed, ascendant lamella of oostegite 1 largely uncovered by oostegite 2. Pleural lamellae of pleomeres 1–4 folded. **Male** head fused with pereomere 1; pleon ventromedial spines absent. **Epicaridium larva** with pereopod 6 much longer than others, strongly prehensile, propodus bearing well-developed terminal process. **Cryptoniscus larva**, body wider anteriorly than posteriorly. Basal 2 joints of antennula denticulate on posterior margins. Maxilla and maxilliped absent. Coxal plates entire on posterior border. Propodus of pereopods 1–6 more or less crenulate on distal margin, carpus very thin, tipped with 1 short spine, merus tipped with 1 long, sharp spine. Pleopods 1–4 with protopod nearly quadrate, bearing 3 long plumose setae and 1 short non-plumose seta at inner distal angle and 2 simple setae at inner proximate angle; exopod with 1 long plumose and 1 short simple seta. Triangular protopod of pleopod 5 with endopod bearing 2 setae.

Subtidal, parasitising xanthid crabs. Temperate Northern Pacific. 1 species (Shiino, 1942).

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Family Ionidae H. Milne Edwards, 1840

Figure 6.24

All members of the Ionidae are branchial ectoparasites of callianassid shrimps. The only species in Ionidae with well-described females, males and cryptoniscus larvae is *Ione thoracica* (Montagu, 1808). This species, and perhaps all the species in the genus, possess the ability for differentiated males to undergo a sex change based on environmental conditions (i.e. loss of the mature female in the branchial chamber of the host); the reverse (females changing to males) may also occur (Reinhard, 1949; Reverberi and Pittoti, 1943). The ramified lateral plates of females and the elongate lateral plates of males are distinctive, as are the denticles on the basal articles of the antennulae of cryptoniscid larvae (bopyroid cryptoniscus larvae typically have smooth basal articles on the antennulae).

Diagnosis. **Female** (fig. 6.24a, c, d) body elongate; pereomeres distinct; head wider than long, oval, partly embedded in pereomere 1. Head entire, not distorted. Frontal lamina present, extending laterally as 2 tapered lobes. Eyes absent. Barbula with 3 smooth, tapered lobes on each side. Antennula and antenna articulated. Maxilliped without palp. Marsupium open or closed. 5 pairs of oostegites; oostegite 1 with short, rounded posterior lobe; internal ridge smooth or digitate. Pereomeres 1–4 with coxal plate and dorsolateral bosses. Middorsal projections absent. 7 pairs of pereopods, progressively longer posteriorly. Pleon of 6 distinct pleomeres; 5 pairs of uniramous lateral plates, each divided into numerous distal rami. 5 pairs of pleopods, usually biramous (1 or 2 pairs sometimes uniramous). Uropods uniramous. **Male** (fig. 6.24b) body with pereomeres subequal in width or widest at middle; head wider than long, narrower than or subequal in width to pereomere 1. Eyes present or absent. Antennula and antenna articulated. Midventral tubercles absent. 7 pairs of pereopods, posterior pairs larger. Pleomeres 1–6 distinct or medially fused, all with elongate lateral plates; pleopods and uropods absent. **Cryptoniscus larva** (fig. 6.24e–g) body teardrop-shaped, eyes present. Antennula with denticles on basal article, without large teeth. Oral sucker absent. Pereomeres without toothed coxal plates. Pereopods 1–7 subequal in size and

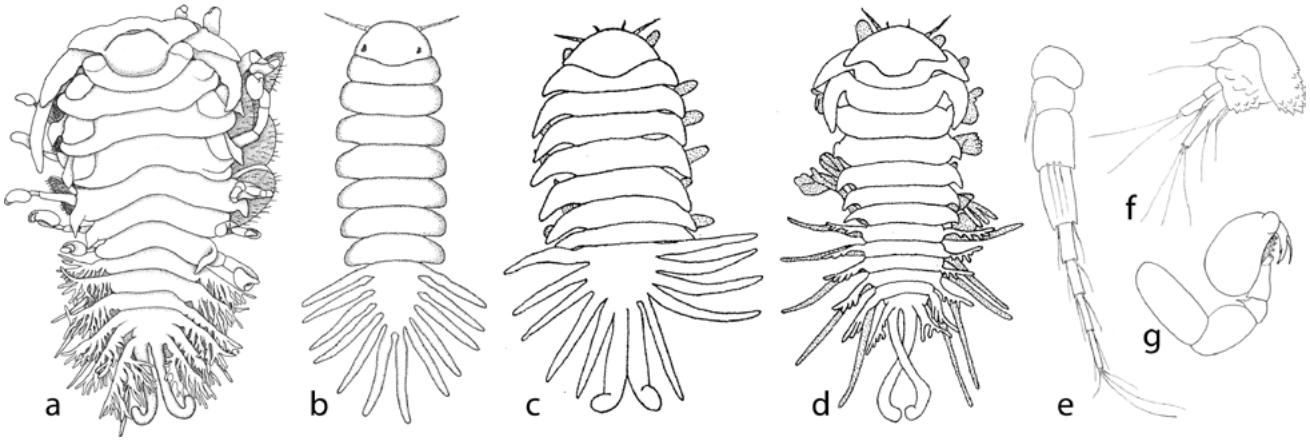


Figure 6.24. Ionidae. *Ione thoracica* (Montagu, 1808): a, female dorsal view; b, male dorsal view; c, d, juvenile females dorsal view; e, cryptoniscus larva antenna; f, cryptoniscus larva antennula; g, cryptoniscus larva pereopod.

shape, dactyli weakly bifid with large dorsal seta, propodi with stout setae on margin. 5 biramous pleopods. Uropodal exopod larger and longer than endopod. Pleotelson heart-shaped, without teeth. Branchial parasites.

Ione Latreille, 1818

Diagnosis. As for family.

Intertidal, parasitising callianassid shrimps. Temperate Northern Atlantic, Western and Central Indo-Pacific, Temperate Northern and Tropical Eastern Pacific, Temperate South America. 7 species (Hernáez et al., 2023).

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Superfamily Cryptoniscoidea Kossmann, 1880

As with Bopyroidea, Cryptoniscoidea is difficult to diagnose. Cryptoniscoids exhibit a wide range of associations with definitive hosts (endoparasitic, mesoparasitic and ectoparasitic, including some hyperparasites). Trilles (1999) stated that all cryptoniscoids are protandrous hermaphrodites (the cryptoniscus larva transforms into a functional male that attaches to a definitive host and become female if one is not present) with species in only one genus, *Scalpelloniscus*, being possibly gonochoristic (Grygier, 1981). However, Trilles (1999) did not include Dajidae and Entophilidae in Cryptoniscoidea, and data for sexual development in most cryptoniscoid species have not been recorded. Functionally adult males (i.e. capable of fertilisation) appear externally indistinguishable from the cryptoniscus larval stage in most families, but in Dajidae and Entophilidae males are of a distinct morphotype and similar to those in Bopyroidea. Females of species in many genera are greatly modified, with body shapes partly or wholly sac-like (Hemioniscidae), globular (Crinoniscidae) or stellate (Stellatoniscidae). However, females in Dajidae and Entophilidae are similar to those in Bopyroidea (i.e. with clear body segmentation and pereopods).

The only morphological character that appears to be a synapomorphy for cryptoniscoids is the number of articles of the antenna of the cryptoniscus larval stage (4 basal plus 5 flagellar articles) (Boyko and Williams, 2015). This is supported by molecular data that distinguishes the epicaridean superfamilies (Boyko et al., 2013).

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Family Asconiscidae Bonnier, 1900

Figure 6.25

The sole species in Asconiscidae can be distinguished from other cryptoniscoid epicarideans by the form of the female, which is reduced to an irregular sac that is extruded from the ventral surface of the cryptoniscus larval stage to which it remains attached, as well as by the strong cuticular ridges on the first two segments of the antennula and the three long thick setae on the first segment of the antennula (Sars, 1899). The sole species is an ectoparasite of mysids.

Diagnosis. **Male** (paedomorphic cryptoniscus larva) (fig. 6.25c–g) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes absent. Antennula article 1 without teeth but with strong cuticular striations, three large setae near posterior margin, article 2 with strong cuticular striations. Coxal plates without teeth. Pereopods 1 and 2 gnathopodal, pereopods 3–7 ambulatory; propodi of pereopods 3–5 quadrate distally, pereopods 6 and 7 tapering distally. Pleotelson margin smooth. **Immature females** with slight indication of segmentation (fig. 6.25a). **Mature females** (fig. 6.25b) without segmentation, sac-like, extending ventrally and attached to cryptoniscus larval body. Ectoparasitic.

Asconiscus G.O. Sars, 1899

Diagnosis. As for family.

Subtidal–bathyal, parasitising *Boreomysis arctica* (Krøyer, 1861) (Mysida). Temperate Northern Atlantic. 1 species (Nielsen and Strömberg, 1973a, b; Sars, 1899).

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Family Cabiropidae Giard and Bonnier, 1887

Figure 6.26

As can be seen from the diagnosis below, Cabiropidae is something of a "wastebasket" family in Cryptoniscoidea. The family contains members that are endoparasitic, mesoparasitic or ectoparasitic (including hyperparasites) in the marsupium of isopods and other hosts. Two genera are known from cryptoniscus larvae only and a third is known from cryptoniscus larvae and immature females only, while five other genera are known only from females, which are highly reduced in morphology. It is likely that some if not most genera in this family will eventually be placed elsewhere in Cryptoniscoidea. If discussing only those genera that share characters with the type genus *Cabirops* (*Arcturocheres*, *Bourdonia*, *Perezina* and *Rolandoniscus*), these five genera can be distinguished from other epicarideans in that the females are compressed laterally and recurved and found unattached in the marsupia of their hosts and pass through 4 stages of development, including a stage with pronounced dorsal lobes and a mature form with a row of chitinous plates along the ventral margin in the centre of the body (the mature stage has not been observed in *Arcturocheres*).

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with or without prominent cuticular striations. Head wider than long, oral cone directed anteriorly or posteriorly. Eyes present or absent. Antennula article 1 with 3–11 posterior teeth or lacking teeth. Coxal plates with teeth. Pereopods 1 and 2 gnathopodal or ambulatory (if ambulatory, propodi quadrate distally), dactyli bifid or entire; pereopods 3–7 ambulatory; propodi of 3–5 quadrate distally, 6 and 7 tapering distally. Pleotelson margin with or without teeth. **Immature female** body compressed laterally, recurved, with numerous dorsal lobes, segmentation indistinct or dorsoventrally compressed, with segmentation visible or body subdivided into 2 portions: a 2-pronged posterior portion anchored in the host's visceral cavity and a segmented anterior end; head distinct with mouthparts and pair of reduced pereopods surrounding it, or indistinct. **Mature female** compressed laterally and recurved, with row of chitinous plates along ventral margin in centre of body or dorsoventrally compressed and rounded, elongate, or quadrate; segmentation present or absent; lobes present or absent; appendages or mouthparts present or absent. Endoparasitic, mesoparasitic and ectoparasitic.

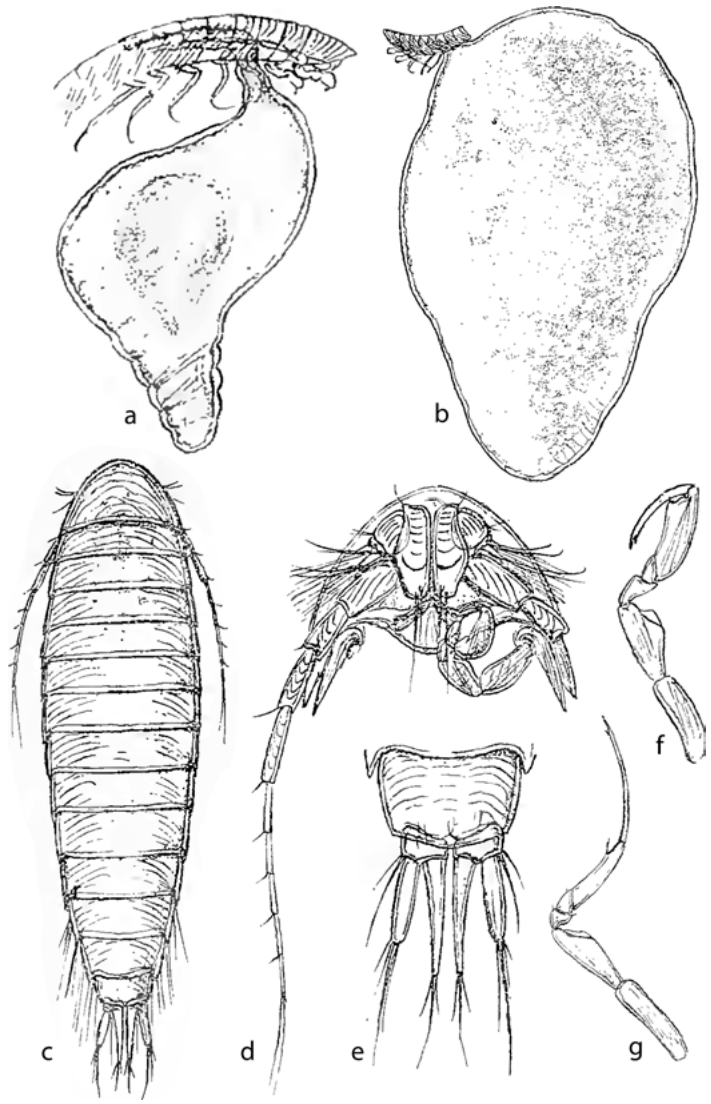


Figure 6.25. Asconiscidae. *Asconiscus simplex* G. O. Sars, 1899: a, immature female lateral view; b, mature female lateral view; c, male dorsal view; d, male head, ventral view; e, male pleon, dorsal view; f, male pereopod 3; g, male pereopod 7.

Key to genera of Cabiropidae

Cironiscus, *Pleuroniscus*, *Podoniscus* and *Rolandoniscus* are not in the key to genera; they are known only from cryptoniscus larvae.

1. Body of mature female body embedded in host 2
– Body of mature female not embedded in host 3
2. Body of mature female (fig. 6.26a) entirely within host rhizocephalan ..... *Perezina*
– Approximately half of body of mature female (fig. 6.26b, c) embedded in host isopod ..... *Ancyroniscus*
3. Body of mature female compressed dorsoventrally, not recurved 4
– Body of mature female compressed laterally, recurved ventrally 10
4. Body of mature female (fig. 6.26d, e) elongate, with lateral bulges ..... *Anthuroniscus*
– Body of mature female not elongate, without lateral bulges 5

5. Body of mature female body heart-shaped 6
– Body of female not heart-shaped 7
6. Mature female (fig. 6.26f) hyperparasitising cryptoniscoid epicarideans on amphipods ..... *Gnomoniscus*
– Mature female (fig. 6.26g) parasitising asellote isopods ..... *Munnoniscus*
7. Body of mature female (fig. 6.26h; see also male fig. 6.26i–l) much longer than wide; found in marsupium of host cirolanid isopods ..... *Cirolanoniscus*
– Body of mature female length and width subequal 8
8. Body of mature female (fig. 6.26m) with flap-like lateral lobes; found in marsupium of host aegid isopods ..... *Aegoniscus*
– Body of mature female with ovate lateral lobes 9
9. Mature female (fig. 6.26n, o) with pereopods; found in marsupium of host nebaliaceans ..... *Apocumoechus*
– Mature female (fig. 6.26p) without pereopods, found in marsupium of host isopods ..... *Clypeoniscus*
10. Cryptoniscus larva (figs. 6.6e, 6.26r–t; see also female, figs. 6.6c, d, 6.26q) with dactylus of pereopod 1 bifurcated at tip; parasites of bopyrid isopods ..... *Cabirops*
– Cryptoniscus larva with dactylus of pereopod 1 not bifurcated at tip 11
11. Cryptoniscus larva (fig. 6.26v; see also female, fig. 6.26u) with dactylus of pereopod 6 deeply bifurcated; parasites of antarcturid isopods ..... *Arcturocheres*
– Cryptoniscus larva (fig. 6.26x; see also female, fig. 6.26w) with dactylus of pereopod 6 not bifurcated, parasites of bopyrid isopods ..... *Bourdonia*

Aegoniscus Barnard, 1925

Diagnosis. **Male** (paedomorphic cryptoniscus larva) not known. **Mature female** dorsoventrally compressed, ventral surface with medial line of 6 pairs of lobes, later margins with row of larger lobes.

Slope, parasitising aegid isopods. Temperate Southern Africa. 1 species (Barnard, 1925).

Ancyroniscus Caullery and Mesnil, 1919

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped (cuticular striations not described). Oral cone not described. Eyes present. Antennula article 1 with 11 posterior teeth. Pereopods 1 and 2 gnathopodal, dactyli not bifid, 3–7 ambulatory. Pleotelson margin with or without teeth. **Immature female** body subdivided into 2 parts: 2-pronged posterior portion anchored in the host's visceral cavity and segmented anterior end, with mouthparts and 2 pairs of rudimentary pereopods, projecting into the marsupium. **Mature female** without appendages or mouthparts; posterior and anterior portions subdivided into multiple rounded lobes filled with eggs.

Subtidal, parasitising aegid and sphaeromatid isopods (egg predators). Temperate Northern Atlantic, Temperate Australasia. 2 species (Bourdon and Bruce, 1980; Caullery and Mesnil, 1919).

Anthuroniscus Shiraki and Kakui, 2024

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped without prominent cuticular striations. Head wider than long, oral cone directed posteriorly. Eyes absent. Antennula article 1 with 8 posterior teeth. Coxal plates with teeth. Pereopods 1 and 2 gnathopodal, dactyli not bifid; pereopods 3–7 ambulatory; propodi of 3–5 quadrate distally, 6 and 7 tapering distally. Pleotelson margin with or without teeth. **Mature female** dorsoventrally compressed, elongate; 6 pairs of lateral bulges indicating segmentation; mouthparts absent; appendages reduced to single putative pereopod 1 stub.

Subtidal, parasitising anthurid isopods (probable egg predators). Central Indo-Pacific. 3 species (Shiraki and Kakui, 2024).

Apocumoechus Nierstrasz and Brender à Brandis, 1931

Diagnosis. **Male** (paedomorphic cryptoniscus larva) not known. **Mature female** without segmentation, body fused into large marsupium with long median slit extending nearly entire length; 2 pairs of (apparently posterior) pereopods near oral area.

Subtidal, parasitising nebaliceans. Tropical Atlantic. 1 species (Nierstrasz and Brender à Brandis, 1931).

Arcturocheres Hansen, 1916

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Oral cone directed anteriorly. Eyes absent. Antennula article 1 with 6 posterior teeth. Pereopods 1 and 2 gnathopodal, dactyli not bifid, 3–7 ambulatory; dactylus of pereopod 6 bifurcated. Pleotelson margin smooth. **Immature female** segmented, body recurved; **mature female** not known.

Slope–bathyal, parasitising antarcturid isopods. Arctic, Southern Ocean. 2 species (Boyko, 2013).

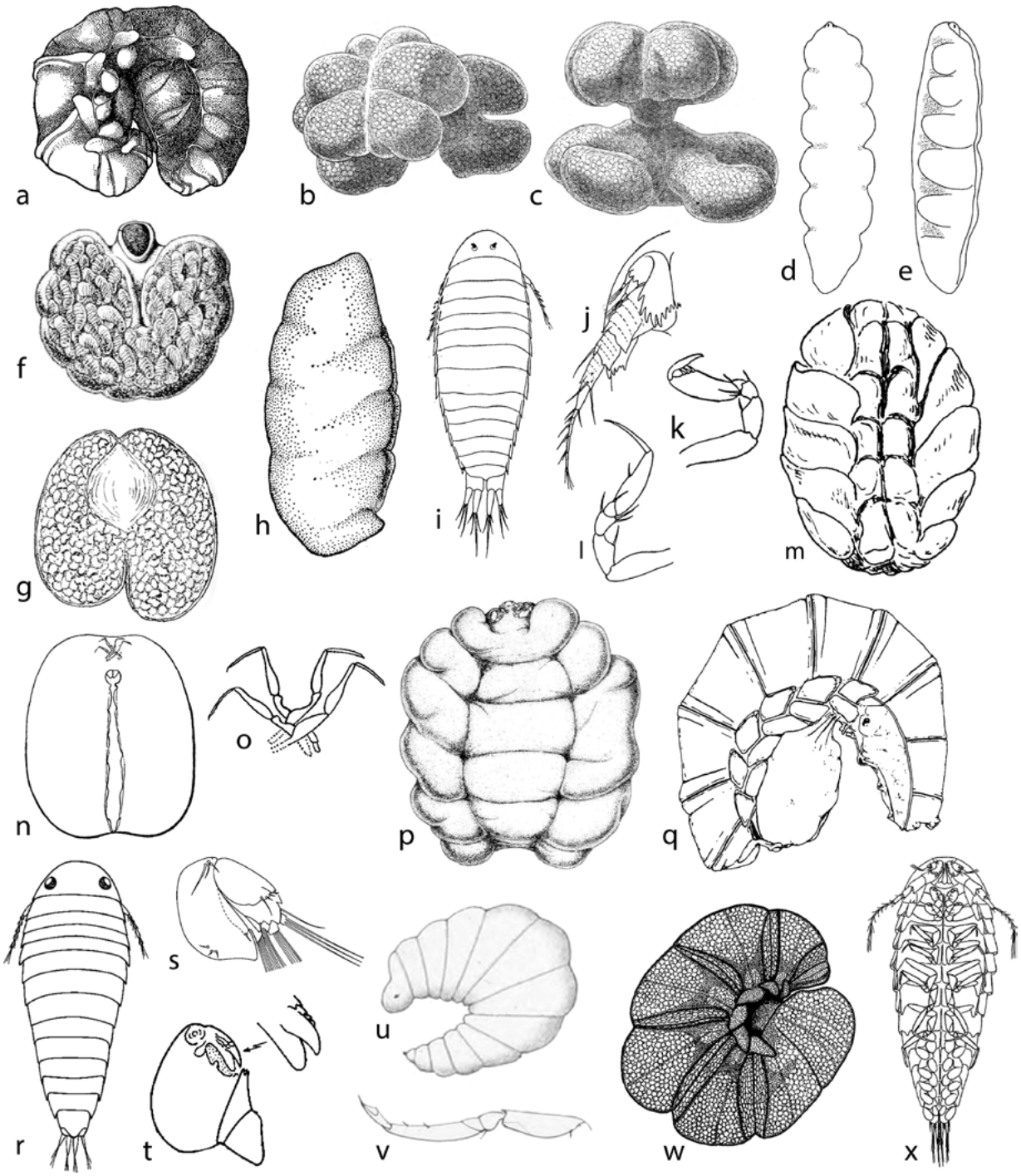


Figure 6.26. Cabiropidae. *Perezina gregaria* (Nierstrasz and Brender à Brandis, 1929): a, female lateral view. *Ancyroniscus bonnieri* Caullery and Mesnil, 1919: b, female dorsal view (segmented region extends from isopod host body); c, female lateral view (top portion extends from isopod host body, bottom portion within body of host). *Anthuroniscus* Shiraki and Kakui, 2024: d, female ventral view; e, female lateral view. *Gnomoniscus podasconis* Giard and Bonnier, 1895: f, female lateral view showing dorsal organ, anterior opening of marsupium and developing embryos. *Munnoniscus marsupialis* (G.O. Sars, 1883): g, female lateral view showing developing embryos in marsupium. *Cirolanoniscus willeyi* Pillai, 1966: h, female lateral view; i, male dorsal view; j, male antennae; k, male pereopod 1; l, male pereopod 7. *Aegoniscus gigas* Barnard, 1925: m, female ventral view. *Apocumoechus paranebaliae* Nierstrasz and Brender à Brandis, 1931: n, female ventral view; o, female pereopods (originally labelled incorrectly as first and second antennae). *Clypeoniscus hanseni* Giard and Bonnier, 1895: p, female ventral view. *Cabirops montereyensis* Sassaman, 1985: q, female lateral view; r, male dorsal view; s, male antennula; t, male pereopod 1, inset shows bifid tip of dactyl; *Arcturocheres pulchripes* Hansen, 1916: u, female lateral view; v, male pereopod 6. *Bourdonia tridentata* Rybakov, 1990: w, female lateral view; x, male ventral view.

***Bourdonia* Rybakov, 1990**

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Oral cone directed anteriorly. Eyes absent. Antennula article 1 with 3 blunt posterior teeth. Pereopods 1 and 2 gnathopodal, dactyli not bifid, 3–7 ambulatory. Pleotelson margin smooth. **Mature female** with segmentation visible, body recurved, row of chitinous plates along ventral margin in centre of body.

Subtidal, slope, hyperparasitising bopyrid isopods. Temperate Australasia, Temperate Northern Pacific. 2 species (Boyko, 2013; Boyko et al., 2024).

***Cabirops* Kossmann, 1884**

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Oral cone directed anteriorly. Eyes present. Antennula article 1 without teeth. Pereopods 1 and 2 gnathopodal, dactylus bifid, 3–7 ambulatory, dactylus less than half length of propodus; 6 and 7 with dactylus as long as propodus. Pleotelson margin smooth. **Immature female** body recurved with numerous dorsal lobes, segmentation indistinct; **mature female** body recurved with segmentation visible, row of chitinous plates along ventral margin in centre of body**.**

Subtidal–slope, hyperparasitising bopyrid isopods. Tropical and Temperate Northern Atlantic, Temperate Southern Africa, Central Indo-Pacific, Temperate Northern Pacific. 15 species (Boyko, 2013).

***Cirolanoniscus* Pillai, 1966**

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped (cuticular striations not described). Oral cone not described. Eyes present. Antennula article 1 with 8 posterior teeth. Pereopods 1–7 ambulatory, dactylus not bifid; propodus of pereopod 1 quadrate distally, 7 tapering distally (other pereopods not described). Pleotelson margin smooth. **Mature female** quadrate, vestigial segmentation visible; anterior 2/3 of body with 2 large rectangular lobes nearly meeting in midline; appendages absent.

Subtidal, parasitising cirolanid isopods. Indo-West Pacific. 1 species (Pillai, 1966).

***Cironiscus* Nielsen, 1967**

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped without prominent cuticular striations. Oral cone directed posteriorly. Eyes absent. Antennula article 1 with 8 posterior teeth. Pereopods 1 and 2 gnathopodal, dactylus not bifid, 3–7 ambulatory; dactyli of 3–5 shorter than propodi, slightly recurved, 6 and 7 longer than propodi, straight. Pleotelson margin with teeth. **Female** not known.

Subtidal, parasitising cirolanid isopods. Temperate Northern Atlantic. 1 species (Nielsen, 1967).

***Clypeoniscus* Giard and Bonnier, 1895**

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped without cuticular striations. Oral cone directed posteriorly. Eyes absent. Antennula article 1 with 11 posterior teeth. Pereopods 1 and 2 gnathopodal, dactyli not bifid, 3–7 ambulatory; dactyli of 3–5 less than half as long as propodi, 6 and 7 with dactyli 3/4 as long as propodi. Pleotelson margin with teeth. **Immature female** dorsoventrally compressed with segmentation visible, head distinct, surrounded by pair of reduced pereopods; **mature female** without segmentation, compressed dorsoventrally, ventral surface with median slit along entire length, dorsal surface with median groove along half of length and rounded "dorsal organ."

Subtidal–slope, parasitising asellote and vavliferan isopods. Arctic, Temperate Northern Atlantic, Temperate Southern Africa, Temperate Northern Pacific. 5 species (Barnard, 1920; Bourdon, 1967; Giard and Bonnier, 1895; Nielsen and Strömberg, 1973a, b; Nierstrasz and Brender à Brandis, 1929a). We herein designate *Clypeoniscus hanseni* Giard and Bonnier, 1895 as the type species of the genus.

***Gnomoniscus* Giard and Bonnier, 1895**

Diagnosis. **Male** (paedomorphic cryptoniscus larva) not known. **Mature female** without segmentation; body compressed dorsoventrally, rounded with 2 large lateral lobes semi-divided by median groove; anterior end raised on short stalk.

Subtidal, hyperparasitising cryptoniscoid isopods. Temperate Northern Atlantic. 1 species (Boyko, 2013; Giard and Bonnier, 1895).

***Munnoniscus* Giard and Bonnier, 1895**

Diagnosis. **Male** (paedomorphic cryptoniscus larva) not known. **Mature female** without segmentation; body compressed dorsoventrally, rounded with 2 large lateral lobes completely divided by median groove; anterior end not raised on short stalk.

Subtidal, parasitising asellote isopods. Temperate Northern Atlantic. 2 species (Boyko, 2013; Giard and Bonnier, 1895; Sars, 1899). We herein designate *Cryptothiria marsupialis* G.O. Sars, 1883 as the type species of the genus.

***Perezina* Nierstrasz and Brender à Brandis, 1930**

Diagnosis. **Male** (paedomorphic cryptoniscus larva) not known. **Mature female** with segmentation visible, body recurved, row of chitinous plates along ventral margin in centre of body.

Subtidal, hyperparasitising rhizocephalan barnacles. Temperate Northern Atlantic. 1 species (Boyko, 2013; Nierstrasz and Brender à Brandis, 1929b).

***Pleuroniscus* Williams and Boyko *in* Williams, Boyko and Stewart, 2024**

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body cylindrical with prominent cuticular striations. Oral cone directed anteriorly. Eyes absent. Antennula article 1 with 7 posterior teeth. Pereopods 1, 2 gnathopodal, 3–7 ambulatory, dactyli not bifid; 1–4 with toothed coxal plates; propodi of 3–5 quadrate distally; 6, 7, tapered distally; dactyli of 1–5 shorter than propodi, 6 and 7 as long as propodi. Pleotelson margin without teeth. **Mature female** not known.

Bathyal, hyperparasitising bopyrid isopods. Indo-West Pacific. 1 species (Williams et al., 2024).

Podoniscus Bourdon, 1981

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Oral cone directed anteriorly. Eyes absent. Antennula article 1 with 8 posterior teeth. Pereopods 1–7 ambulatory, dactyli not bifid; propodi of 1–5 quadrate distally; dactyli of 1 and 2 as long as propodi, 3 and 4 as long as propodi and carpi combined, 5–7 as long as propodi, carpi and meri combined. Pleotelson margin with teeth. **Female** not known.

Bathypelagic, host(s) unknown. Southern Ocean. 1 species (Bourdon, 1981).

Rolandoniscus Boyko, 2013

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped (cuticular striations not described). Oral cone not described. Eyes absent. Antennula article 1 with 8 posterior teeth. Pereopods 1 and 2 gnathopodal, dactyli not bifid, 3–7 ambulatory; dactyli of 3–5 shorter than propodi, 6 and 7 longer than propodi. Pleon with 5 medioventral tubercles. Pleotelson margin indented medially, smooth. **Female** poorly known (based on single damaged specimen), body with bilobed marsupium and lateral plates.

Slope, hyperparasitising bopyrid isopods. Temperate Northern Atlantic. 1 species (Bourdon, 1967; Boyko, 2013).

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Family Capitoniscidae Boyko and Williams, 2023

Figure 6.27

Members of Capitoniscidae are ectoparasitic in the marsupium of cumaceans and an unknown host. They can be distinguished from other epicarideans by the greatly swollen head, lack of teeth on antennula segment 1, lack of teeth on the coxal plates, and morphology of pereopods 1 and 2 of the cryptoniscus larvae; the female appears to be spheroid and unsegmented with some appendages present, but is poorly described (Bourdon, 1972; Boyko and Williams, 2023).

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body elongate. Head wider than long, inflated anteroposteriorly, posterior margin wider than pereomere 1; eyes absent. Antennula article 1 short, rounded, without marginal teeth; dense setal brush present. Coxal plates with weak marginal crenulations but without teeth. Pereopods 1–3 gnathopodal, 1 and 2 with globular propodi and thick dactyli extending to distal margin of merus, pereopod 3 with ovate propodus and slender dactylus extending to distal margin of carpus; pereopods 4–7 ambulatory with propodi tapering distally; each pereopodal dactylus bearing a distal tooth. Pleotelson triangular, with or without distal row of few stout teeth. **Mature female** spheroid in dorsal view, unsegmented, possibly with two pairs of pereopods and two pairs of posterior tubercles. Ectoparasitic.

Key to cryptoniscus larvae of genera of Capitoniscidae

1. Cryptoniscus larva (fig. 6.27a–e; see female fig. 6.27f) pleotelson with terminal teeth, pereopods 3–5 of similar structure and segment proportions and different from pereopods 6 and 7; parasites of cumaceans ..... *Capitoniscus*

– Cryptoniscus larva (fig. 6.27g–l) pleotelson without terminal teeth, pereopods 3 of different structure and proportions than pereopods 4–7, all similar; host unknown ..... *Carocryptus*

Capitoniscus Bourdon, 1972

Diagnosis. **Male** (paedomorphic cryptoniscus larva) pereopods 3–5 of similar structure and segment proportions and different from those of pereopods 6 and 7. Pleotelson triangular, with distal row of few stout teeth.

Bathypelagic, parasitising cumaceans, Temperate Southern Africa, Southern Ocean, Temperate South America. 3 species (Bourdon, 1972, 1981; Menzies and George, 1972).

Carocryptus Schultz, 1977

Diagnosis. **Male** (paedomorphic cryptoniscus larva) pereopod 3 of different structure and segment proportions from pereopods 4–7. Pleotelson triangular, without distal row of teeth.

Bathypelagic, host unknown. Southern Ocean. 1 species (Schultz, 1977).

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Family Crinoniscidae Bonnier, 1900

Figure 6.28

Members of Crinoniscidae are endoparasitic and can be distinguished from other isopod parasites of barnacles by the lack of teeth on the basal segment of the antennula in males (= cryptoniscus larval stage); females are egg predators (Williams and Boyko, 2006; Buhl-Mortensen et al., 2020.

Diagnosis. **Male** (paedomorphic cryptoniscus larva) (fig. 6.28d–h) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes present. Antennula article 1 without posterior teeth. Coxal plates without teeth. Pereopods 1 and 2 gnathopodal, pereopods 3–7 ambulatory; propodi of pereopods 3–5 quadrate distally with dactyli shorter than propodi, pereopods 6 and 7 tapering distally, dactyli subequal to propodi in length. Pleotelson margin smooth. **Immature female** (fig. 6.28b, c) segments incompletely fused, lacking appendages except for uniarticulated antenna in some species, mandibles and elongate second pereopods. **Mature female** (fig. 6.28a) fusiform or anteriorly globose, posteriorly annulated, lacking appendages (remnants of pereopod 2 present in some species). Endoparasitic.

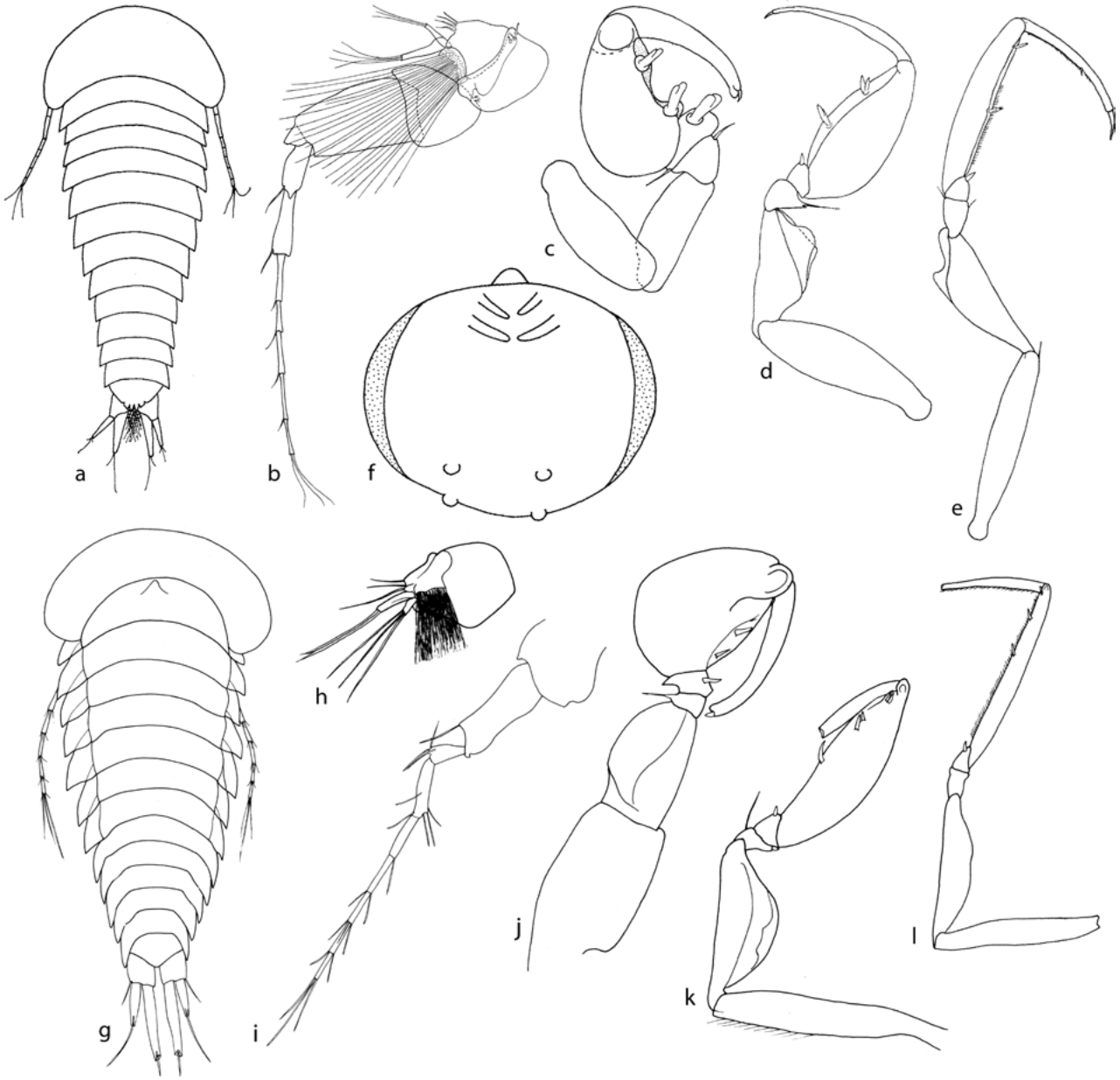


Figure 6.27. Capitoniscidae. *Capitoniscus cumacei* Bourdon, 1972: a, male dorsal view; b, male antennula and antenna; c, male pereopod 1; d, male pereopod 3; e, male pereopod 7; f, female ventral view. *Carocryptus laticephalus* Schultz, 1977: g, male dorsal view; h, male antennula; i, male antenna; j, male pereopod 1; k, male pereopod 3; l, male pereopod 7.

Crinoniscus Pérez, 1900

Diagnosis. As for family.

Subtidal–slope, parasitising sessile and pedunculate barnacles. Temperate Northern Atlantic, Temperate Australasia. 5 species (Buhl-Mortensen et al., 2020).

Proteolepas Darwin, 1854 *nomen dubium*

Diagnosis. As for family (only the immature female is known and is indistinguishable from those of *Crinoniscus* spp.).

Subtidal, parasitising pedunculate barnacles. Tropical Atlantic. 1 species (Buhl-Mortensen et al., 2020).

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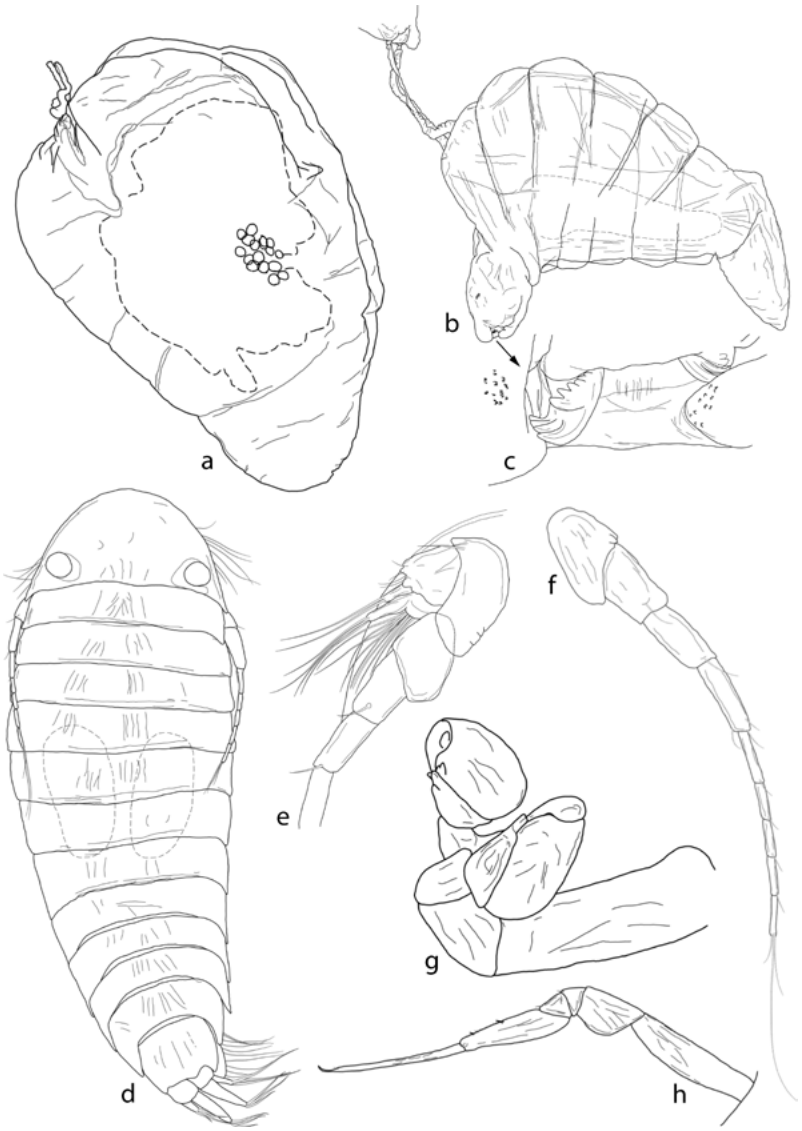


Figure 6.28. Crinoniscidae. *Crinoniscus stroembergi* Buhl-Mortensen, Williams and Boyko, 2020: a, mature female lateral view; b, immature female lateral view; c, close-up of mandibles of immature female; d, male dorsal view; e, male antennula; f, male antenna; g, male pereopods 1 and 2; h, male pereopod 7.

Family Cryptoniscidae Kossmann, 1880

Figure 6.29

Members of Cryptoniscidae are endoparasitic or mesoparasitic, and can be distinguished from other epicarideans by the presence of an elongate rapier-like dactylus (or dactylus and propodus) on at least the seventh (sometimes also the sixth) pereopod of males (= cryptoniscus larval stage). In addition, in at least one genus (*Liriopsis*) the epicaridium larvae exhibit a modified pereopod 6, the dactyl of which is needle-like (Fraisse, 1878; Peresan and Roccatagliata, 2005). Aside from Entoniscidae, this is the only group of epicarideans presently known to exhibit such modification of the sixth legs of

epicaridium larvae. Mature females (except for those of species in *Liriopsis*) have a subdivided attachment process inserted into the host (Boyko, 2014; Peresan and Roccatagliata, 2005). It should be noted that several genera lack a description of one of the life history stages (male, immature female and/or mature female) and their placement in this family is tentative. Some cryptoniscids are hyperparasites of rhizocephalan barnacles.

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped without prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes present. Antennula article 1 without teeth. Coxal plates without teeth. Pereopods 1 and 2 gnathopodal; pereopods 3–5 or 3–6 ambulatory, propodi tapering or quadrate distally, dactyli shorter than propodi; if 3–5 ambulatory then pereopod 6 of 3 segments (third segment extremely long and slender, tapering toward recurved tip, more than twice as long as ischium and basis combined) or 4 segments (terminal segment long and slender, tapering toward tip, approximately as long as ischium and basis combined or terminal segment long and slender, acute at tip, twice as long as all other segments combined) or 6 segments (terminal segment long and slender, acute at tip, as long as all other segments combined); pereopod 7 of 4 segments (terminal segment elongate or globular, undivided or divided, tapering to distal tip, recurved at tip) or 6 segments (propodus tapering distally, dactylus elongate, slender, longer than propodus or as long as all other segments combined). Pleotelson margin smooth. **Mature female** linear (flattened dorsoventrally with 5 lateral lobes on each side or as an elongate smooth sac), recurved strongly (dorsal margin smooth or divided into 6–10 lobes) or body divided by narrow neck into anchor portion embedded in host body and subspherical portion (marsupium) extending from host mantle. Attachment trunk, if present, with 2 or 4 attachment lobes. Mesoparasitic or endoparasitic.

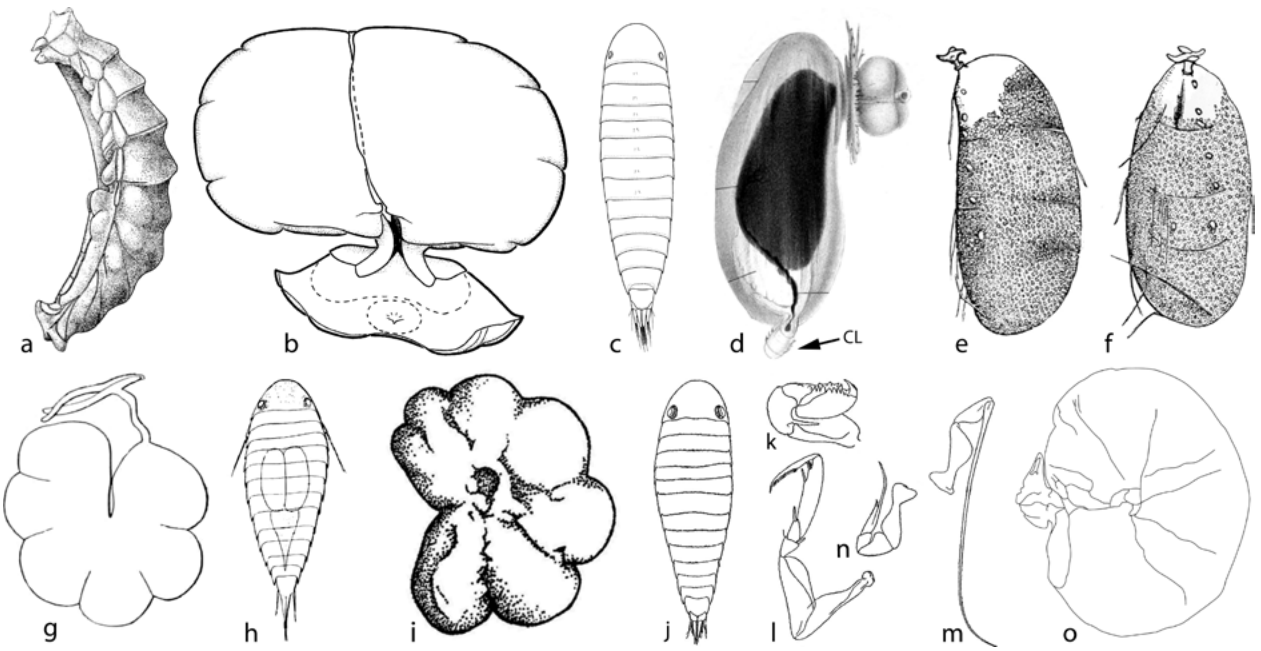


Figure 6.29. Cryptoniscidae. *Enthylacus trivinctus* Pérez, 1920: a, female lateral view. *Liriopsis pygmaea* (Rathke, 1843): b, mature female ventral view; c, male dorsal view. *Cryptoniscus paguri* Fraisse, 1878: d, female lateral view. *Zeuxokoma setosa* (Nierstrasz and Brender à Brandis, 1930): e, female lateral view; f, female ventral view. *Danalia curvata* (Fraisse, 1878): g, mature female lateral view; h, male dorsal view. *Avada kedavra* Boyko, 2014: i, mature female lateral view; j, male dorsal view; k, male pereopod 2; l, male pereopod 4; m, male pereopod 6; n, male pereopod 7. *Cabirnalia nausicaa* Boyko and van der Meij, 2018: o, mature female lateral view. Abbreviations: CL, cryptoniscus larva.

Key to mature females of genera of Cryptoniscidae

Eumetor not included in key; it was poorly described and placement in Cryptoniscidae is not certain.

1. Found inside of host body unattached (fig. 6.29a) ..... *Enthylacus*
– External to host and attached to host body 2
2. Approximately half of body (fig. 6.29b; see also male, fig. 62.8c) embedded in host; attachment process lacking ..... *Liriopsis*
– Most of body not embedded in host; attachment via process with terminal lobes 3

3. Body of mature female not recurved 4
– Body of mature female recurved 5
4. Body (fig. 6.29d) attached to host by short process with 2 terminal bulbous lobes ..... *Cryptoniscus*
– Body (fig. 6.29e, f) attached to host by short process with 4 terminal hook-like lobes ..... *Zeuxokoma*
5. Body (fig. 6.29g; see also male, fig. 6.29h) attached to host with long process bearing 4 terminal slender lobes ..... *Danalia*
– Body attached to host with short process bearing stout terminal lobes 6
6. Attachment process (fig. 6.29i; see also male, fig. 6.29j–n) with 4 hook-like terminal lobes ..... *Avada*
– Attachment process (fig. 6.29o) with 2 flattened, triangular, terminal lobes 7
7. Dorsal margin of body smooth, terminal lobes triangular ..... *Cabirnalia*
– Dorsal margin of body lobed, terminal lobes ovate ..... *Cryptodanalia*

Avada Boyko, 2014

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body with striations not described. Head anterior margin with triangular median region reflexed posteroventrally (visible in ventral view). Coxal plates not described. Pereopods 3–5 ambulatory, propodi tapering distally; pereopod 6 of 3 segments, segment 3 extremely long and slender, tapering toward recurved tip, more than 2 times as long as ischium and basis combined; pereopod 7 of 4 segments, terminal segment long, slender, subdivided by median slit into ventral and dorsal portions, dorsal portion twice length of ventral, recurved at tip. **Mature female** with strongly convex smooth dorsal margin smooth or divided into 7–9 lobes, ventral side shorter, shallow medial indentation present. Attachment trunk short with 4 short strongly sclerotised attachment lobes.

Intertidal, parasitising sacculinid rhizocephalans, and anomuran and brachyuran decapods. Central Indo-Pacific, Temperate Northern Pacific, and Eastern Indo-Pacific. 3 species (Boyko, 2014).

Cabirnalia Boyko and van der Meij, 2018

Diagnosis. **Male** (paedomorphic cryptoniscus larva) not described. **Mature female** body recurved strongly, circular in outline; strongly convex dorsal margin without lobes but with cuticular indentations indicating segmentation; ventral sides meeting medially, with several small, platelike areas demarcated at midpoint. Attachment trunk short, with 1 attachment lobe, medially divided and expanded into 2 broad sections.

Subtidal, parasitising cryptochirid crabs. Eastern Indo-Pacific. 1 species (Boyko and van der Meij, 2018).

Cryptodanalia Williams, Boyko and Zheng, 2026

Diagnosis. **Male** (paedomorphic cryptoniscus larva) not described. **Mature female** body recurved strongly, U-shaped in outline; strongly convex dorsal margin with lobes; ventral sides not meeting medially, with several small, platelike areas demarcated at midpoint. Attachment trunk short, with 2 ovate, swollen attachment lobes.

Slope, parasitising galatheid squat lobsters. Temperate Australasia. 1 species (Williams et al., 2026).

Cryptoniscus Müller, 1864

Diagnosis. **Male** coxal plates not described. Pereopods 3–6 ambulatory, propodi quadrate distally, dactyli shorter than propodi; pereopod 7 of 6 segments, propodus tapering distally, dactylus elongate, slender, longer than propodus. **Immature females** vermiform, swollen; head as pair of inflated lobes extending through cuticle of host. **Mature female** body flattened dorsoventrally with 5 lateral lobes on each side; anterior and posterior ends tapered, anterior end more strongly; ventral surface with medial slit terminating in rounded area where head extends out through body wall of host.

Subtidal, parasitising rhizocephalan barnacles on hermit crabs. Tropical Atlantic, Temperate North Atlantic. 2 species (Fraisse, 1878).

Danalia Giard, 1887

Diagnosis. **Male** oral cone not described. Pereopods 3–5 ambulatory, propodi quadrate distally; pereopod 6 of 4 segments, terminal segment long and slender, tapering toward tip, approximately as long as ischium and basis combined; pereopod 7 of 4 segments, terminal segment elongate, undivided, tapering to distal tip, recurved at tip. **Mature female** elongate and strongly recurved; strongly convex dorsal margin with 6–10 weakly to moderately pronounced lobes, ventral side strongly concave, with large median gap between lobes. Attachment trunk variable in length with 4 short to elongate flexible and fragile attachment lobes. Thickened anteroventral shield area small to moderate in size.

Subtidal, parasitising galatheid squat lobsters, brachyuran crabs, and rhizocephalans on brachyuran crabs. Tropical Atlantic, Temperate Northern Atlantic, Western and Central Indo-Pacific, Eastern Indo-Pacific. 14 species (Boyko, 2014).

Enthylacus Pérez, 1920

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body cuticular striations not described. Oral cone not described. Antennula not described. Coxal plates not described. Pereopods 3–5 ambulatory; propodi of 3–5 tapering distally; pereopod 6 of 4 segments, terminal segment long and slender, acute at tip,

twice as long as all other segments combined; pereopod 7 of 4 segments, terminal segment globular at base, tapering in distal half to acute tip, undivided, recurved at tip. Pleotelson margin not described. **Immature female** with dorsal segmentation and ventral medial lobes, body recurved slightly; anterior and posterior ends with triangular shield-like projection. **Mature female** not described.

Subtidal, parasitising rhizocephalan barnacles on brachyuran crabs. Western Indo-Pacific. 1 species (Pérez, 1920).

Eumetor Kossmann, 1872

Diagnosis. **Male** (paedomorphic cryptoniscus larva) illustrated but with relevant characters not described. **Mature female** not described but Kossmann (1872) noted the mature female differed little from *Liriopsis pygmaea* (Rathke, 1843).

Subtidal, parasitising rhizocephalans on brachyuran crabs. Central Indo-Pacific. 1 species (Kossmann, 1872).

Liriopsis Schultze *in* Müller, 1859

Diagnosis. **Male** (paedomorphic cryptoniscus larva) pereopods 3–5 ambulatory, propodi quadrate distally; pereopods 6 and 7 of 6 segments each, terminal segment long and slender, acute at tip, as long as all other segments combined. **Mature female** body divided by narrow neck into anchor portion embedded in host body and subspherical portion (marsupium) extending from host mantle; anchor portion with 3 parallel hollow bars, ventral surface concave; marsupium ventral surface with longitudinal median slit bearing finger-shaped process at anterior end and 6 internal digitations at posterior end.

Subtidal, parasitising rhizocephalans on hermit crabs and king crabs. Temperate Northern Atlantic and Pacific, Temperate South America. 2 species (Peresan and Roccatagliata, 2005).

Zeuxokoma Grygier, 1993

Diagnosis. **Male** (paedomorphic cryptoniscus larva) not described. **Mature female** body elongate, relatively linear smooth sac with pronounced thickened anteroventral shield; internal subdivisions present but external lobes lacking; trunk short relative to body with 4 stout strongly sclerotized attachment hooks.

Subtidal–slope, parasitising caridean shrimps. Tropical Atlantic, Central Indo-Pacific, Temperate Northern Pacific, Eastern Indo-Pacific. 6 species (Boyko, 2014).

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Family Cumoechidae Boyko and Williams, 2023

Figure 6.30

Members of Cumoechidae are ectoparasitic in the marsupium of cumacean hosts. They can be distinguished from other isopod parasites by a conical head and an elongate antennular segment 1 with c. 16 acute marginal teeth of the cryptoniscus larva and the shape of the female body with a long median cleft bearing antennae and pereopods at the anterior end (Hansen, 1916).

Diagnosis. **Epicaridium larva** (fig. 6.30h) with antenna as long as body; setae on antenna and uropodal exopod and endopod as long as or longer than body. **Male** (paedomorphic cryptoniscus larva) body elongate (fig. 6.30b–g). Head longer than wide, conical, posterior margin no wider than pereomere 1; eyes absent. Antennula article 1 elongate with c. 16 marginal acute teeth. Coxal plates with posterior margins toothed. Pereopods 1–3 gnathopodal, pereopods 4–7 ambulatory with propodi tapering distally, dactyli as long as propodi. Pleotelson margin with 10 teeth, distalmost pair longest. **Mature female** (fig. 6.30a) spheroid in dorsal view, compressed dorsoventrally, segmented, ventral surface with long median cleft and raised segmented pad surrounding cleft; anterior region with reduced antennae and pair of pereopods. Ectoparasitic.

Cumoechus Hansen, 1916

Diagnosis. As for family.

Slope–bathyal, parasitising cumaceans. Arctic. 1 species (Boyko and Williams, 2023; Hansen, 1916).

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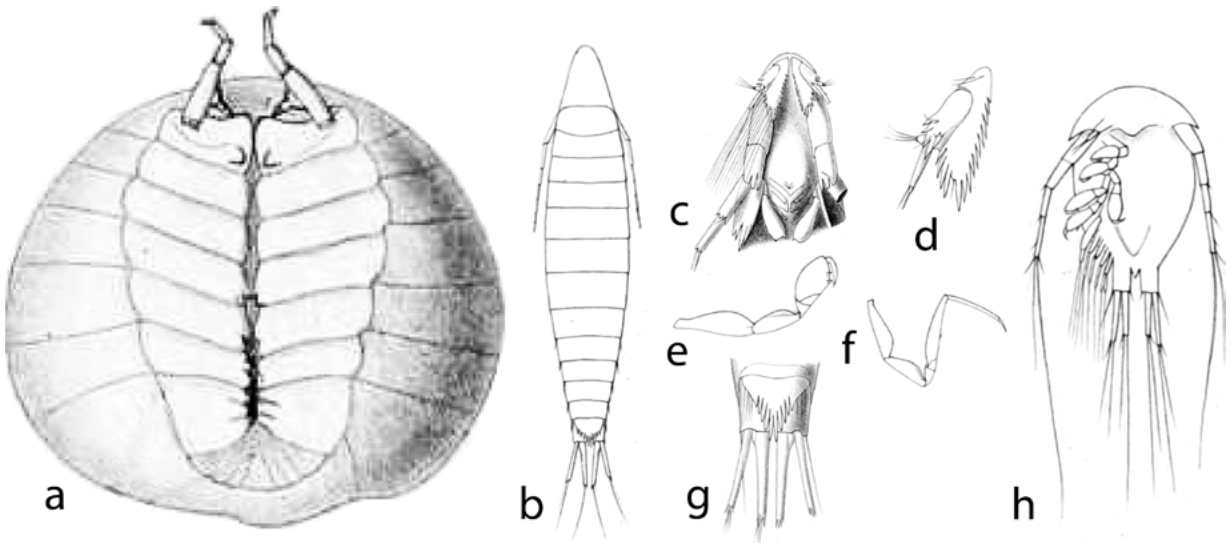


Figure 6.30. Cumoechidae. *Cumoechus insignis* Hansen, 1916: a, female dorsal view; b, male dorsal view; c, male head, ventral view; d, male antennula; e, male pereopod 1; f, male pereopod 7; g, male pleon, dorsal view; h, epicaridium larva ventral view.

Family Cyproniscidae Giard and Bonnier, 1887

Figure 6.31

Members of Cyproniscidae are ectoparasitic within the carapace of ostracod hosts; no other epicarideans are known to parasitise ostracods. There are no clear synapomorphies for the family because the two genera have very different cryptoniscus larval and female morphologies, as well as feeding strategies (Hosie, 2008; Buhl-Mortensen et al., 2020.

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly or posteriorly. Eyes present or absent. Antennula article 1 with 6–12 posterior teeth. Coxal plates with 5–8 teeth. Pereopods 1 and 2 gnathopodal, subequal in size or with 2 much larger than 1; pereopods 3–7 ambulatory, propodi of pereopods 3–5 distally quadrate, 6 and 7 tapering distally or 3–7 all tapering distally. Pleotelson margin with or without teeth; anal tube present or absent. **Mature females** with or without rudimentary segmentation; rudimentary mouthpart and pereopodal appendages present or absent. Attachment tube to host present or absent. Ectoparasitic.

Key to genera of Cyproniscidae

1. Cryptoniscus larvae (fig. 6.31c) without anal tube; mature female (fig. 31a, b) attached to host via slender tube; direct feeding on host. ..... *Cyproniscus*[1]

– Cryptoniscus larvae (fig. 6.31g–i) with anal tube; mature female (fig. 6.31d–f) not attached to host via slender tube; cryptoniscus larvae are egg predators. ..... *Onisocryptus*

[1] Four species described in *Cyproniscus* do not belong to this genus: *C. binoculis* Menzies and George, 1972 was transferred to *Scalpelloniscus* (Hemioniscidae) by Grygier (1981), *C. peruvicus* Menzies and George, 1972 was transferred to *Capitoniscus* Bourdon, 1972 (Capitoniscidae) by Boyko and Williams (2023); *C. decemspinosus* Menzies and George, 1972 and *C. octospinosus* Menzies and George, 1972 are left in *Cyproniscus* for now because there is no other taxon to accommodate them and erecting a new genera is unwarranted until they are fully redescribed. We do not consider the characters of the latter two species in the diagnosis for *Cyproniscus*.

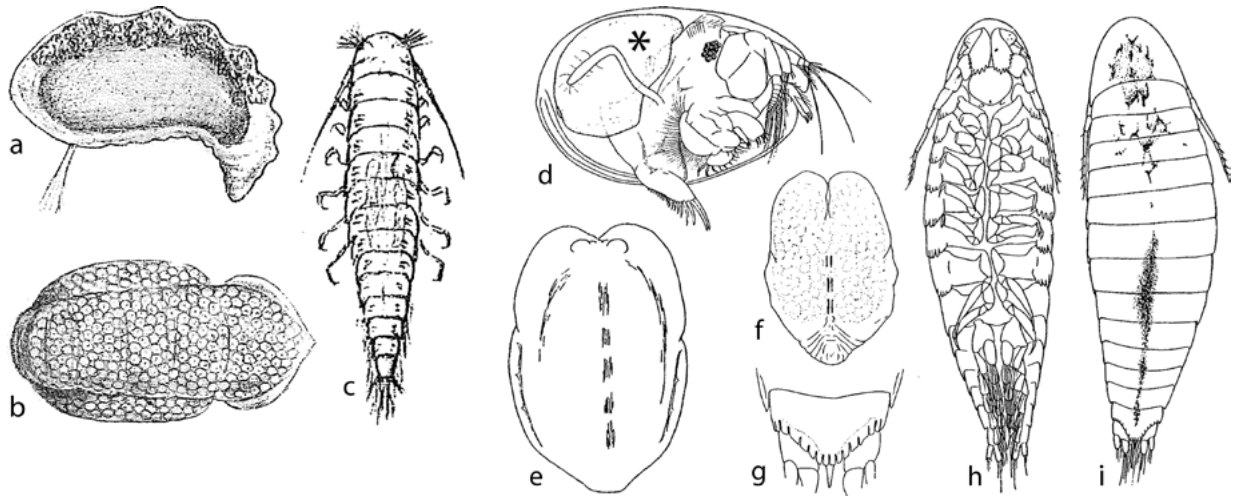


Figure 6.31. Cyproniscidae. *Cyproniscus cypridinae* (G.O. Sars, 1883): a, female lateral view; b, ovigerous female dorsal view; c, male dorsal view. *Onisocryptus ovalis* (Shiino, 1942): d, female within host ostracod (parasite shown by asterisk); e, female dorsal view; f, female ventral view; g, male pleon and anal tube, dorsal view; h, male ventral view; i, male dorsal view.

Cyproniscus Kossmann, 1884

Diagnosis. **Male** (paedomorphic cryptoniscus larva) oral cone directed anteriorly. Eyes absent. Antennula article 1 with 6–10 posterior teeth. Coxal plates with 8 teeth. Pereopods 1 and 2 gnathopodal, subequal in size; pereopods 3–7 ambulatory, propodi of pereopods 3–5 distally quadrate, 6 and 7 tapering distally. Pleotelson margin without teeth; anal tube absent. **Mature female** with rudimentary segmentation, pleon recurved, much smaller than pereon; mouthpart and pereopodal appendages lacking. Attachment tube to host present.

Subtidal–shelf, parasitising ostracods. Temperate Northern Atlantic, Temperate Southern Africa, Southern Ocean. 4 species and 1 subspecies (Nielsen and Strömberg, 1973a, b; Sars, 1899).

Onisocryptus Schultz, 1977

Diagnosis. **Male** (paedomorphic cryptoniscus larva) oral cone directed posteriorly. Eyes present or absent. Antennula article 1 with 10–12 posterior teeth. Coxal plates with 5 teeth. Pereopods 1 and 2 gnathopodal, pereopod 2 much larger than 1; pereopods 3–7 ambulatory, subequal in size and shape, propodi of pereopods 3–7 tapering distally or 3–5 distally quadrate and 6 and 7 tapering distally. Pleotelson margin with teeth; anal tube present. **Mature female** without distinct segmentation; some rudimentary mouthpart and pereopodal appendages at anterior end present. Attachment tube to host absent; egg predators.

Subtidal–bathyal, parasitising ostracods. Temperate Northern Pacific, Southern Ocean. 3 species (Abe and Horiuchi, 2000; Strömberg, 1983).

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Family Dajidae G.O. Sars, 1883

Figures 6.32, 6.33

Dajidae is a rather heterogeneous grouping of ectoparasitic genera with body shapes ranging from dorsoventrally flattened and ovate to heart-shaped, elongate, pyriform or spheroid. Future analyses, using molecular data and morphological data from presently unknown cryptoniscus larvae will, at a minimum, change the allocation of species to genera and likely break up the taxon into two or more families. Characters of females, males and cryptoniscus larvae are included, as all these life history stages exhibit phylogenetically informative traits; those of epicaridium larvae may also be informative but they are known from too few species to warrant inclusion here. Females of species in some genera, such as *Akrophryxus* and *Telephryxus*, are radically divergent from the "typical" "back-pack isopod" shape seen in species of *Holophryxus* and *Zonophryxus*, whereas species in other genera (e.g. *Antephrya* and *Streptodajus*) are very similar to each other.

Diagnosis. **Female** body semicircular, heart-shaped, elongate, pyriform, ovate or spheroid, pereomeres segmented or unsegmented; head visible or not visible dorsally (with or without frontal lamina), displaced facing anteriorly, or internalised into pereon; anterolateral corners of lateral lobes rounded or modified into recurved, elongate lobes with spoon-like tips. Eyes absent. Antennula present (segmented or unsegmented) or absent; antenna present (segmented or unsegmented) or absent. Oral sucker present or absent. 4–6 pairs of oostegites or oostegites fused. 4–6 pairs of gnathopodal pereopods, subequal in size and shape, or pereopod 5 modified into large clasper, all at anterior end of pereon, pereopods 1–4 at anterior end and 5 at posterolateral margin, or widely spaced. Pleon segmented, unsegmented, vermiform, or modified into thickened plate with medial holes; pleopods and uropods present or absent. **Male** body flat or recurved, pereomeres subequal in width, head wider than long, rounded or triangular, distinct from or fused with pereomere 1. Eyes present or absent. Antennula and antenna unsegmented or segmented. Pereomere 7 distinct from or fused to pleon. 6 or 7 pairs of pereopods (7 reduced or absent). Pleon segments distinct or fused, pleopods absent, anal cone and uropods present or absent. **Cryptoniscus larva** body teardrop-shaped or elongate, head with posterolateral lobes or not, head rounded, horseshoe-shaped, helmet-shaped, or triangular, eyes present or absent. Antennula with or without teeth on basal segment. Oral sucker present or absent. Pereomeres with toothed, serrate or smooth coxal plates. Pereopods 1, 1 and 2, or 1–6 gnathopodal, others ambulatory, longer, anterior pairs with or without multifid setae on propodi and carpi, posterior pairs always with multifid setae on propodi and carpi. Pleotelson rounded, quadrate, or triangular, with or without teeth. Ectoparasitic.

Key to females of genera of Dajidae, including some characters of males

Cryptocisus, *Dolichophryxus*, *Neritoniscus* and *Paraspidophryxus* are not in the key to genera; they are known only from cryptoniscus larvae. For these genera see figs 6.38 and 6.39.

1. Body of mature female spherical 2
– Body of mature female not spherical, compressed dorsoventrally 3
2. Mature female (fig. 6.32a) without antennula, attachment plate (pleon) triangular, male (fig. 6.32b) with 6 pairs of pereopods; parasites of brachyurans (Ethusidae, Goneplacidae and Palicidae) ..... *Akrophryxus*
– Mature female (fig. 6.32c) with antennula, attachment plate (pleon) subquadrate, male (fig. 6.32d) with 7 pairs of pereopods (seventh pair reduced); parasites of anomurans (Munidopsidae) ..... *Telephryxus*
3. Mature female with attachment processes 4
– Mature female without attachment processes 5
4. Mature female (fig. 6.32e, f) with attachment processes at anterior end, male with rudimentary pereopod 7; parasites of euphausiids ..... *Oculophryxus*
– Mature female (fig. 6.32g) with attachment processes at posterior end, male with well-developed pereopod 7; parasites of euphausiids ..... *Heterophryxus*
5. Mature female (fig. 6.32h; see also male, fig. 6.32i) pleon modified as slender, whip-like structure used by males for attachment; parasites of mysids ..... *Aspidophryxus*
– Mature female pleon not modified as slender, whip-like structure 6
6. Mature female pleotelson distinct, bilobed, posterolateral margins of marsupium extend posteriorly to or beyond pleotelson 7
– Mature female pleotelson indistinct, posterolateral margins of marsupium not extending posteriorly to or beyond pleotelson 8

7. Mature female (fig. 6.32j–l) body unsegmented, heart-shaped; parasites of mysids ..... *Prodajus*

– Mature female (fig. 6.32m) body segmented anteriorly and posteriorly, ovate; parasites of mysids ..... *Prophryxus*

8. Mature female with segmented pleon 9

– Mature female with unsegmented pleon 13

9. Mature female (fig. 6.32n; see also male, fig. 6.32o) with lateral portions of marsupium directed laterally, host(s) unknown ..... *Allophryxus*

– Mature female with lateral portions of marsupium directed medioventrally, meeting in midline of ventral surface or nearly so 10

10. Mature female with pleon indistinctly segmented dorsally 12

– Mature female with pleon distinctly segmented dorsally 11

11. Mature female (fig. 6.32p, q) marsupium with distinct anterior "shoulders" extending anterior to frontal margin of head, male with unsegmented pleon; parasites of mysids ..... *Dajus*

– Mature female (fig. 6.33a) marsupium without distinct anterior "shoulders," head and anterolateral margins of marsupium on same plane, male with segmented pleon; parasites of lophogastrids ..... *Arthrophryxus*

12. Mature female (fig. 6.33b–d) with pereopods and mouthparts directed anteriorly; parasites of mysids ..... *Streptodajus*

– Mature female (fig. 6.33e) with pereopods and mouthparts directed ventrally; parasites of mysids and euphausiids ..... *Notophryxus*

13. Mature female with distinct dorsal pereon segmentation 14

– Mature female with indistinct or absent dorsal pereon segmentation 15

14. Mature female (fig. 6.33f) with 5 distinct pereon segments indicated dorsally; host(s) unknown ..... *Colophryxus*

– Mature female (fig. 6.33g) with three distinct pereon segments indicated dorsally; host(s) unknown ..... *Antephrya*

15. Mature female (fig. 6.33h) length and width approximately subequal; parasites of aegid isopods ..... *Aegophila*

– Mature female longer than wide 16

16. Mature female (fig. 6.33i, j; see also male fig. 6.33k) with posterior margin of body bearing row of triangular processes; parasites of caridean shrimps ..... *Zonophryxus*

– Mature female with posterior margin of body smooth 17

17. Mature female (fig. 6.33l, m; see also male fig. 6.33n) with frontal lamina projecting anterior to head, posterior lobe extending beyond posterior margins of marsupium; parasites of dendrobranchiate and caridean shrimps ..... *Holophryxus*

– Mature female (fig. 6.33o, p; see also male, fig. 6.33q) without frontal lamina or posterior lobe extending beyond posterior margins of marsupium; parasites of euphausiids ..... *Branchiophryxus*

Aegophila Bresciani, 1966

Diagnosis. **Female** body semicircular, wider than long; pereomeres with faint dorsal indications; head subsumed into pereon, not extending anteriorly beyond anterior margins of lateral lobes. Eyes absent. Antennula and antenna absent. Oostegites 1 large, ovate, 2–5 small, slender to subquadrate. Pereopods 1–5 gnathopodal, subequal in size and shape; distoventral margin of propodi expanded into cup to receive tips of dactyli. Pleon minute, vermiform, segments fused. **Male** with pereomeres subequal in width, head wider than long, fused with pereomere 1. Eyes absent. Antennula of one segment; antenna segmented, short. Pleon segments fused, pleopods absent, anal cone present, uropods absent. **Cryptoniscus larva** body teardrop-shaped, eyes absent. Antennula without teeth on basal segment. Oral sucker present. Pereomeres without toothed coxal plates. Pereopods 1 gnathopodal, dactyli short, slightly curved, propodus inner margin folded, bearing 2 flat multifid setae; carpus without multifid setae. Pereopods 3–6 dactyli more elongate than 1 and 2, propodi more elongate, narrower than 1

and 2, bearing 2 flat multifid setae; carpi without multifid setae. Pereopod 7 dactylus and propodus subequal in length to those of pereopods 3–5, propodus bearing 2 large, erect, multifid setae, carpus without multifid setae. Pleotelson without teeth.

Slope, parasitising aegid isopods. Arctic, Temperate Northern Pacific. 2 species (Williams and Boyko, 2021).

Akrophryxus Williams and Boyko, 2021

Diagnosis. **Female** body spheroid, unsegmented; head not visible externally. Eyes absent. Antennula absent; antenna as oblong flat plate lateral to oral cone. Oostegite 1 largest, ovate with small posterior accessory lobe; oostegites 2–5 small, becoming larger posteriorly. Pereopods 1–5 gnathopodal, subequal in size and shape. Pleon modified as oblong, narrow, thickened plate with 3 circular medial holes, largest surrounding antennula of host. **Male** with pereomeres subequal in width, head wider than long, fused with pereomere 1. Eyes absent. Antennula of few small, stacked, disc-like segments; antenna as broad elongate lobes lateral to oral cone. Pereomere 7 fused to pleon. 6 pairs of subequal pereopods (pereopod 7 absent). Pleon segments fused, pleopods, anal cone, and uropods absent. **Cryptoniscus larva** body teardrop-shaped, eyes present. Antennula without teeth on basal segment. Oral sucker absent. Pereomeres without toothed coxal plates. Pereopods 1 and 2 subequal, dactyli short, slightly curved, propodus inner margin folded, bearing 2 flat multifid setae; carpus with 1 distal multifid seta. Pereopods 3–5 dactyli more elongate than 1 and 2, curved, propodi more elongate, narrower, than 1 and 2, inner margin of each folded, bearing 2 flat multifid setae; carpi each with 1 distal multifid seta. Pereopod 6 dactylus subequal in length to those of pereopods 3–5, propodus more elongate and narrower than those of pereopods 3–5, inner margin slightly folded, bearing 2 erect, multifid setae, carpus with 1 distal multifid seta. Pereopod 7 similar to pereopod 6 but with elongate dactylus extending to distal margin of merus, carpus with 1 flat multifid seta. Pleotelson without teeth.

Slope, parasitising ethusiid, goneplacid, and palicid brachyurans. Western and Central Indo-Pacific, Temperate Northern Pacific. 3 species (Williams et al., 2022).

Allophryxus Koehler, 1911

Diagnosis. **Female** body heart-shaped; pereomeres indicated dorsally and ventrally; head with subquadrate frontal lamina, directed anteriorly, extending well beyond anterior margins of lateral lobes. Antennula (or antenna) of 1 segment, other absent. 5 pairs of oostegites. Pereopods 1–5 gnathopodal, subequal in size. Pleon segmented, extending posteriorly beyond posterior margins of lateral lobes; pleomeres 1–3 with medial projection. Possible pleopods present on last 2 pleomeres; uropods present, displaced to same side of pleotelson. **Male** body recurved with pereomeres subequal in width, head wider than long, fused to pereomere 1. Eyes absent. Antennula not described; antenna segmented. Pleon large, triangular, segments fused; pleopods and anal cone absent; minute uropods present. **Cryptoniscus larva** unknown.

Mesopelagic–bathypelagic, host(s) unknown. Temperate Northern Atlantic. 1 species (Koehler, 1911).

Antephrya Schultz, 1978

Diagnosis. **Female** body elongate ovate, tapering posteriorly; some pereomeres indicated dorsally; head with frontal lamina scarcely visible dorsally, directed anterodorsally, extending anteriorly slightly beyond anterior margins of lateral lobes. Antennula and antenna not described. Oral sucker present. Oostegites not described. Pereopods 1–5 gnathopodal, subequal in size, displaced to anterior margin below head. Pleon not segmented, extending posteriorly beyond posterior margins of lateral lobes; pleomeres with 4 medial irregular projections. Pleopods and uropods absent. **Male** and **cryptoniscus larva** unknown.

Bathypelagic, host(s) unknown. Southern Ocean. 1 species (Schultz, 1978).

Arthrophryxus Richardson, 1908

Diagnosis. **Female** body ovate; pereomeres segmented dorsally; head without frontal lamina, not extending beyond anterior margins of lateral lobes. Eyes absent. Antennula as 1 flat lobe, antenna segmented. 5 pairs of oostegites. Pereopods 1–5 gnathopodal, subequal in size and shape. Pleon segmented, pleopods and uropods absent. **Male** body recurved, pereomeres subequal in width; head triangular, wider than long, fused with pereomere 1. Eyes absent. Antennula and antenna not described. 7 pairs of pereopods. Pleon segmentation visible dorsally, pleopods, anal cone and uropods absent. **Cryptoniscus larva** unknown.

Bathypelagic, parasitising lophogastrids. Temperate Northern Pacific. 1 species (Richardson, 1908a).

Aspidophryxus G.O. Sars, 1883

Diagnosis. **Female** body heart-shaped; pereomeres with faint dorsal indications; head with subquadrate frontal lamina, ventrally directed, slightly extending anteriorly beyond anterior margins of lateral lobes. Eyes absent. Antennula and antenna of one segment each. Oostegites fused. Pereopods 1–5 gnathopodal, ischia progressively longer in posterior pairs. Pleon vermiform, segments fused. **Male** with pereomeres subequal in width, head wider than long, distinct from pereomere 1. Eyes absent. Antennula of one segment; antenna segmented, long. Pleon segments fused, pleopods absent, anal cone and uropods present. **Cryptoniscus larva** body teardrop-shaped, eyes absent. Antennula without teeth on basal segment. Oral sucker present. Pereomeres without toothed coxal plates. Pereopods 1–5 not described. Pereopod 6 dactylus elongate, propodus bearing 3 short, multifid setae, carpus with 1 simple(?) seta. Pereopod 7 similar to pereopod 6 but propodus bearing 2 large, erect multifid setae, carpus with 1 simple(?) seta. Pleotelson without teeth.

Subtidal–shelf, parasitising mysids, Tropical Atlantic, Temperate Northern Atlantic, Temperate Northern Pacific. 5 species (Shimomura, 2017).

Branchiophryxus Caullery, 1897

Diagnosis. **Female** body elongate ovate; pereomeres indicated dorsally only in median; head without narrow frontal lamina, not extending anteriorly beyond anterior margins of lateral

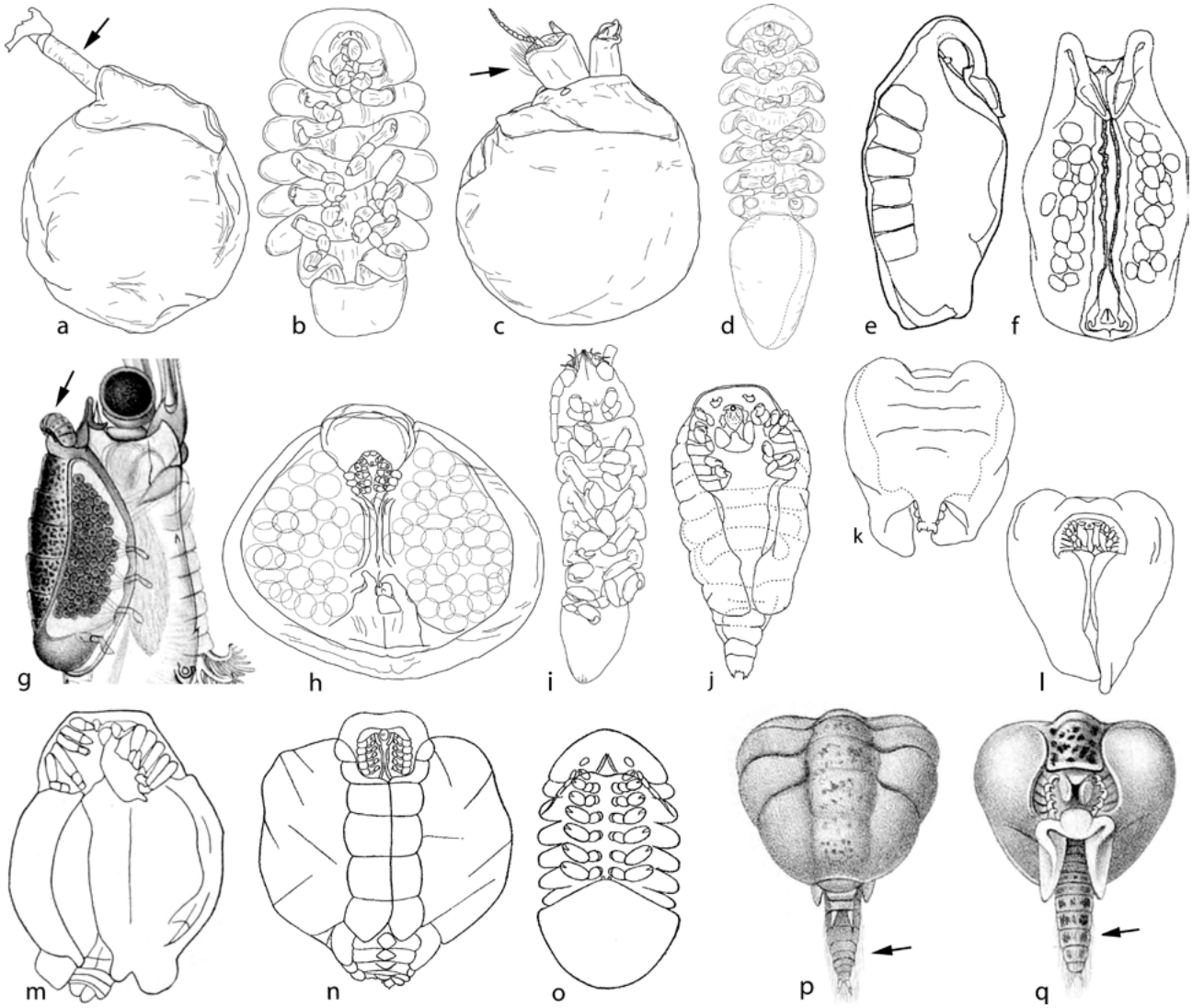


Figure 6.32. Dajidae. *Akrophryxus milvus* Williams and Boyko, 2021: a, female lateral view, shown attached to host antenna (arrow); b, male ventral view. *Telephryxus clypeus* Williams and Boyko, 2021: c, female lateral view, shown attached to host antennula (arrow); d, male ventral view. *Oculophryxus bicaulis* Shields and Gómez-Gutiérrez, 1996: e, female lateral view; f, female ventral view. *Heterophryxus appendiculatus* G.O. Sars, 1885: g, female lateral view, shown attached to host *Euphausia pellucida* Dana, 1850, male shown by arrow. *Aspidophryxus discoformis* Boyko and Williams, 2012: h, female ventral view; i, male ventral view. *Prodajus curviabdominalis* Shimomura, Ohtsuka and Naito, 2005: j, immature female (stage 2) ventral view; k, mature female dorsal view; l, mature female ventral view. *Prophryxus alascensis* Richardson, 1909: m, mature female ventral view. *Allophryxus ruber* Koehler, 1911: n, female ventral view; o, male ventral view. *Dajus siriellae* G.O. Sars, 1885: p, female dorsal view, arrow shows male attached; q, female ventral view, arrow shows male attached.

lobes. Antennula as flat plates, antenna absent. 4 pairs of oostegites. Pereopods 1–4 gnathopodal, subequal in size. Pleon minute, fused; pleopods and uropods absent. **Male** body flattened with pereomeres subequal in width, head wider than long, posterior margin raised and sloping towards anterior margin, fused to pereomere 1. Eyes absent. Antennula rudimentary, antenna segmented. Pleon rounded, unsegmented; pleopods, anal cone and uropods absent. **Cryptoniscus larva** body elongate, head triangular; eyes absent. Antennula basal segment not described. Oral sucker present. Pereomere coxal plates not described. Pereopods 1–5 short, 6 and 7 greatly elongated (pereopods otherwise not described). Pleotelson without teeth.

Shelf–bathypelagic, parasitising euphausiids. Temperate Northern Atlantic. 3 species (Nierstrasz and Brender à Brandis, 1931).

Colophryxus Richardson, 1908

Diagnosis. **Female** body ovate; pereomeres indicated dorsally; head with narrow frontal lamina, directed anteriorly and

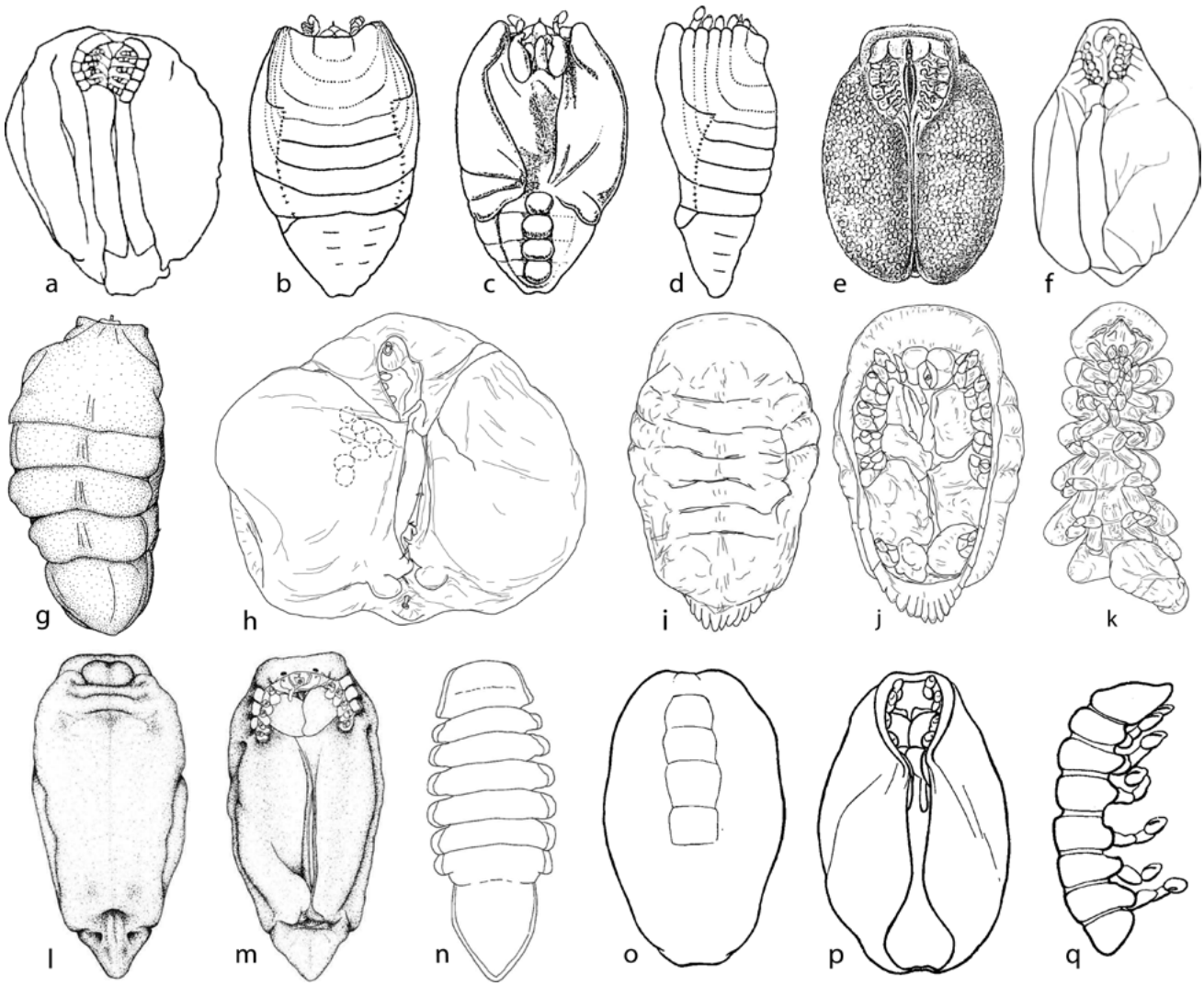


Figure 6.33. Dajidae. *Arthrophryxus beringanus* Richardson, 1908: a, female ventral view. *Streptodajus equilibrans* Nierstrasz and Brender à Brandis, 1923: b, female dorsal view; c, female ventral view; d, female lateral view. *Notophryxus ovoides* G.O. Sars, 1883: e, female with brood of eggs, ventral view. *Colophryxus novangliae* Richardson, 1908: f, female ventral view. *Antephrya limacis* Schultz, 1978: g, female dorsal view. *Aegophila cappa* Williams and Boyko, 2021: h, female ventral view. *Zonophryxus probisowa* Boyko and Williams, 2021: i, female dorsal view; j, female ventral view; k, male ventral view. *Holophryxus acanthephyrae* Stephensen, 1912: l, female dorsal view; m, female ventral view; n, male dorsal view. *Branchiophryxus koehleri* Nierstrasz and Brender à Brandis, 1931: o, female dorsal view; p, female ventral view; q, male lateral view.

extending well beyond anterior margins of lateral lobes. Antennula and antenna not described. 4 pairs of oostegites. Pereopods 1–5 gnathopodal, subequal in size. Pleon fused, extending slightly beyond posterior margins of lateral lobes; pleopods and uropods absent. **Male** body recurved with pereomeres subequal in width, head wider than long, posterior margin raised and sloping towards anterior margin, fused to pereomere 1. Eyes absent. Antennula and antenna not described. Pleon large, swollen, indistinctly segmented; pleopods, anal cone and uropods absent. **Cryptoniscus larva** unknown.

Bathypelagic, host(s) unknown. Temperate Northern Atlantic. 1 species (Richardson, 1908b).

Cryptocisus Schultz, 1977

Diagnosis. **Female** and **male** unknown. **Cryptoniscus larva** body elongate, head horseshoe-shaped; eyes absent. Antennula without teeth on basal segment. Oral sucker absent. Pereomeres with serrate coxal plates margins, without teeth. Pereopods 1–6 gnathopodal, 1 shorter than 2–6, dactyli stout, ventrally serrate; 1 with stout setae on propodus and carpus, 2–6 propodi with 2 erect multifid setae, carpus with 1 multifid seta; pereopod 7 ambulatory, dactylus, propodus and ischium long; dactylus smooth ventrally, bearing distal tooth; propodus with 2 erect multifid setae ventrally and row of spines dorsally, carpus with 1 erect multifid setae. Pleotelson with distomedial region

quadrate, bearing 1 small spine at each posterolateral corner.

Shelf–bathypelagic, host(s) unknown. Southern Ocean. 1 species (Schultz, 1977).

Dajus Krøyer, [1842]

Diagnosis. **Female** body heart-shaped; pereomeres with dorsal segmentation; head with narrow frontal lamina, directed anteriorly, not extending beyond anterior margins of lateral lobes. Eyes absent. Antennula and antenna segmented. 5 pairs of oostegites. Pereopods 1–5 gnathopodal, subequal in shape, all at anterior end. Pleon segmented, pleopods present as 1 pair of large lobes on pleomere 1 and rudimentary pairs on other pleomeres, uropods present. **Male** with pereomeres subequal in width, head wider than long, rounded, fused to pereomere 1. Eyes absent. Antennula and antenna segmented. Pleon unsegmented, pleopods absent and anal cone absent (anal slit present), rudimentary uropods present. **Cryptoniscus larva** body teardrop-shaped, eyes absent. Antennula with teeth on basal segment. Oral sucker present. Pereomeres with serrations on coxal plates but without teeth. Pereopods 1 and 2 gnathopodal, dactylus stout, without robust setae on propodi or carpi. Pereopods 3–7 ambulatory, 3–5 subequal in size, 6 and 7 with longer ischia; setal patterns of 3–5 unknown; 6 and 7 with 2 large erect multifid setae on propodus, 1 large erect multifid seta on carpus. Pleotelson posterior margin rounded, without teeth.

Subtidal–bathypelagic, parasitising mysids. Temperate Northern Atlantic, Arctic, Western Indo-Pacific. 4 species (Pillai, 1964).

Dolichophryxus Schultz, 1977

Diagnosis. **Female** and **male** unknown. **Cryptoniscus larva** body teardrop-shaped, head helmet-shaped with small lobes at posterolateral corners; eyes absent. Antennula with teeth on basal segment. Oral sucker present. Pereomeres with serrate coxal plates margins, without teeth. Pereopod 1 gnathopodal, dactylus short, large setae on propodus or carpus absent; pereopods 2–6 ambulatory, dactyli long, ventrally smooth with distal tooth; propodi with 2 erect multifid setae; carpi with 1 erect multifid seta; pereopod 7 ambulatory, dactylus long; dactylus setose ventrally, subdivided at midlength; propodus with 2 erect multifid setae ventrally and row of spines dorsally, carpus with 1 erect multifid setae. Pleotelson with distomedial region triangular.

Mesopelagic–bathypelagic, host(s) unknown. Southern Ocean. 1 species (Schultz, 1977).

Heterophryxus G.O. Sars, 1885

Diagnosis. **Female** body elongate ovate; pereomeres with medial dorsal segmentation; head with square frontal lamina, projecting beyond anterolateral margins of pereon. Eyes absent. Antennula absent; antenna rudimentary. 5 pairs of oostegites. Pereopods 1–4 gnathopodal, subequal in shape and size, widely spaced along pereon; pereopod 5 modified into enlarged clasper at posterior end of body. Pleon small, fused, rounded, projecting slightly posteriorly beyond lateral lobes, pleopods and uropods absent. **Male** with pereomeres subequal in width, head wider than long, rounded, fused to pereomere 1. Eyes absent. Antennula and antenna segmented. Pleon fused, rounded, swollen; pleopods, anal cone, and uropods absent. **Cryptoniscus larva** unknown.

Subtidal–bathypelagic, parasitising euphausiids. Central Pacific Ocean, Temperate Southern Pacific, Southern Ocean. 4 species (Ariyama et al., 2016).

Holophryxus Richardson, 1905

Diagnosis. **Female** body elongate ovate; pereomeres with faint or no dorsal segmentation; head with rounded or square frontal lamina, projecting beyond anterolateral margins of pereon. Eyes absent. Antennula and antenna rudimentary. 5 pairs of oostegites. Pereopods 1–5 gnathopodal, subequal in shape. Pleon fused, projecting posteriorly beyond lateral lobes, pleopods and uropods absent. **Male** with pereomeres subequal in width, head wider than long, fused to pereomere 1. Eyes absent. Antennula 2 segmented. Antenna unsegmented. Pleon fused, elongate, pleopods and uropods absent. Anal cone present. **Cryptoniscus larva** body teardrop-shaped, eyes absent. Antennula without teeth on basal segment. Oral sucker absent. Pereomeres without toothed coxal plates. Pereopods 1–6 gnathopodal, 1 shorter than 2–6, dactyli stout, ventrally serrate; 1 with stout setae on propodus and carpus, 2–6 with 2 transverse rows of 1 to several setae on propodi, carpi with stout bifid seta; 7 dactylus, propodus, ischium longer than 1–6, dactylus smooth ventrally, propodus with 2 erect multifid setae, carpus with 1 bifid seta. Pleotelson without teeth.

Mesopelagic–bathypelagic, parasitising sergestoid and caridean shrimps. Temperate Northern Atlantic, Central Atlantic, Central Indo-Pacific, Temperate Northern Pacific, South Pacific, Temperate South America. 10 species (Boyko and Williams, 2021a; Huys et al., 2023).

Neritoniscus Schultz, 1977

Diagnosis. **Female** and **male** unknown. **Cryptoniscus larva** body teardrop-shaped, eyes present with multiple ocelli. Antennula without teeth on basal segment. Pereomeres without toothed coxal plates. Pereopods 1 smallest, dactylus shorter than propodus, propodus bearing 2 erect, multifid setae, carpus with 1 multifid seta; pereopods 2–7 subequal in size, dactyli approximately as long as propodi, propodi each bearing 2 erect, multifid setae, carpi each with 1 multifid seta. Pleotelson without teeth.

Shelf, host(s) unknown. Temperate South America. 1 species (Schultz, 1977).

Notophryxus G.O. Sars, 1883

Diagnosis. **Female** body ovate; pereomere segmentation visible medially on dorsal surface; head with broad lamina, extending beyond anterior margins of lateral lobes. Eyes absent. Antennula segmented, antenna absent. Oostegites fused into single unit. Pereopods 1–5 gnathopodal, subequal in size. Pleon segmented, terminal segment bifurcated; pleopods and lateral plates present. **Male** body recurved with pereomeres subequal in width, head wider than long, fused to pereomere 1; anterior margin sloping. Eyes absent. Antennula unsegmented, antenna segmented. 7 pairs of pereopods, pereopods 1–4 smaller than

5–7. Pleon segmented or unsegmented; pleopods, anal cone, and uropods absent. **Cryptoniscus larva** unknown.

Subtidal–bathypelagic, parasitising mysids and euphausiids. Temperate Northern Atlantic, Tropical Atlantic, Southern Ocean, Western Indo-Pacific, Temperate Northern Pacific. 9 species (Shimomura and Ohtsuka, 2011).

Oculophryxus Shields and Gómez-Gutiérrez, 1996

Diagnosis. **Female** body pyriform; pereomere segmentation absent; head without frontal lamina, not extending beyond anterior margins of lateral lobes. Antennula of 1 segment, antenna absent. Anterolateral margins of body modified into recurved, elongate lobes with spoon-like tips. Oostegites fused into 1 unit. Pereopods 1–4 gnathopodal, subequal in size; pereopod 5 absent. Pleon fused with pereon; pleopods and uropods absent. **Male** body flat with pereomeres subequal in width, head wider than long, fused to pereomere 1; anterior margin with medial indentation. Eyes absent. Antennula and antenna segmented. 6 pairs of subequal fully developed pereopods; pereopod 7 reduced, of 2 segments, dactylus absent. Pleon large, ovate, segments fused; pleopods, anal cone, and uropods absent. **Cryptoniscus larva** unknown.

Shelf, parasitising euphausiids. Tropical Atlantic, Central Indo-Pacific, Tropical Eastern Pacific. 1 species (Shields and Gómez-Gutiérrez, 1996).

Paraspidophryxus Schultz, 1977

Diagnosis. **Female** and **male** unknown. **Cryptoniscus larva** body elongate, head triangular; eyes absent. Antennula not described. Oral sucker present. Pereomeres with coxal plates not described. Pereopod 1 gnathopodal, dactylus stout; 2–6 ambulatory, dactyli longer than propodi, propodi with 2 erect multifid setae, carpus with 1 multifid seta; 7 ambulatory, dactylus, propodus and ischium long; dactylus smooth ventrally, bearing 1 distal tooth; propodus with 2 erect multifid setae ventrally, carpus with 1 erect multifid setae. Pleotelson with distomedial region rounded, smooth.

Mesopelagic–bathypelagic, host(s) unknown. Southern Ocean. 1 species (Schultz, 1977).

Prodajus Bonnier, 1903

Diagnosis. **Female** body heart-shaped; pereomeres with faint or no dorsal segmentation; head with subquadrate frontal lamina, directed ventrally, not extending beyond anterior margins of lateral lobes. Eyes present or absent. Antennula 1 or 4 segmented. Antenna absent or 4 segmented. 5 pairs of oostegites. Pereopods 1–5 gnathopodal, subequal in shape, pereopod 1 slightly smaller than 2–5. Pleon of 3 or 4 pleomeres plus pleotelson, pleopods absent, pair of recurved posterolateral lobes ("uropods") present. **Male** with pereomeres subequal in width, head wider than long, fused to pereomere 1. Eyes present or absent. Antennula 2 segmented. Antenna of 5 or 6 segments. Pleon 1 or 2 segmented, pleopods absent. Anal cone absent (anal slit present). Pair of tapered posterolateral lobes ("uropods") present, distal tips bifurcated. **Cryptoniscus larva** body teardrop-shaped, eyes present or absent. Antennula with teeth on basal segment. Oral sucker present. Pereomeres with toothed coxal plates. Pereopod 1 gnathopodal, dactylus stout, without robust setae on propodus or carpus. Pereopods 2–7 ambulatory, subequal in size except 7 with longer ischium; pereopods 2–6 each with 2 stout setae on propodus, 1 stout seta on carpus; pereopod 7 with 2 large erect multifid setae on propodus, 1 large erect multifid seta on carpus. Pleotelson with or without teeth.

Subtidal, parasitising mysids. Temperate Northern Atlantic, Western Indo-Pacific, Temperate Northern Pacific. 7 species (Shimomura et al., 2005).

Prophryxus Richardson, 1909

Diagnosis. **Female** body irregularly ovate; pereomeres 1–3 segmented, 4–7 with indications of segmentation dorsally; head with thin frontal lamina, head and pereomeres 1–3 extending beyond anterior margins of lateral lobes. Eyes absent. Antennula and antenna not described. Oostegites not described. Pereopods 1–5 gnathopodal, subequal in size and shape. Pleon segmented, pleopods rudimentary (number unknown), uropods not described but possibly present. **Male** and **cryptoniscus larva** unknown.

Bathypelagic, parasitising a "schizopod" (euphausiid or mysid; species of both were collected at the type locality). Temperate Northern Pacific. 1 species (Richardson, 1909).

Streptodajus Nierstrasz and Brender à Brandis, 1923

Diagnosis. **Female** body ovate, tapering posteriorly; pereomeres indicated dorsally; head with frontal lamina not visible dorsally, directed anterodorsally, extending anteriorly slightly beyond anterior margins of lateral lobes. Oral sucker present. Antennula (or antenna) of 1 segment, other absent. Oostegites of 1 pair, large, fused. Pereopods 1–5 gnathopodal, subequal in size, displaced to anterior margin below head. Pleon indistinctly segmented dorsally and ventrally, segmented ventrally, extending posteriorly beyond posterior margins of lateral lobes; pleomeres 1–4 with medial rounded projections. Pleopods and uropods absent. **Male** and **cryptoniscus larva** unknown.

Bathypelagic, parasitising mysids. Central Indo-Pacific. 1 species (Nierstrasz and Brender à Brandis, 1923).

Telephryxus Williams and Boyko, 2021

Diagnosis. **Female** body spheroid, unsegmented; head not visible. Eyes absent. Antennula as 1 flat triangular plate; antenna as 1 flat rectangular plate lateral to oral cone. Oostegite 1 largest, broadly ovate with large triangular posterior accessory lobe; oostegites 2–4 flat, ovate; oostegite 5 flat, tapering. Pereopods 1–5 gnathopodal, subequal in size and shape. Pleon modified as subquadrate, broad, thickened plate with 2 circular medial holes, subequal in size; hole surrounding distal portion of host antennular peduncle with 1 small additional hole on each lateral margin. **Male** with pereomeres subequal in width; head wider than long, triangular, fused with pereomere 1. Antennula as 1 ovate plate lateral to and extending posterior to oral cone; antenna of 2 segments. Pereomeres 2–7 distinct, lateral margins recurved ventrally. Pereopods 1–6 subequal in size and shape; pereopod 7 reduced to stub. Pleon tapering to rounded tip, all segments fused, distinct from pereomere 7; pleopods, anal cone,

and uropods absent. **Cryptoniscus larva** body teardrop-shaped, head extended posterolaterally; eyes present. Antennula without teeth on basal segment. Oral sucker absent. Pereomeres without toothed coxal plates. Pereopod 1 with short, slightly curved dactylus, propodus semi-spherical bearing 2 stout, simple setae, carpus with 1 stout simple seta; pereopods 2–6 each with more elongate curved dactyli, propodi progressively more elongate, bearing 2 stout simple setae, carpi each with 1 stout, simple seta. Pereopod 7 with long, slightly curved dactylus, propodus elongate with 2 large multifid setae near base of dactylus; carpus with 1 distal large multifid seta; merus triangular with anterodorsal edge extending into spine-like extension. Pleotelson without teeth.

Abyssal, parasitising munidopsid squat lobsters. Tropical Atlantic. 1 species (Williams and Boyko, 2021).

Zonophryxus Richardson, 1903

Diagnosis. **Female** body ovate; pereomeres with faint dorsal indications; head with large frontal lamina, fused with lateral margins of pereomeres. Eyes absent. Antennula as recurved flat lobe; antenna small, digitiform. 6 pairs of oostegites, sixth pair fused to fifth. Pereopods gnathopodal, 5 or 6 pairs, sixth pair (if present) near posterior margin of body at base of oostegite 6. Pleon without pleopods or uropods. Posterior margin of pleon with row of triangular-shaped processes. **Male** body flattened; head ovate, fused with pereomere 1. Eyes absent. Antennula minute, rounded; antennae elongate, blade-like. Pereon with 6 free segments. 7 pairs of subequal pereopods. Pleomeres fused; pleopods, anal cone, and uropods absent. Type 1 male head sloping from anterior to posterior, smooth. Pereomere 7 smaller than pereomere 2. Pleon extending posteriorly from pereomere 7. Type 2 male head with distinct medial and lateral lobes. Pereomere 7 larger than pereomere 2. Pleon ventrally displaced under pereomere 7. **Cryptoniscus larva** body teardrop-shaped, eyes absent. Antennula without teeth on basal segment. Pereomeres without toothed coxal plates. Pereopods 1 and 2 subequal, dactyli short, slightly curved, propodus bearing 2 stout, simple setae; carpus without setae. Pereopods 3–5 dactyli more elongate, curved, propodi more elongate, narrower, bearing 2 stout simple setae; carpi without setae. Pereopod 6 and 7 dactyli subequal in length to those of pereopods 3–5, propodi more elongate and narrower than those of pereopods 3–5, bearing 2 erect, multifid setae, carpus with 1 distal multifid seta. Pleotelson without teeth.

Shelf–bathypelagic, parasitising caridean shrimps. Tropical Atlantic, Temperate Northern Atlantic, Temperate Southern Africa, Southern Ocean, Central and Eastern Indo-Pacific, Temperate Northern Pacific, Temperate South America. 7 species (Williams and Boyko, 2021b).

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Family Entophilidae Richardson, 1903

Figure 6.34

Members of Entophilidae are endoparasitic; they can be distinguished from all other epicarideans by the symmetrical body form of the females, the pleopods and lateral plates forming a cylindrical tube surrounding the pleomeres, and thread-like form of some pleopodal endopods and/or uropods. Within Epicaridea, entoniscids are the only other fully internal parasites; female entoniscids are vermiform (Boyko and Williams, 2015; McDermott et al., 2019).

Diagnosis. **Female** body nearly symmetrical, ovoid with tapering posterior end. Pereomeres distinctly segmented dorsally; head bilobed, not distorted. Frontal lamina present. Eyes absent. Barbula with single (irregularly shaped or smooth) lobe on each side. Antennula as rounded unsegmented flap, antenna as elongate, unsegmented flap or 2-segmented. Maxilliped without palp. Marsupium closed. 5 pairs of oostegites; oostegite 1 with triangular or ovate posterior lobe; internal ridge smooth. Coxal plates present. Dorsolateral bosses absent. Middorsal projections absent. 7 pairs of subequal pereopods. Pleon of 5 or 6 segments, pleomeres 1 and 2 with medioventral tubercles or tubercles absent; uniramous lateral plates on pleomeres 1–4 or 1–5. Biramous pleopods on pleomeres 1–4 or 1–6, exopods lamellar, unsegmented or 2-segmented, endopods long and thin; pleopod 5 uniramous, lamellar or thread-like. Pleopods and lateral plates forming cylindrical tube surrounding pleomeres. Slender or thread-like uniramous uropods inserted ventrally between fifth pleopods. **Male** with pereomeres slightly narrowing posteriorly or with tubular body shape. Head wider than long, diamond-shaped or ovate; eyes present or absent. Antennula rounded, unsegmented lobe, sparsely setose, antenna absent or antennula and antenna as bilobed flaps, densely setose. Midventral tubercles absent. 6 pairs of subequal pereopods plus pereopod 7 as an unsegmented stub or 7 pairs of subequal pereopods. 6 distinct pleomeres, pleopods present on pleomeres 1–4 as rounded stubs, pleomere 5 without pleopods or bilobed flap-like pleopods present on pleomeres 1–5. Pleotelson ovate, with pair of slender uropods inserted posteromedially or posterolaterally, with or without scales, marginally setose. Endoparasitic.

Key to genera of Entophilidae

1. Mature female (fig. 6.34a–d) with unsegmented antenna, 5 pairs of biramous pleopods, pleopod 5 a stout tapered lobe, male (fig. 6.34f, g) with antenna as pair of simple flaps, pereopod 7 reduced to stub, 4 pairs of uniramous pleopods. ..... *Axiophilus*

– Mature female (fig. 6.34h–k) with 2-segmented antenna, 6 pairs of pleopods, pleopod 5 minute and thread-like, male (fig. 6.34l–n) with antenna as 2 pairs of bilobed flaps, pereopod 7 not reduced, 5 pairs of uniramous pleopods. ..... *Entophilus*

Axiophilus Boyko and Williams, 2015

Diagnosis. **Female** with barbula as single irregularly shaped lobe on each side. Antennula and antenna as elongate, unsegmented flaps. Oostegite 1 with triangular posterior lobe. Pleon of 5 segments, medioventral tubercles absent; uniramous lateral plates on pleomeres 1–4. Biramous pleopods on pleomeres 1–4, exopods lamellar, 2-segmented, endopods long and thin; pleopod 5 uniramous, lamellar (lacking endopod). Uropods slender, uniramous, inserted ventrally between fifth pleopods. **Male** with pereomeres slightly narrowing posteriorly. Head diamond-shaped; eyes present. Antennula a rounded, unsegmented lobe, sparsely setose; antenna absent. Midventral tubercles absent. 6 pairs of subequal pereopods plus pereopod 7 as unsegmented stub. Pleopods present on pleomeres 1–4 as rounded stubs, pleomere 5 without pleopods. Pleotelson with slender uropods inserted posteromedially, without scales.

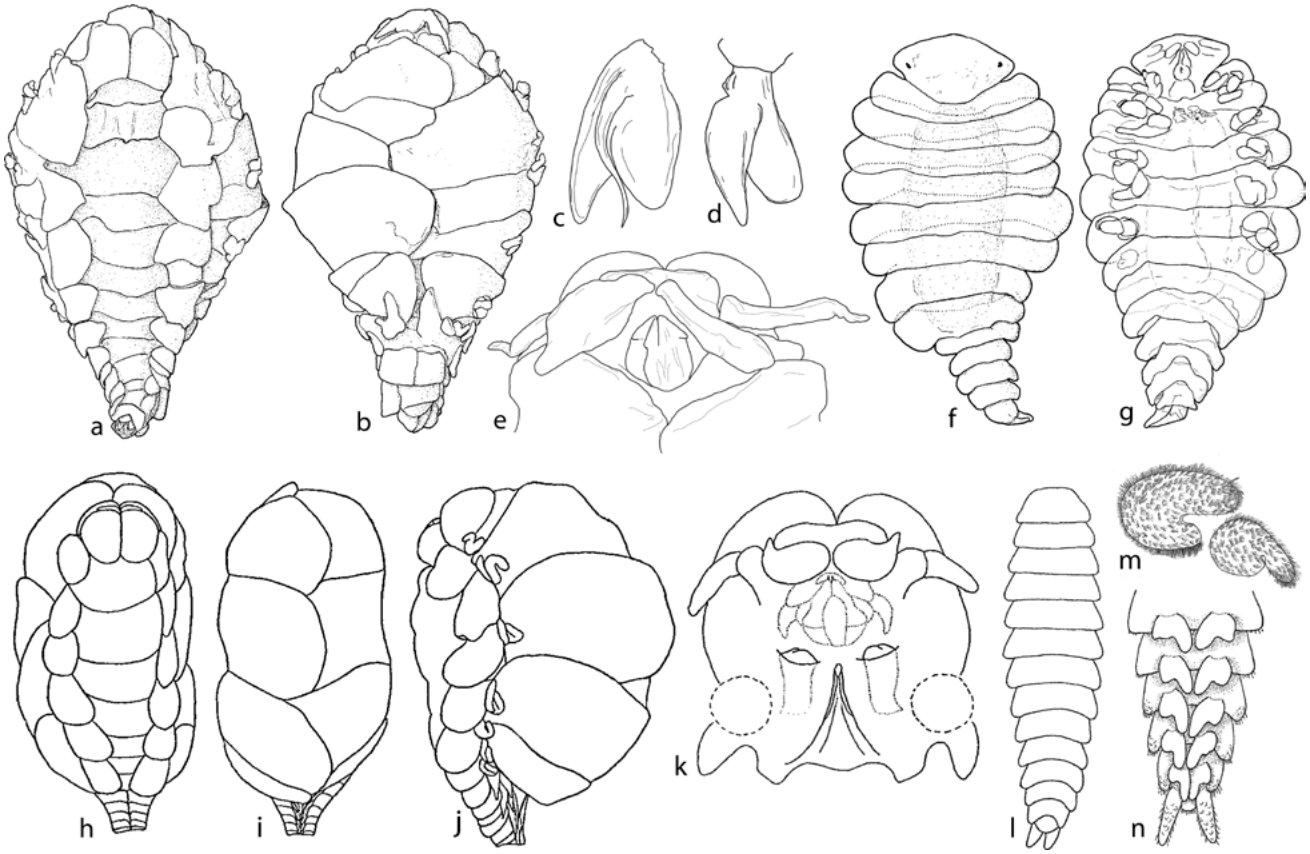


Figure 6.34. Entophilidae *Axiophilus mirabiledictu* (Markham and Dworschak, 2005): a, female dorsal view; b, female ventral view; c, female pleopod 4; d, female, pleopod 5 and terminal pleomere, lateral view; e, female head, ventral view; f, male dorsal view; g, male ventral view. *Entophilus omnitectus* Richardson, 1903: h, female dorsal view; i, female ventral view; j, female lateral view; k, female head, ventral view; l, male dorsal view; m, male antennula and antenna; n, male pleon, ventral view.

Subtidal, parasitising callianassid shrimps. Western Indo-Pacific. 1 species (Boyko and Williams, 2015).

Entophilus Richardson, 1903

Diagnosis. **Female** with barbula as single, smooth lobe on each side. Antennula as rounded, unsegmented flap; antenna with 2-segments. Oostegite 1 with ovate posterior lobe. Pleon of 6 segments, medioventral tubercles on pleomeres 1 and 2; uniramous lateral plates on pleomeres 1–5. Biramous pleopods on pleomeres 1–6, exopods and endopods lamellar, unsegmented; pleopod 5 minute, thread-like (lacking endopod). Uropods uniramous, minute, thread-like. **Male** with tubular body shape, pereomere and pleomere width subequal. Head ovate; eyes absent. Antennula and antenna as bilobed flaps, densely setose. Midventral tubercles absent. 7 pairs of subequal pereopods. Bilobed flap-like pleopods present on pleomeres 1–5. Pleotelson with slender uropods inserted posterolaterally, with scales.

Shelf-Slope, parasitising munidid squat lobsters. Tropical Atlantic, Temperate Northern Atlantic, Western and Eastern Indo-Pacific. 1 species (Boyko and Williams, 2015).

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Family Hemioniscidae Bonnier, 1900

Figure 6.35

Members of Hemioniscidae are endoparasitic. They can be distinguished from other isopod parasites of barnacles by the presence of distinct teeth on the basal segment of the antennula in males (= cryptoniscus larval stage) (Buhl-Mortensen et al., 2020; Williams and Boyko, 2006).

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes present or absent. Antennula article 1 with 5–9 posterior teeth. Coxal plates with or without teeth. Pereopods 1 and 2 gnathopodal, pereopods 3–7 ambulatory, pereopods 3–5 with propodi quadrate distally, 6 and 7 tapering distally. Pleotelson margin smooth. **Mature females** with some segmentation visible, most of body fused into large marsupium. Endoparasitic.

Key to genera of Hemioniscidae

Cryptothir taxon inquirendum excluded

1. Cryptoniscus larva (fig. 6.35b, c) antennular basal segment with fewer than 6 teeth (fig. 6.35d); mature female spheroid with dorsal segmentation, lacking appendages (fig. 6.35a); parasitic in ascothoracicans ..... *Gorgoniscus*

– Cryptoniscus larva antennular basal segment with more than 6 teeth; mature female retains some cryptoniscus segmentation with appendages (fig. 6.35e, h) 2

2. Cryptoniscus larva (fig. 6.35f, g) antennular basal segment with 7 teeth, female (fig. 6.35e) parasitic in balanid, lepadid and trypetesid cirripedes ..... *Hemioniscus*

– Cryptoniscus larva (fig. 6.35i, j) antennular basal segment with 8 or 9 teeth, female (fig. 6.35h) parasitic in scalpellid cirripedes ..... *Scalpelloniscus*

Cryptothir Dana, 1853 (*taxon inquirendum*)

Diagnosis. As for family (only the cryptoniscus larva is known and was described and figured incompletely).

Subtidal, parasitising pyrgomatid barnacles. Eastern Indo-Pacific. 1 species (Williams and Boyko, 2006).

Gorgoniscus Grygier, 1981

Diagnosis. **Male** (paedomorphic cryptoniscus larva) eyes absent. Antennula article 1 with 5 posterior teeth. Coxal plates longitudinally ridged, posterior margins smooth. Pleotelson margin smooth. **Mature female** spheroid in dorsal view, compressed dorsoventrally with anterior and posterior ends curled ventrally; cryptoniscus segmentation not retained, lacking appendages.

Slope, parasitising ascothoracican barnacles. Eastern Indo-Pacific. 1 species (Grygier, 1981a).

Hemioniscus Buchholz, 1866

Diagnosis. **Male** (paedomorphic cryptoniscus larva) eyes present. Antennula article 1 with 7 bluntly rounded teeth. Coxal plates with or without teeth. Pleotelson with smooth evenly rounded distal margin. **Mature female** with anterior segments unmodified from cryptoniscus form; posterior segments fused into enlarged marsupium.

Intertidal–subtidal, parasitising acrothoracican, lepadid and sessile thoracican barnacles. Central Indo-Pacific, Temperate Northern Pacific, Temperate Northern Atlantic, and Temperate Southern Africa. 3 species and 1 subspecies (Goudeau, 1967, 1970, 1972; Williams and Boyko, 2006). *Leponiscus* Giard, 1887 is treated here as a junior subjective synonym.

Scalpelloniscus Grygier, 1981

Diagnosis. **Male** (paedomorphic cryptoniscus larva) eyes absent. Antennula article 1 with 8 or 9 bluntly rounded teeth. Coxal plates with teeth. Pleotelson with bell curve-shaped posterior lobe. **Mature female** with anterior segments as in cryptoniscus larva; posterior segments as in cryptoniscus larva dorsally (sac-like ventrally) or entirely sac-like.

Slope–abyssal, parasitising pedunculate thoracican barnacles. Temperate Southern Africa, Temperate Australasia, Temperate South America. 4 species (Grygier, 1981b; Hosie, 2008).

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Buhl-Mortensen, L., Williams, J.D., and Boyko, C.B. 2020. A new species of *Crinoniscus* Pérez, 1900 (Crustacea: Isopoda: Crinoniscidae) parasitising the pedunculate barnacle *Heteralepas newmani* Buhl-Mortensen & Mifsud (Cirripedia: Heteralepadidae) with notes on its ecology and a review of the genus. *Systematic Parasitology* 97: 179–192. https://doi.org/10.1007/s11230-020-09903-x.

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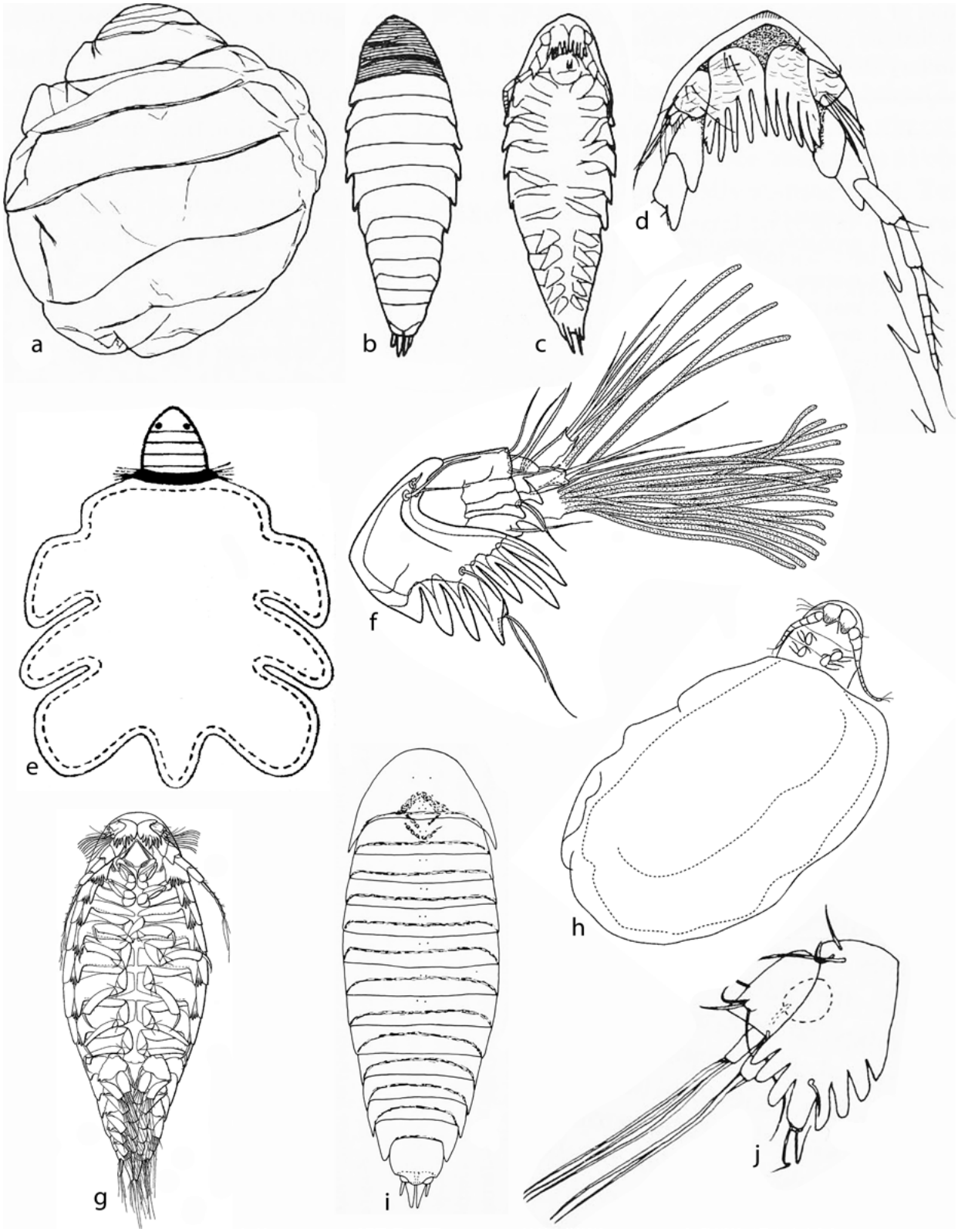


Figure 6.35. Hemioniscidae. *Gorgoniscus incisodactylus* Grygier, 1981: a, female dorsal view; b, male dorsal view; c, male ventral view; d, male head, ventral view showing antennulae and antenna. *Hemioniscus balani* Buchholz, 1866: e, female dorsal view; f, male antennula; g, male ventral view. *Scalpelloniscus nieli* Hosie, 2008: h, female ventral view. *Scalpelloniscus penicillatus* Grygier, 1981b: i, male dorsal view; j, male antennula.

chez l'isopode épicaride *Hemioniscus balani* Buchholz. *Cahiers de Biologie Marine* 8: 437–448.
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Family Podasconidae Giard and Bonnier, 1895

Figure 6.36

Members of Podasconidae are the only known direct epicaridean ectoparasites of amphipods (*Gnomoniscus podasconis* Giard and Bonnier, 1895 is a hyperparasite of *Podascon haploopis* Giard and Bonnier, 1895; fig. 6.36a) (Giard and Bonnier, 1895; Hansen, 1916). It is possible, however, that the two included genera do not belong to the same family or even that the family is not valid; they were likely placed in the same family on the basis of host choice rather than morphological affinities. Females of species of *Podascon* are very similar to those of *Cirolanoniscus* (Pillai, 1966; Cabiropidae) but cryptoniscus larvae are not known from either genus. The females of species of *Parapodascon* are similar to those of *Cumoechus* (Cumoechidae) but the cryptoniscus larvae are very different. A complete redescription of species in both genera is needed, as well as collection of material for molecular analysis, to determine their relationships to each other and to other cryptoniscoids. The family-level diagnosis below includes only the characters for the type genus.

Diagnosis. **Male** (paedomorphic cryptoniscus larva) unknown. **Mature female** ovate, swollen dorsoventrally, dorsal surface with segmentation, marsupium closed by 2 large smooth lateral lobes; pleon distinct, segmented. Ectoparasitic.

Key to mature females of genera of Podasconidae

1. With dorsal segmentation; ventrally with 2 large lateral lobes meeting in midline; pleon distinguishable (fig. 6.36a–d) ..... *Podascon*
– Without any segmentation; ventrally with narrow slit in midline; pleon indistinguishable (fig. 636e–j) ..... *Parapodascon*

Parapodascon Hansen, 1916

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with poorly developed cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes absent. Antennula article 1 with 7 posterior teeth. Coxal plates with teeth. Pereopods 1 and 2 gnathopodal, pereopods 3–7 ambulatory; propodi of pereopods 3–5 quadrate distally, 6 and 7 tapering distally; dactylus of pereopods 5 and 7 with terminal spine, that of pereopod 6 with 1 long dorsal spine and 1 short ventral spine. Pleotelson margin smooth. **Mature female** ovate, without any segmentation, lacking most appendages; median half of ventral surface with longitudinal slit flanked by 5 pairs of rounded lobes and bearing minute conical antennae at anterior end; pleon indistinguishable.

Intertidal–slope, parasitising lysianassoid amphipods. Arctic. 1 species (Coyle and Mueller, 1981; Hansen, 1916).

Podascon Giard and Bonnier, 1889

Diagnosis. **Mature female** ovate, swollen dorsoventrally, dorsal surface with segmentation; pleon distinct.

Subtidal, parasitising lysianassoid amphipods. Temperate Northern Atlantic. 3 species (Giard and Bonnier, 1895).

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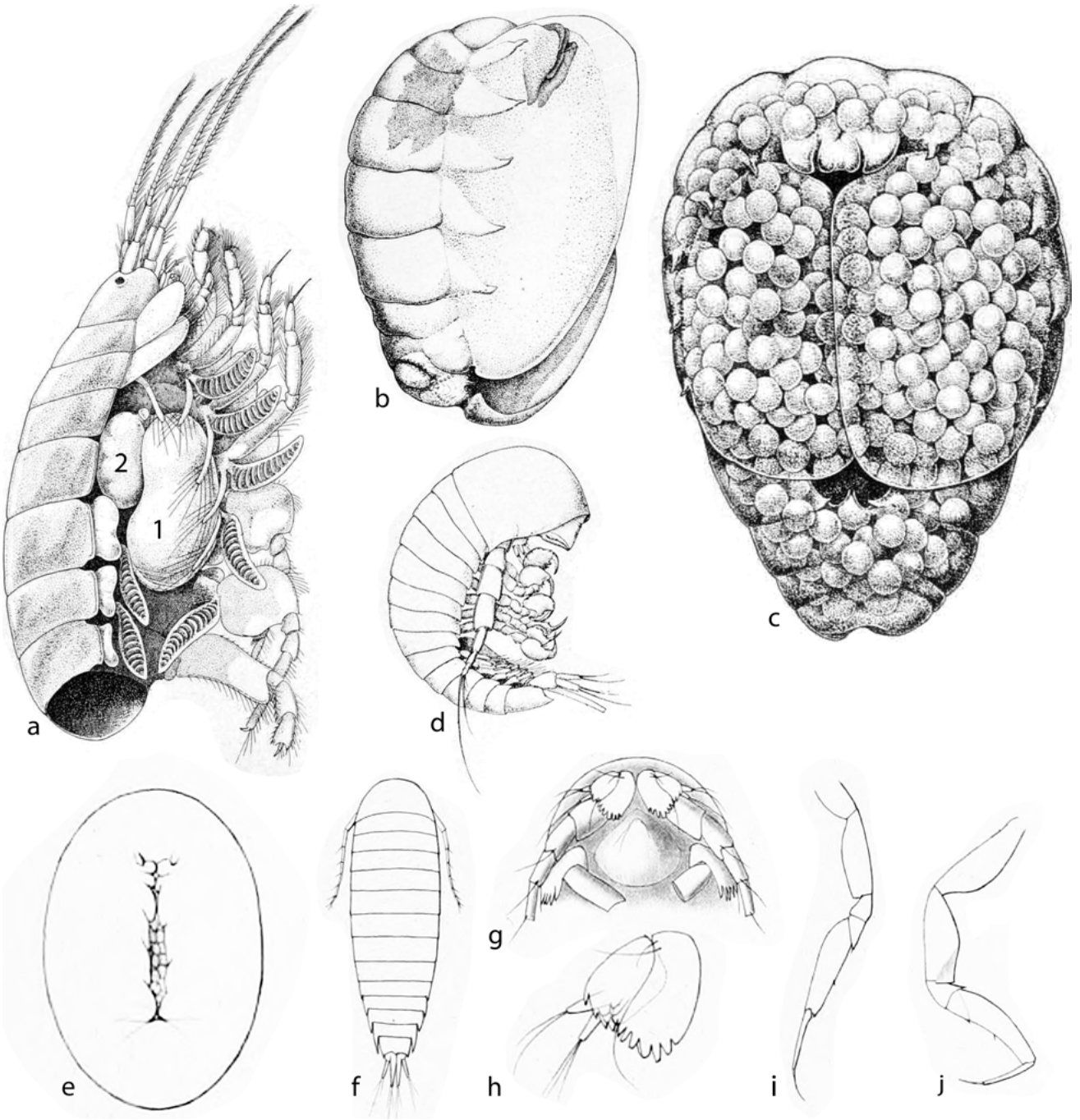


Figure 6.36. Podasconidae. a, host amphipod with *Podascon haploopis* Giard and Bonnier, 1895 (labeled 1) and hyperparasitic cabiropid isopod *Gnomoniscus podasconis* Giard and Bonnier, 1895 (labeled 2), lateral view of host and parasites. *Podascon dellavallei* Giard and Bonnier, 1889: b, female lateral view; c, ovigerous female ventral view. *Podascon chevreuxi* Giard and Bonnier, 1895: d, epicaridium larvae, lateral view. *Parapodascon stebbingi* (Giard and Bonnier, 1895): e, female ventral view; f, male dorsal view; g, male head, ventral view; h, male antennula; i, male pereopod 5; j, male pereopod 7.

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Family Stellatoniscidae Oanh and Boyko, 2020

Figure 6.37

Members of Stellatoniscidae are ectoparasitic in the marsupium of entoniscid isopods as hyperparasites. They can be distinguished from other epicaridean parasites by the mature females possessing numerous thin tentacular extensions and the cryptoniscus larva having a mesial demarcated area on antennular segment 1, pereomere 7 lacking coxal plates, pereopod 1 with a ridged surface on the carpus and merus, and pereopods 1 and 2 dissimilar (Oanh and Boyko, 2020).

Diagnosis. **Epicaridium larva** (fig. 6.37e) antenna approximately 3/4 as long as body. 6 pairs of gnathopodal pereopods subequal in size and shape; pleon with 5 pairs of biramous pleopods; uropods biramous. **Male** (paedomorphic cryptoniscus larva; fig. 6.36e–j), body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes present. Antennula article 1 with 6 or 7 posterior teeth and mesial demarcated area. Coxal plates 1–6 entire, covered with scales, pereomere 7 lacking coxal plate. Pereopods 1 and 2 gnathopodal, pereopod 2 larger than 1 and with greatly enlarged dactylus; pereopod 1 carpus and merus with ridged surface, pereopods 3–7 ambulatory, subequal in size and shape, propodi subquadrate distally, ischia and bases with mediodorsal lobes. Pleotelson margin smooth. **Immature female** (fig. 6.37b–d) developing from 4-lobed stage to 4 lobes with short thin mediodistal extensions to reduced body with 8 short tentacular extensions; **mature female** (fig. 6.37a) with 10 tentacular thin extensions radiating out from central body. Ectoparasitic.

Stellatoniscus Oanh and Boyko, 2020

Diagnosis. As for family.

Subtidal, parasitising entoniscid isopods. Central Indo-Pacific. 2 species (Oanh and Boyko, 2020).

Reference

Oanh, L.T.K., and Boyko, C.B. 2020. *Cancrion khanhensis* sp. nov. (Crustacea: Isopoda: Entoniscidae) infesting *Monomia haanii* (Stimpson, 1858) (Crustacea: Brachyura: Portunidae) from Nha Trang Bay, Khanh Hoa, Vietnam, with remarks on larval stages of entoniscids and description of a new family, genus and two new species of hyperparasites infesting entoniscids. *Zootaxa* 4894(3): 366–386. https://doi.org/10.11646/zootaxa.4894.3.4

Cryptoniscoidea genera known only from cryptoniscus larvae

Figures 6.38–6.41

Some epicaridean species and 20 genera have been described solely from the cryptoniscus larval stage and, as such, present some difficulties in taxonomic placement. Although some have characters that allow them to be included in existing families (with unclear position), others are of uncertain placement within Cryptoniscoidea. *Vacuotheca* Schädel, Perrichot and Haug, 2019, a monotypic genus known only from fossil cryptoniscus specimens that was not placed within a superfamily when described, is clearly a member of Cryptoniscoidea (4 basal + 5 flagellar antennal segments; fig. 6.41o). Due to the lack of knowledge of adult stages, it is unknown if species in these genera are endoparasitic, mesoparasitic or ectoparasitic associates of definitive hosts.

The following key includes taxa known only from cryptoniscus larval stages. Users should be aware that unknown cryptoniscus larvae they encounter may correspond to taxa included here, or possibly to those covered in preceding sections for which adult forms may be known. The key is intended as a practical tool to aid in narrowing down identifications and encouraging comparison across cryptoniscoid genera. We hope to facilitate efforts to link cryptoniscoid larval and adult stages, resolve taxonomic placement, and expand understanding of their life histories and host associations. Researchers should also be aware that findings of cryptoniscus larvae on female epicarideans may represent hyperparasites (e.g., Cabiropidae) rather than recently settled larva of the same species.

The cryptoniscus larvae of the type species of the monotypic *Eumetor* Kossman, 1872 (Cryptoniscidae?) and *Crytpothir* Dana, 1853 (Cryptothiridae; possible synonym of Crinoniscidae or Hemioniscidae) are poorly described and not included in the key.

Diagnoses are given below only for genera placed *incertae sedis*. For all others, see Cabiropidae and Dajidae.

Key to genera known only from cryptoniscus larvae

1. Oral sucker (fig. 6.38b, j, o) present 2
– Oral sucker absent 4

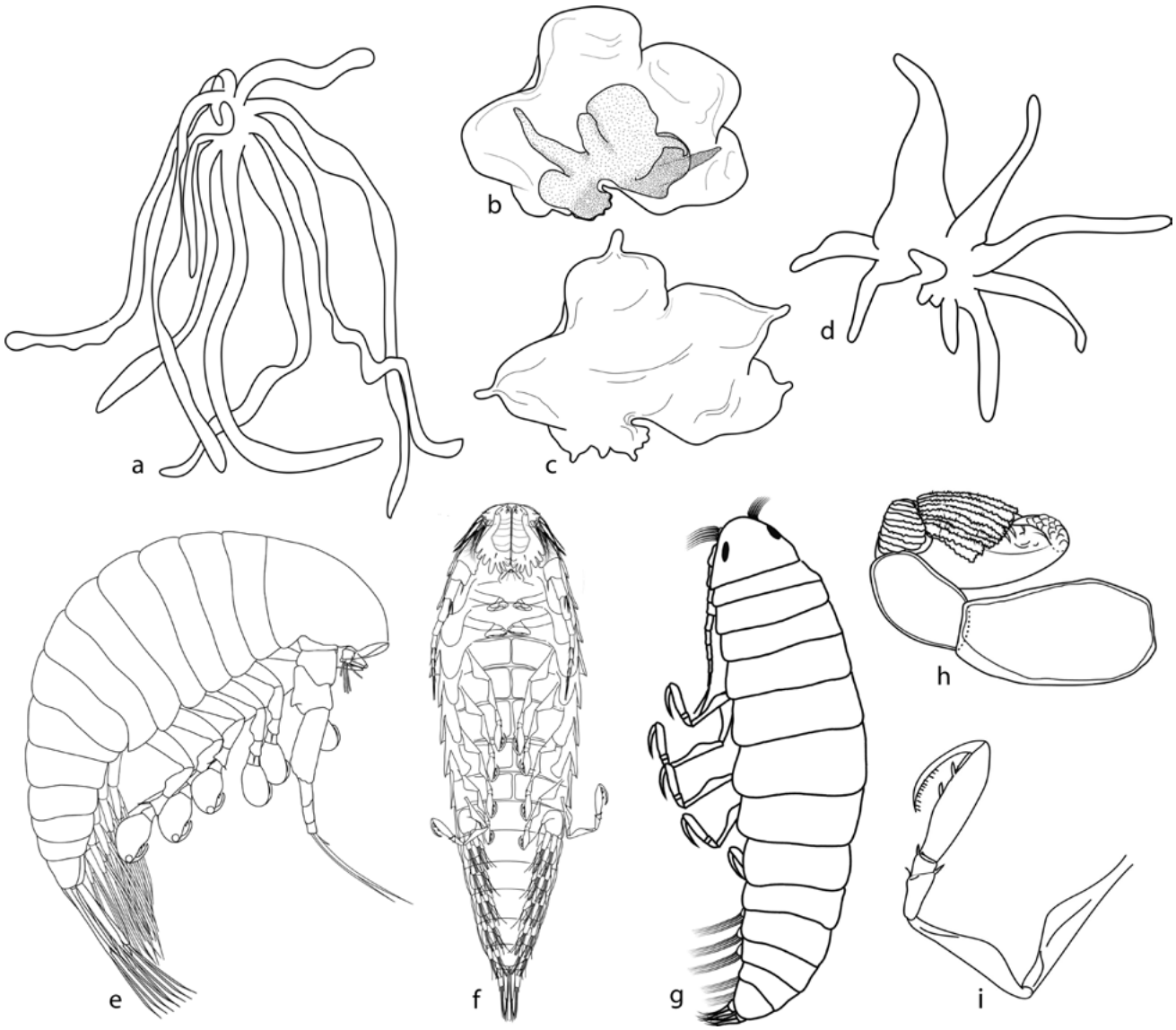


Figure 6.37. Stellatoniscidae. *Stellatoniscus tentaculus* Oanh and Boyko, 2020: a, mature female; b, immature female (stage 1); c, immature female (stage 2); d, immature female (stage 3); e, epicaridium larva lateral view; f, male ventral view; g, male dorsolateral view; h, male pereopod 1; i, male pereopod 7.

2. Pereopod 7 with large multifid teeth on propodus and carpus 3
– Pereopod 7 (fig. 6.38h) without large multifid teeth on propodus and carpus (see also fig. 6.38a–g) ..... *Thermaloniscus* (*incertae sedis*)
3. Antenna (fig. 6.38i, n) reaching past anterior margin of pleomere 1, dorsal margin of pereopod 7 (fig. 6.38m) propodus spinose (see also fig. 6.38j–l) ..... *Dolichophryxus* (Dajidae)
– Antenna (fig. 6.38o) reaching past anterior margin of pereomere 5; dorsal margin of pereopod 7 (fig. 6.38q) propodus smooth (see also fig. 6.38p) ..... *Paraspidophryxus* (Dajidae)
4. Pereopod 7 with large multifid teeth on propodus and carpus (fig. 6.39d, h) 5
– Pereopod 7 without large multifid teeth on propodus and carpus 6
5. Coxal plate margins smooth (figs. 6.39a–d) ..... *Neritoniscus* (Dajidae)

– Coxal plate margins serrated (figs. 6.39e–i) ..... *Cryptocisus* (Dajidae)

6. Antennular basal segment with marginal teeth (fig. 6.39k, m, u) 7

– Antennular basal segment smooth 13

7. Pleotelson posterior margin with teeth (fig. 6.39j, n) 8

– Pleotelson posterior margin without teeth 10

8. Pleotelson (fig. 6.39j) posterior margin with fewer than 10 teeth 9

– Pleotelson (fig. 6.39n) posterior margin with more than 10 teeth (see also fig. 6.39l, m, o) ..... *Podoniscus* (Cabiropidae)

9. Dactylus of pereopods 6 and 7 (fig. 6.39k) as long as propodus, pleotelson (fig. 6.39j) posterior margin with 5 teeth ..... *Cironiscus* (Cabiropidae)

– Dactylus of pereopods 6 and 7 (fig. 6.41p) shorter than propodus, pleotelson (fig. 6.41n, q) posterior margin with 6 teeth (see also fig. 6.41o) ..... *Vacuotheca* (*incertae sedis*)

10. Coxal plate margins with 4 or fewer teeth 11

– Coxal plate (compare to fig. 6.39f) margins with more than 10 teeth (see also fig. 6.39p–s) ..... *Osicryptus* (*incertae sedis*)

11. Pleon with medioventral tubercules; pleotelson (fig. 6.40d) medially indented (see also fig. 6.40a–c, e, f). ..... *Rolandoniscus* (Cabiropidae)

– Pleon without medioventral tubercules; pleotelson rounded 12

12. Coxal plate margins on pereomeres 5–7 lacking teeth (fig. 6.40w; see also fig. 6.40t–v) ..... *Pleuroniscus* (Cabiropidae)

– Coxal plate margins with 3 or 4 teeth on pereomeres 5–7 (fig. 6.39w; see also fig. 6.39t–v) ..... *Chimaeroniscus* (*incertae sedis*)

13. Antennula (fig. 6.40g) with large subquadrate basal plate (see also fig. 6.40h–k) ..... *Trisopodoniscus* (*incertae sedis*)

– Antennula without large subquadrate basal plate 14

14. Head inflated and posterolaterally extended (fig. 6.40l, p) 15

– Head not inflated or posterolaterally extended 16

15. Pleotelson (fig. 6.40l) triangular with marginal teeth (see also fig. 6.40m–o) ..... *Nalocryptus* (*incertae sedis*)

– Pleotelson (fig. 6.40p) subquadrate with smooth margins (see also fig. 6.40q–s) ..... *Onocryptus* (*incertae sedis*)

16. Propodus of pereopod 6 (fig. 6.41d) greatly reduced, dactylus more than 4 times as long as propodus (see also fig. 6.41a–c, e) ..... *Nococryptus* (*incertae sedis*)

– Propodus of pereopod 6 not greatly reduced, dactylus less than twice as long as propodus 17

17. Pereopod 3 similar in shape and size to pereopods 1 and 2 (fig. 6.41f–i) ..... *Cryptocotitus* (*incertae sedis*)

– Pereopod 3 similar in shape and size to pereopods 4–7 (fig. 6.41j–m) ..... *Elocryptus* (*incertae sedis*)

Chimaeroniscus Williams, Boyko and Moritaki, 2022

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body linear with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes absent. Antennula article 1 with teeth. Coxal plates with teeth. Pereopods 1–2 gnathopodal, 3–7 ambulatory; propodi of 3–7 rounded distally, dactyli shorter than propodi in anterior pairs, gradually becoming longer than propodi in posterior pairs. Pleotelson margin smooth.

Slope, parasitising dajid isopods. Central Indo-Pacific, Southern Ocean. 1 species (Williams et al., 2022).

Cryptocotitus Schultz, 1977

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes absent. Antennula article 1 with few low bumps, without large teeth. Coxal plates with teeth. Pereopods 1–3 gnathopodal, 4–5 ambulatory, propodi quadrate distally; propodi of 6 and 7 tapering distally, dactylus of 6 as long as propodus, dactlyus of 7 as long as propodus, merus, and carpus combined. Pleotelson margin smooth.

Bathypelagic, host unknown. Southern Ocean. 1 species (Schultz, 1977).

Elocryptus Schultz, 1977

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body widest at pereomere 5, tapering anteriorly and posteriorly with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes absent. Antennula article 1 without teeth. Coxal plates without teeth. Pereopods 1–2 gnathopodal, 3–7 ambulatory, propodi quadrate distally; dactyli of 3–5 shorter than propodi, 6 and 7 longer than propodi. Pleotelson margin smooth.

Mesopelagic, host unknown. Southern Ocean. 1 species (Schultz, 1977).

Nalocryptus Schultz, 1977

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body linear with prominent cuticular striations. Head much wider than long with posterolateral tapered extensions directed posteriorly, oral cone directed anteriorly. Eyes absent. Antennula article 1 without teeth. Coxal plates with teeth. Pereopods 1–3 gnathopodal, 4–7 ambulatory; propodi of 4–7 tapering distally, dactyli shorter than propodi. Pleotelson margin triangular, with teeth.

Mesopelagic, host unknown. Southern Ocean. 1 species (Schultz, 1977).

Nococryptus Schultz, 1977

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes absent. Antennula article 1 without teeth. Coxal plates with teeth. Pereopods 1 and 2 gnathopodal, 3–7 ambulatory; propodi of 3 broadly quadrate distally, distal end wider than proximal end; propodi of 4 and 5 narrowly quadrate distally, distal end approximately as wide as proximal end; propodus of pereopod 6 short, rounded, as long as carpus and merus combined, dactylus slender, elongate, as long as all other segments combined; pereopod 7 subequal to 4 and 5 in shape and size. Pleotelson margin smooth.

Slope, host unknown. Southern Ocean. 1 species (Schultz, 1977).

Onocryptus Schultz, 1977

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Head much wider than long with posterolateral tapered extensions directed posteriorly, oral cone directed anteriorly. Eyes absent. Antennula article 1 without teeth. Coxal plates with teeth. Pereopods 1 and 2 gnathopodal, 3–7 ambulatory; propodi of 3–5 rounded distally, dactyli shorter than propodi, recurved; propodus of 6 tapering in middle then slightly expanded to distal rounded tip, dactylus as long as propodus, straight; propodus of 7 tapering distally, dactylus as long as propodus, recurved. Pleotelson margin smooth.

Bathypelagic, host unknown. Southern Ocean. 1 species (Schultz, 1977).

Osicryptus Schultz, 1977

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes absent. Antennula article 1 with teeth and robust setal brush. Coxal plates with teeth. Pereopods 1 and 2 gnathopodal, 3–7 ambulatory; propodi of 3–6 quadrate distally, dactyli shorter than propodi; propodus of 7 rounded distally, dactylus shorter than propodus. Pleotelson margin smooth.

Bathypelagic, host unknown. Southern Ocean. 1 species (Schultz, 1977).

Thermaloniscus Bourdon, 1983

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly, oral sucker present. Eyes present. Antennula article 1 without teeth. Coxal plates without teeth. Pereopods 1 and 2 gnathopodal, 3–7 ambulatory; propodi of 3–7 quadrate distally, dactyli longer than propodi. Pleotelson margin smooth.

Bathyal, host unknown. Tropical Eastern Pacific. 1 species (Bourdon, 1983).

Trisopodoniscus Bourdon, 1981

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes absent. Antennula article 1 without teeth. Coxal plates without teeth. Pereopods 1–3 gnathopodal, 4–7 ambulatory; propodus of 4 quadrate distally, dactylus shorter than propodus; propodi of 5–7 elongate, tapering distally, dactyli approximately 1/4 of propodus length. Pleotelson margin smooth.

Bathypelagic, host unknown. Southern Ocean. 1 species (Bourdon, 1981).

Vacuotheca Schädel, Perrichot and Haug, 2019†

Diagnosis. **Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes absent. Antennula article 1 with teeth. Coxal plates with teeth. Pereopods 1–3 gnathopodal, 4–7 ambulatory; dactyli of all pereopods shorter than propodi. Pleotelson margin with teeth.

Fossil only, host unknown. Ex Vendean amber (France). 1 species (Schädel et al., 2019).

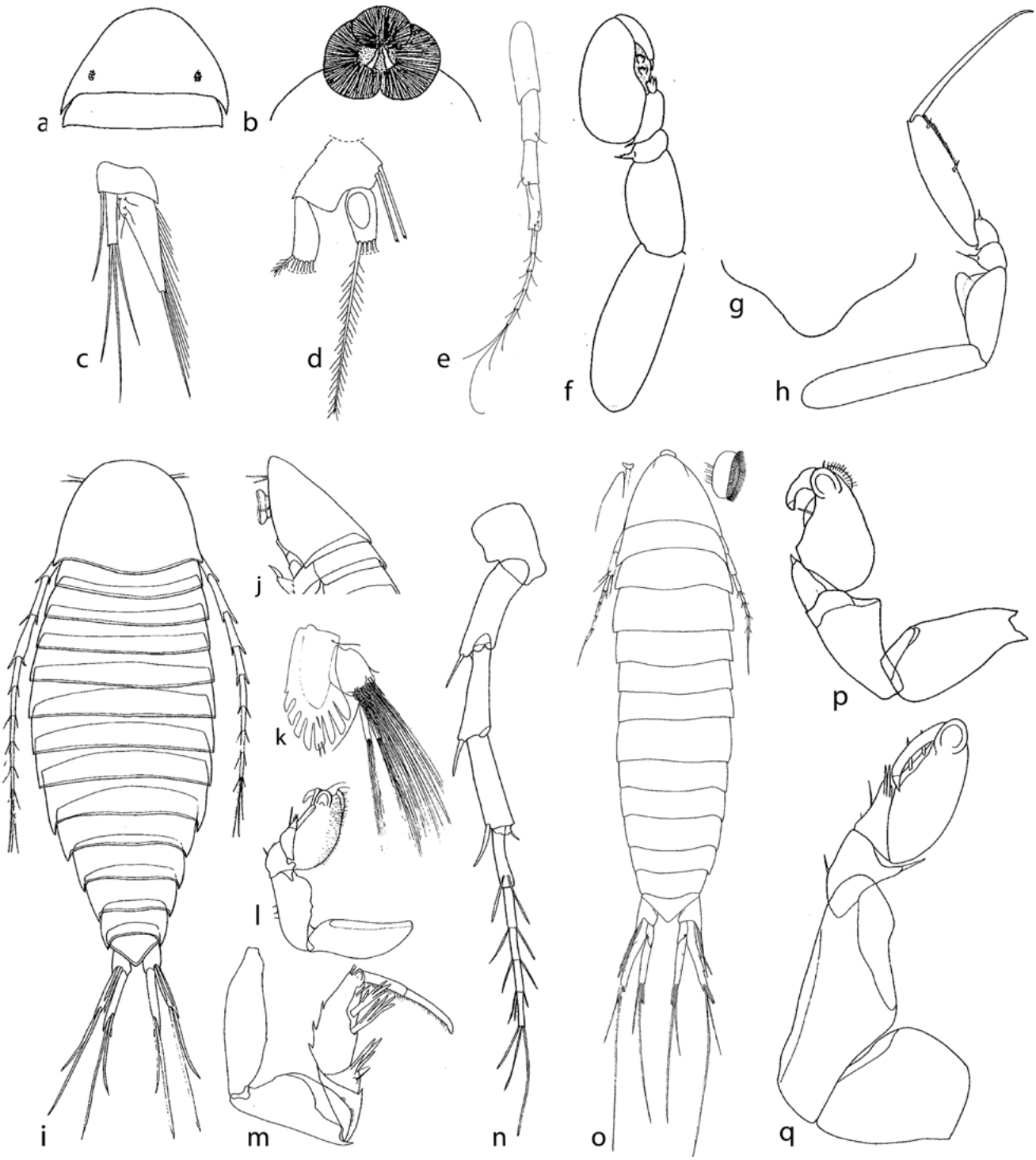


Figure 6.38. Cryptoniscoidea known only from cryptoniscus larvae. *Thermaloniscus cotylophorus* Bourdon, 1983: a, head dorsal view; b, oral sucker; c, uropod; d, pleopod 1; e, antenna; f, pereopod 1; g, pleotelson dorsal view; h, pereopod 7. *Dolichophryxus geminatus* Schultz, 1977: i, dorsal view; j, head and oral sucker lateral view; k, antennula; l, pereopod 1; m, pereopod 7; n, antenna. *Paraspidophryxus terminalis* Schultz, 1977: o, dorsal view with close-ups of oral sucker in lateral view; p, pereopod 1; q, pereopod 6.

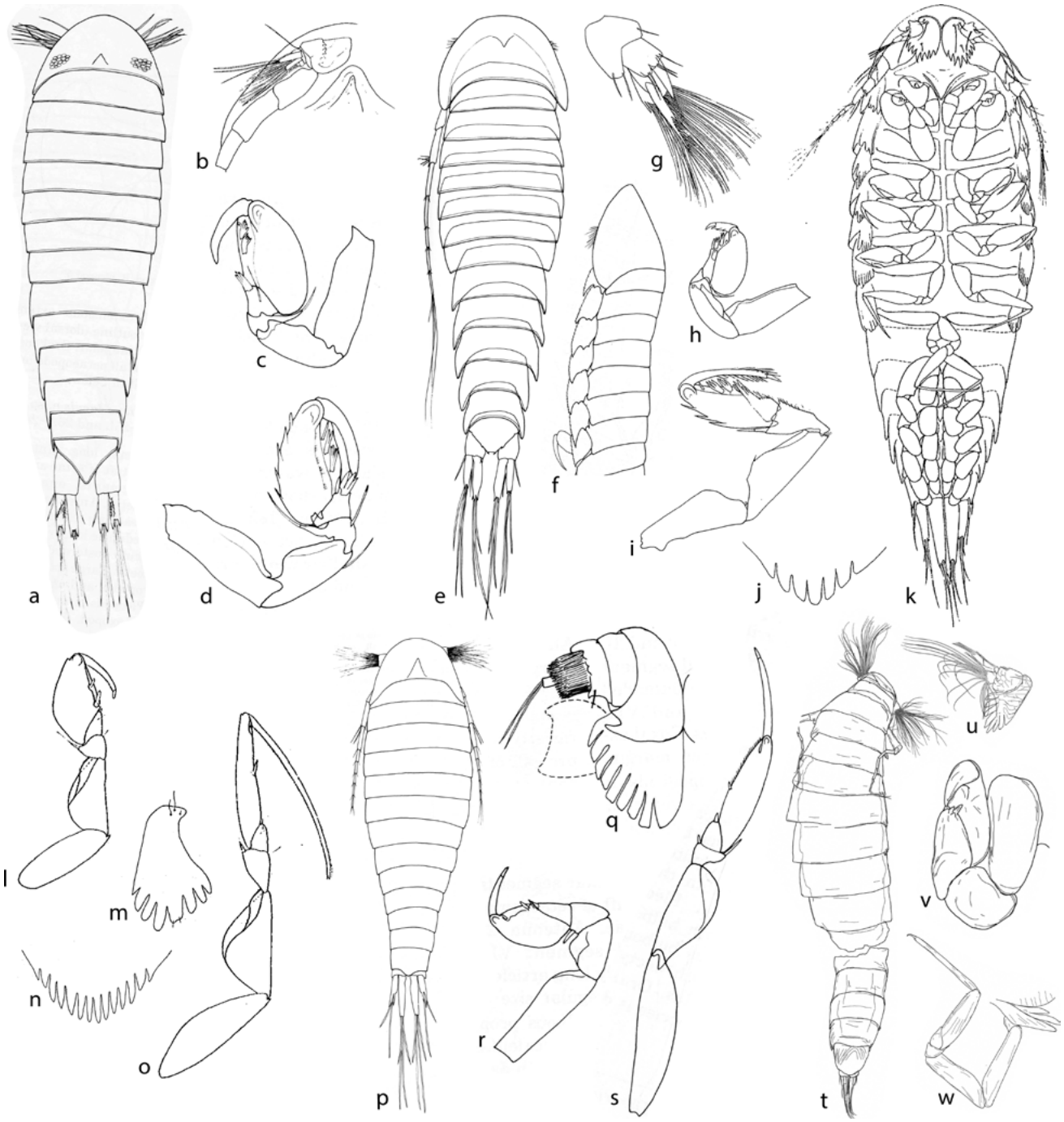


Figure 6.39. Cryptoniscoidea known only from cryptoniscus larvae. *Neritoniscus euphoticus* Schultz, 1977: a, dorsal view; b, antennula, oral cone and part of antenna; c, pereopod 1; d, pereopod 7. *Cryptocisus laevis* Schultz, 1977: e, dorsal view; f, lateral view of head and pereon showing serrated coxal plates; g, antennula; h, pereopod 1; i, pereopod 7. *Cironiscus dahli* Nielsen, 1967: j, pleotelson, dorsal view; k, ventral view. *Podoniscus multidentatus* Bourdon, 1981: l, pereopod 1; m, basal article of antennula; n, pleotelson, dorsal view; o, pereopod 7. *Osicryptus hirsutus* Schultz, 1977: p, dorsal view; q, antennula; r, pereopod 1; s, pereopod 7. *Chimaeroniscus spheramator* Williams, Boyko and Moritaki, 2022: t, dorsal view; u, antennula; v, pereopod 1; w, pereopod 7.

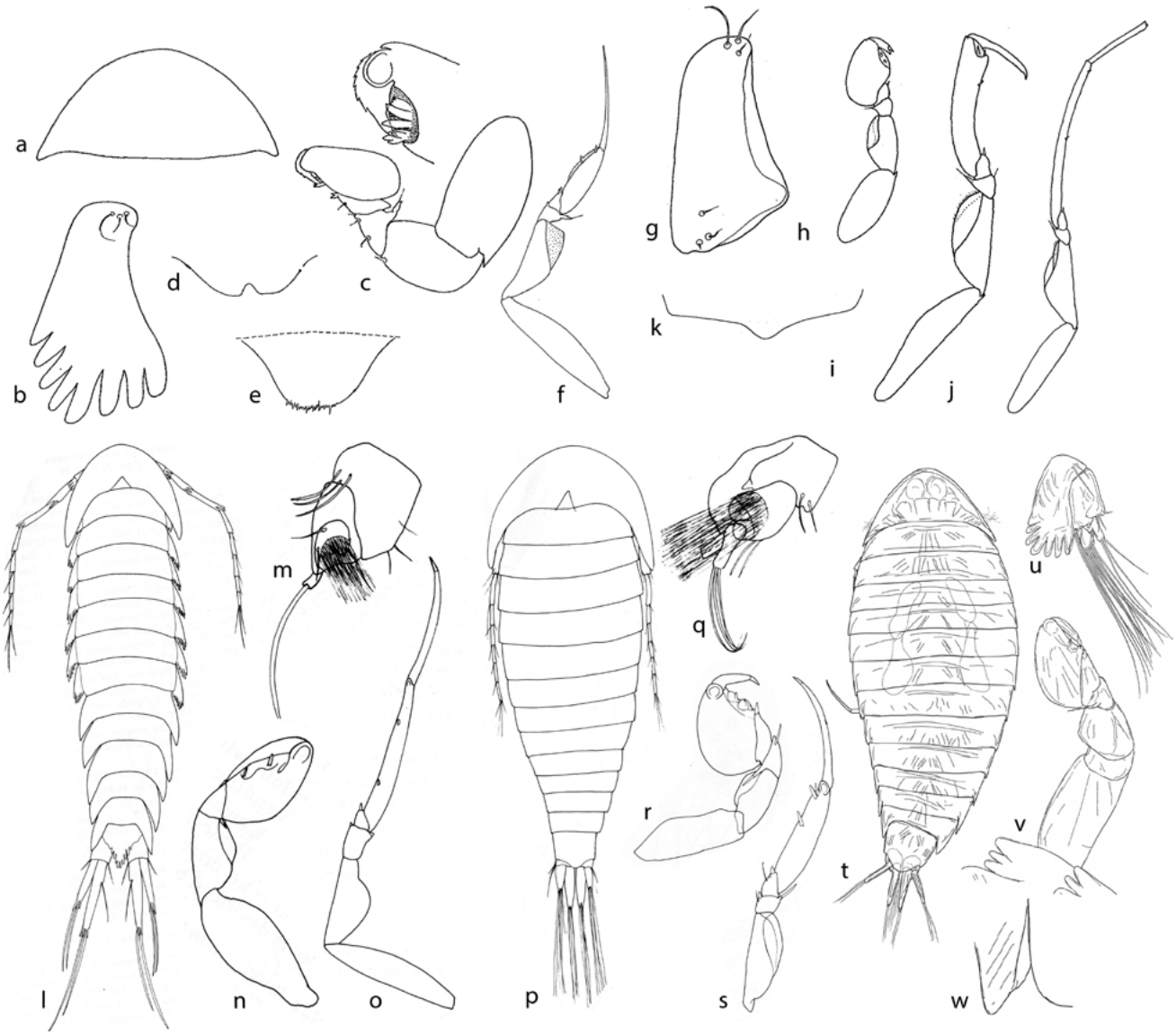


Figure 6.40. Cryptoniscoidea known only from cryptoniscus larvae. *Rolandoniscus serratus* (Bourdon, 1967): a, head, dorsal view; b, basal article of antennula; c, pereopod 1 and close-up; d, pleotelson, dorsal view; e, midventral tubercule; f, pereopod 7. *Trisopodoniscus abyssorum* Bourdon, 1981: g, basal article of antennula; h, pereopod 1; i, pereopod 4; j, pereopod 7; k, pleotelson dorsal view. *Nalocryptus longicaudatus* Schultz, 1977: l, dorsal view; m, antennula; n, pereopod 1; o, pereopod 7. *Onocryptus alatus* Schultz, 1977: p, dorsal view; q, antennula; r, pereopod 1; s, pereopod 7. *Pleuroniscus bellisamans* Williams and Boyko *in* Williams, Boyko and Stewart, 2024: t, dorsal view; u, antennula; v, right pereopod 2, base shown with coxal plates 1 and 2; w, coxal pate 5.

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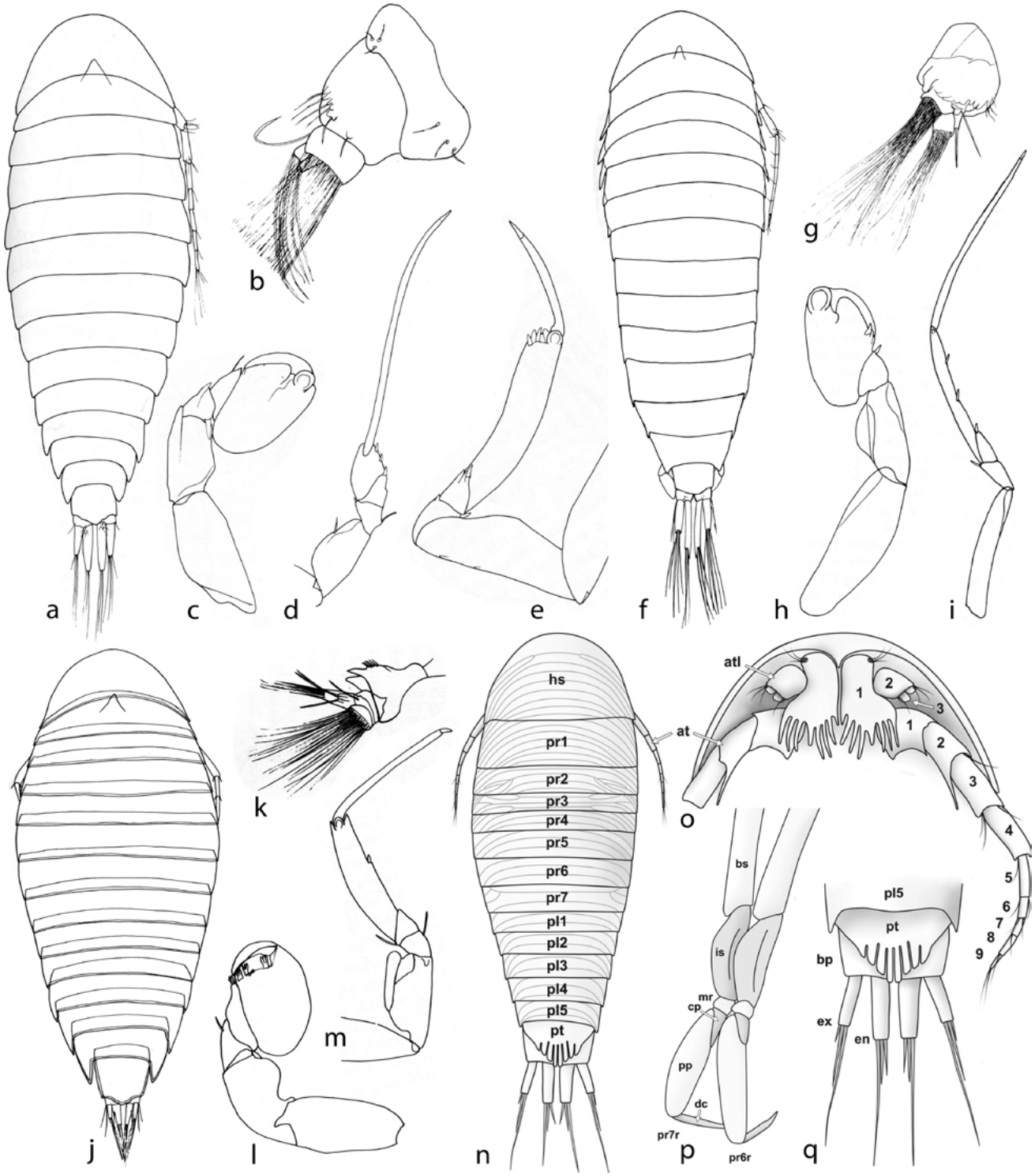


Figure 6.41. Cryptoniscoidea known only from cryptoniscus larvae, including the fossil genus *Vacuotheca* Schädel, Perrichot and Haug, 2019. *Nococryptus angustus* Schultz, 1977: a, dorsal view; b, antennula; c, pereopod 1; d, pereopod 6; e, pereopod 7. *Cryptocotitus acus* Schultz, 1977: f, dorsal view; g, antennula; h, pereopod 1; i, pereopod 7. *Elocryptus amplitruncus* Schultz, 1977: j, dorsal view; k, antennula; l, pereopod 1; m, pereopod 7. *Vacuotheca dupeorum* Schädel, Perrichot and Haug, 2019: n, dorsal view; o, antennulae and antennae; p, pereopods 6 and 7; q, pleotelson and uropods, dorsal view. Abbreviations: at, antenna (with number of articles indicated); atl, antennula (with number of articles indicated); bp, basipod of uropod; bs, basis; cp, carpus; dc, dactylus; en, endopod of uropod; ex, exopod of uropod; hs, head shield; is, ischium; mr, merus; pl1–5, pleomeres 1–5; pr1–7, pereomeres 1–7; pp, propodus; pr6r, right pereopod 6; pr7r, right pereopod 7; pt, pleotelson.

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Chapter 7. Suborder Phoratopidea

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Abstract Poore, G.C.B. 2026. Chapter 7. Suborder Phoratopidea. *In*: Poore, G.C.B. (ed.) Marine Crustacea Isopoda: guide to families and genera of the world. *Memoirs of Museum Victoria* 86: 355–356.

A diagnosis is provided for one family containing one genus and one species of marine isopod of the suborder Phoratopidea. Ecology and distribution are discussed with citation of literature critical for further investigation.

Keywords Phoratopodidae

Introduction

The single species, known from two specimens from South Australia (Hale, 1925), was redescribed by Bruce (1981). While superficially similar to cymothoidans, the species has uniquely wide merus–propodus on pereopods 4 and 5 with greatly reduced dactyli. Bruce (1981) noted similarities with some idoteid valviferans. Brandt and Poore (2003) placed the species in its own suborder.

Diagnosis. Head-pereonite 1 free. Pereopodal coxal dorsal plates 1–6 present; coxal dorsal plate 1 fused to tergite; coxal dorsal plate 7 absent (coxal dorsal plate 6 and pleonal 1 or 2 epimeron in contact); ventral coxal plates 1–7 (medial extension of coxa replacing sternite) obsolete (not distinguished from sternite). Pleotelson incorporating pleonite 6 only, pleonites 1–5 free. Pleotelson underside flat, without ventrolateral ridges (pleopods not enclosed laterally). Mandibular lacinia mobilis present on both sides; molar flat triangular blade-like or conical process; palp present. Maxilla trilobed. Maxillipedal endite reaching at least distal margin of palp article 2, usually distally truncate and setose. Pereopods 4 and 5 merus–propodus much wider than those of pereopods 2 and 3, with reduced dactyli. Pleopodal exopods uniarticulate. Pleopods 1 and 2 biramous. Pleopod 3 biramous; endopod more or less oval or rectangular, rounded distally. Telsonic region of pleotelson elongate, anus situated anteriorly on pleotelson. Uropod situated anterolaterally on pleotelson; peduncle not operculate; rami ventral to pleotelson, articulating from side to side in vertical axis inside branchial chamber.

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Phoratopodidae Hale, 1925

Figure 7.1

Phoratopus Hale, 1925

Shelf (79 m). Temperate South Australia. 1 species, *Phoratopus remex* Hale, 1925.

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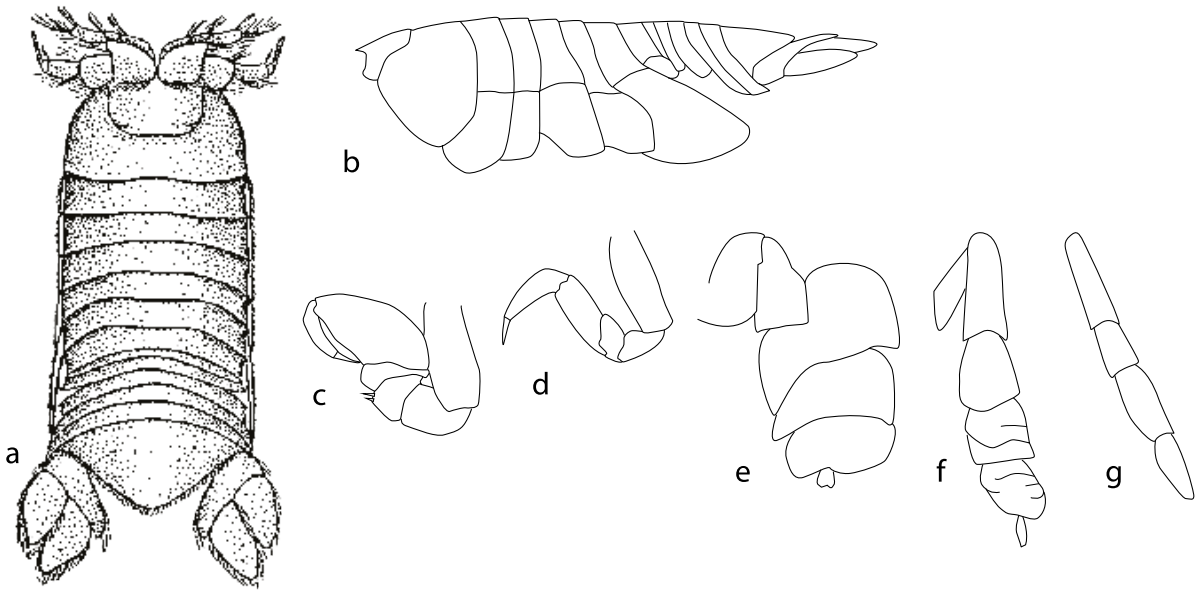


Figure 7.1. Phoratopodidae, *Phoratopus remex* Hale, 1925. a, b, habitus; c–g, pereopods 1, 2, 5, 6, 7. Fig. 7.1a from Hale (1925).

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Chapter 8. Suborder Limnoriidea

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Abstract Poore, G.C.B. 2026. Chapter 8. Suborder Limnoriidea. *In*: Poore, G.C.B. (ed.) Marine Crustacea Isopoda: guide to families and genera of the world. *Memoirs of Museum Victoria* 86: 357–362.

Diagnoses and illustrated keys are provided for three families and five genera of marine isopods of the suborder Limnoriidea. The ecology and distribution of each taxon are discussed with citation of literature critical for further investigation.

Keywords Hadromastacidae, Keuphyliidae, Limnoriidae, dichotomous keys

Introduction

The Limnoriidea Brandt and Poore *in* Poore, 2002 include three families whose similarity was recognised by Bruce (1988) and Wägele (1989). While the Limnoriidae are all wood, algal or seagrass borers and therefore herbivores, the other two families are not. Both are flattened and, as far as is known, free-living. The group is unified by the absence of a mandibular molar and long maxillipedal endite, the maxilliped usually being slender.

The suborder name was introduced in Poore (2002) and justified in a cladistic analysis by Brandt and Poore (2003). The Limnoriidea include three families, of which the Limnoriidae includes the junior synonym Lynseiidae Poore, 1994.

Diagnosis. Head-pereonite 1 free. Dorsal pereopodal coxal plates present (secondarily reduced in some species); coxal plate of pereopod 1 fused to tergite, or free from tergite; coxal plate 7 present; ventral coxal plates 1–7 (medial extension of coxa replacing sternite) obsolete (not distinguished from sternite). Pleotelson incorporating pleonite 6 only, pleonites 1–5 free. Pleotelson underside flat, without ventrolateral ridges (pleopods not enclosed laterally). Penial processes medial, closer to midpoint than to pereopods. Mandibular lacinia mobilis present on both sides, or absent; molar absent; palp present, or absent. Maxilla trilobed. Maxillipedal endite reaching at least distal margin of palp article 2, usually distally truncate and setose. Pereopods 1–3 more or less prehensile, directed anteriorly; pereopods 4–7 directed posteriorly. Pleopodal exopods uniarticulate. Pleopod 1 biramous. Pleopod 2 biramous. Pleopod 3 biramous; endopod more or less oval or rectangular, rounded distally. Telsonic region of pleotelson elongate, anus situated anteriorly on pleotelson. Uropod situated anterolaterally on pleotelson; peduncle not operculate; rami ventral to pleotelson, articulating from side to side in vertical axis inside branchial chamber.

Key to families of Limnoriidea

1. Body vaulted; head massive, capable of lateral rotation. Uropodal rami inserting widely separately on peduncle (fig. 8.1) ..... Hadromastacidae
– Body dorsoventrally compressed or semicircular in cross-section; head flat or cylindrical, not capable of lateral rotation. Uropodal rami inserting adjacently on peduncle 2
2. Body dorsoventrally compressed; head flat. Eyes dorsal (fig. 8.2) ..... Keuphyliidae
– Body semicircular in cross-section; head more or less spherical. Eyes lateral (fig. 8.3) ..... Limnoriidae

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Credits

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Fig. 8.1a, b, Bruce (1988). Fig. 8.2a, b, Bruce (1980). Fig. 8.3a, Poore (1987); b, c, Cookson (1991).

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Hadromastacidae Bruce and Müller, 1991

Figure 8.1

The Hadromastacidae comprise three species in one genus from the south-western Pacific and Indian Ocean. The genus *Hadromastax* Bruce, 1988 was originally placed in the Limnoriidae, but it bears little similarity to this family (Bruce and Müller, 1991).

Diagnosis. Head massive, capable of lateral rotation (offset from pereonite 1). Eyes lateral. Coxa 1 and pereonite 1 distinctly separated; pleonites 1–2 distinct, 3–4 laterally marked, pereonite 5 fused to pleotelson. Antennula flagellum with 2–4 articles. Frontal lamina absent; clypeus absent. Mandibular incisor massive in female; lacinia mobilis absent; palp with 3 articles. Maxillipedal epipod present. Pereopod 7 smaller and more slender than other pereopods. Uropodal rami inserting widely seperately on peduncle; endopod without apical claw.

Hadromastax Bruce, 1988

Subtidal, shelf; associated with coral. Western and Eastern Indo-Pacific, Temperate Australasia. 3 species (Bruce, 1988: species description; Bruce and Müller, 1991: genus diagnosis; Bruce, 2004: species description).

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Keuphyliidae Bruce, 1980

Figure 8.2

The family comprises a single species, epizoic on coral reefs in the region of Australia. Bruce (1980, 1988) believed the family to be most closely related to the Limnoriidae, a relationship supported by Brandt and Poore (2003).

Diagnosis. Head flat, not capable of lateral rotation (laterally encompassed by pereonite 1). Eyes dorsal. Coxa 1 and pereonite 1 fused; pleonites 1–5 free. Antennula flagellum with 3 articles. Frontal lamina present; clypeus present. Mandibular incisor not enlarged; lacinia mobilis present; palp absent. Maxillipedal epipod present. Pereopods 1–7 similar. Uropodal rami inserting adjacently on peduncle; endopod with apical claw.

Keuphylia Bruce, 1980

Subtidal; associated with coral. Central Indo-Pacific. 1 species (Bruce, 1980).

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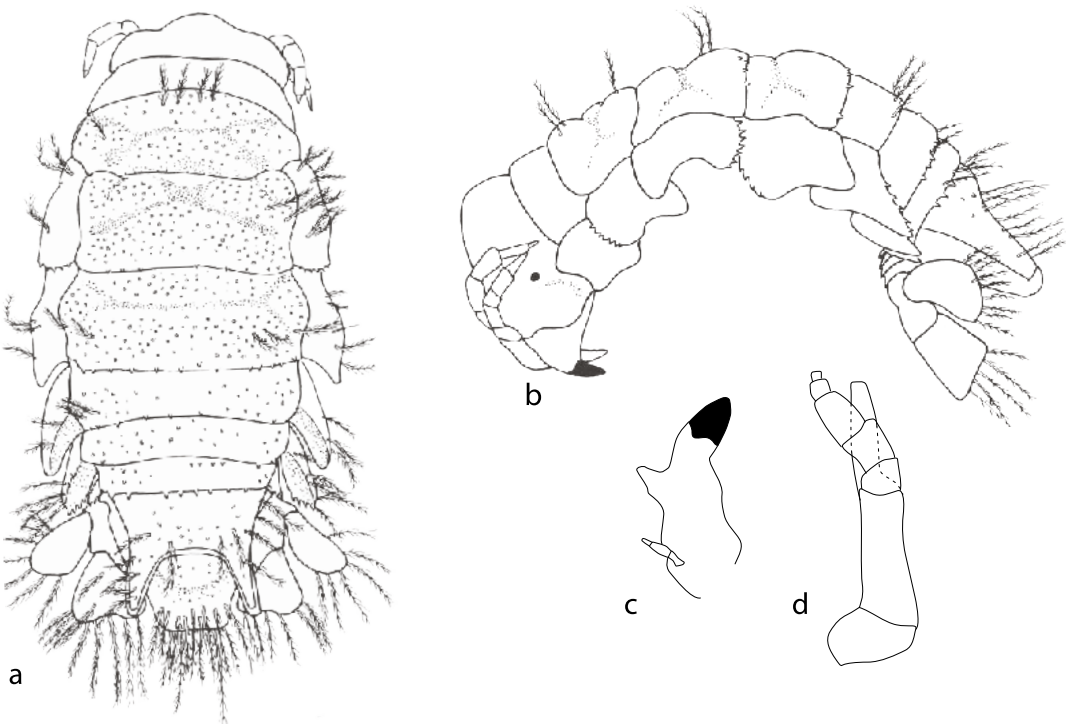


Figure 8.1. Hadromastacidae, *Hadromastax merga* Bruce, 1988. a, b, habitus, female; c, mandible, female; d, maxilliped (without setae).

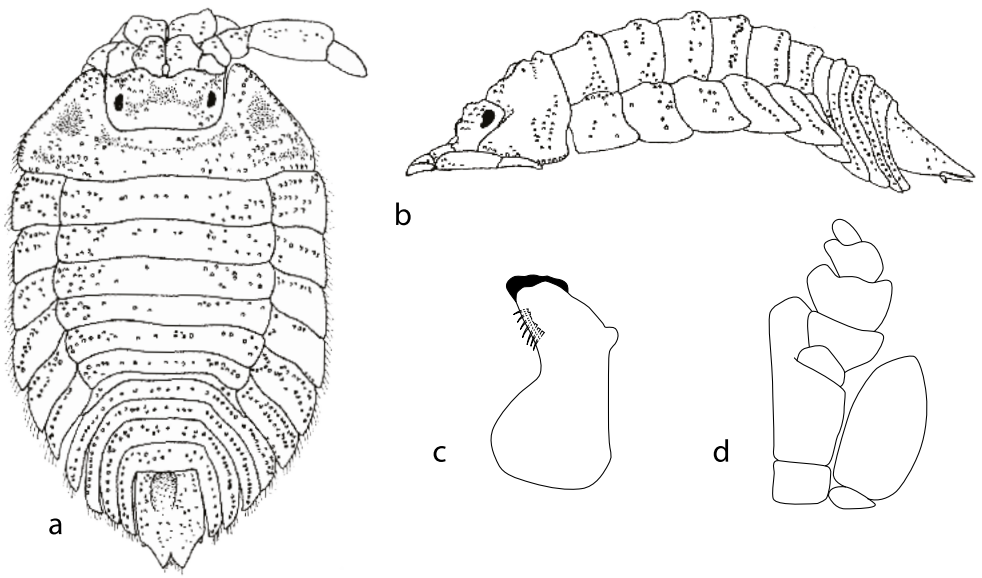


Figure 8.2. Keuphylidae, *Keuphylia nodosa* Bruce, 1980. a, b, habitus; c, mandible; d, maxilliped (without setae).

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Limnoriidae White, 1850

Figure 8.3

The Limnoriidae are a cosmopolitan family of marine borers from intertidal to slope depths. Species of *Paralimnoria* are wood borers, those of *Limnoria* are either wood or algal borers, and those of *Lynseia* are from seagrasses. The term "gribble" is applied to species of *Limnoria*. Mature specimens are between 2 and 8.5 mm long. Species of *Limnoria* are found boring in saturated wood and the holdfasts of algae of the genera *Macrocystis, Egregia, Laminaria, Postelsia, Eisenia*, *Ecklonia, Durvillaea*, *Sargassum*, *Lessonia, Corallina* and other red algae (Menzies, 1957). Four species have been found in the rhizomes of seagrasses, *Posidonia*, *Thalassia*, *Phyllospadix*, *Amphibolis* and *Zostera* (Brearley et al., 2008; Cookson and Lorenti, 2001; van Tussenbroek and Brearley, 1998). *Lynseia* is an Australian genus of three species that mines the leaves of sea-grasses of the genera *Zostera* and *Posidonia* (Brearley and Walker, 1995).

The wood borers are of major economic importance; the most-studied species is *L. tripunctata* Menzies, 1951. Damage to wooden piles and ships is well studied (Cragg et al., 1999), but gribble also attack cultural heritage (Pournou, 2020). *Limnoria* are usually found in pairs in burrows, with the female at the blind end of the tunnel (Eltringham and Hockley, 1961). Cookson's (1991) review of the Australasian species surpassed that of Menzies (1957). Both authors discussed the history of the family and defined the genera and species then known. *Lynseia* was added later (Cookson and Poore, 1994).

Diagnosis. Head more or less spherical, not capable of lateral rotation (laterally encompassed by pereonite 1). Eyes lateral. Coxa 1 and pereonite 1 fused; pleonites 1–5 free. Antennula flagellum with 3 or 4 articles. Frontal lamina absent; clypeus present. Mandibular incisor not enlarged; lacinia mobilis present; palp absent, reduced to seta or of 1–3 articles. Maxillipedal epipod present. Pereopod 7 longer than other pereopods. Uropodal rami inserting adjacently on peduncle.

Key to genera of Limnoriidae

1. Body 7–15 times as long as wide. Pereopods 6 and 7 much longer than pereopod 5 (fig. 8.3a) ..... *Lynseia*
– Body less than 5 times as long as wide. Pereopods 6 and 7 not longer than pereopod 5 (fig. 8.3b, c) 2
2. Uropodal rami elongate, with apical claw (fig. 8.3n). Antennula flagellum with 5 articles (fig. 8.3f). Pereopod 1 secondary unguis trifid (fig. 8.3k) ..... *Paralimnoria*
– Uropodal exopod much shorter than endopod, endopod without apical claw (fig. 8.3l). Antennula with 4 or fewer flagellar articles (fig. 8.3d). Pereopod 1 secondary unguis bifid (Fig. 8.3a) or undivided, sometimes with accessory spinules (fig. 8.3j) ..... *Limnoria*

Limnoria Leach, 1814

Diagnosis. Body less than 5 times as long as wide. Antennula flagellum with 3 or 4 articles. Maxillipedal palp of 5 articles. Pereopods 6 and 7 not significantly longer than pereopod 5. Uropodal endopod without apical claw; exopod much shorter than endopod.

Subtidal–slope (0–1100 m); burrowing in decaying wood, large brown algae and seagrass. Temperate Northern and Tropical Atlantic, Temperate Northern Pacific, Indo-West Pacific, Temperate Southern Africa, Temperate Australasia, Southern Ocean. 55 species (Cookson, 1991: rediagnosis, key to 41 species).

Lynseia Poore, 1987

Diagnosis. Body 7–15 times as long as wide. Antennula flagellum with 2 articles. Maxillipedal palp of 1 or 3 articles. Pereopod 1 secondary unguis trifid; pereopods 6 and 7 much longer than pereopod 5. Uropodal endopod without apical claw; exopod much shorter than endopod.

Subtidal; burrowing into leaf bases of seagrasses, *Zostera* and *Posidonia*. Temperate Australasia. 3 species (Poore, 1987: diagnosis, species description; Cookson and Poore, 1994: diagnosis, family placement, species descriptions; Brearley and Walker, 1995: ecology; 1996: ecology).

Paralimnoria Menzies, 1957

Diagnosis. Body less than 5 times as long as wide. Antennula flagellum with 5 articles. Maxillipedal palp of 5 articles. Pereopod 1 secondary unguis bifid; pereopods 6 and 7 not significantly longer than pereopod 5. Uropodal endopod with apical claw; exopod more than half as long as endopod.

Subtidal; burrowing in decaying wood. Western and Central Indo-Pacific. 2 species (Menzies, 1957: foundation study; Cookson and Cragg, 1988: second species; Cookson, 1991: rediagnosis).

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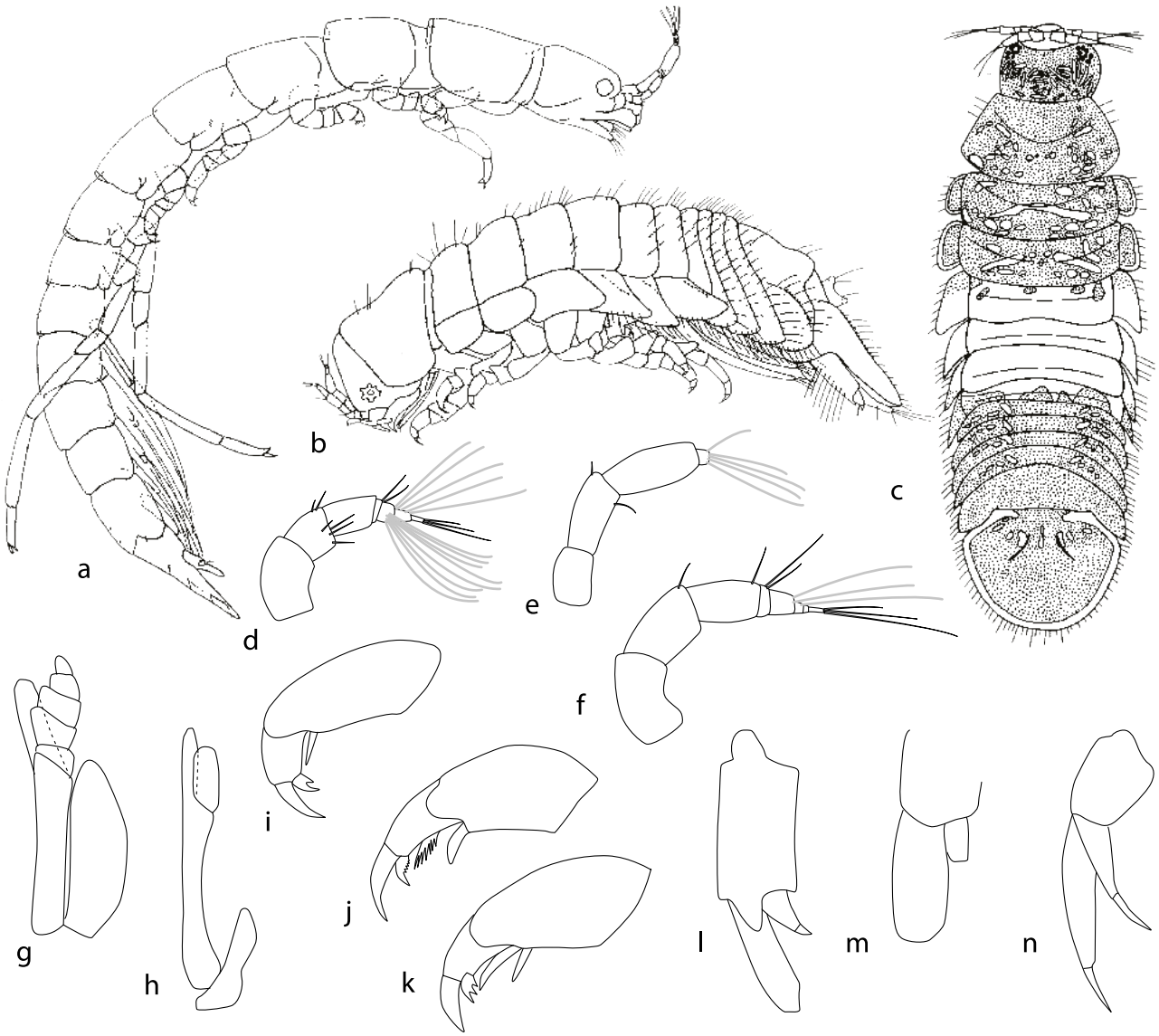


Figure 8.3. Limnoriidae. a, *Lynseia himantopoda* Poore, 1987; b, *Limnoria indica* Becker and Kampf, 1958; c, *Limnoria glaucinosa* Cookson, 1991. Antennula: d, *Limnoria*; e, *Lynseia*; f, *Paralimnoria*. Maxilliped: g, *Limnoria*; h, *Lynseia*. Pereopod 1 propodus, dactylus: i, j, *Limnoria*; k, *Paralimnoria*. Uropod: l, *Limnoria*; m, *Lynseia*; n, *Paralimnoria*.

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Chapter 9. Suborder Sphaeromatidea

(http://zoobank.org/urn:lsid:zoobank.org:pub:92D63170-6096-4600-8E4B-2C49A9CCE92B)

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Abstract Poore, G.C.B., and Bruce, N.L. 2026. Chapter 9. Suborder Sphaeromatidea. *In*: Poore, G.C.B. (ed.) Marine Crustacea Isopoda: guide to families and genera of the world. *Memoirs of Museum Victoria* 86: 363–432.

Diagnoses and illustrated keys are provided for eight families and 124 genera of the Isopoda suborder Sphaeromatidea. Paravireiidae fam. nov. is erected for the genus *Paravireia* Chilton, 1925. The ecology and distribution of each taxon are discussed with citation of literature critical for further investigation and identification to species.

Keywords Ancinidae, Basserolidae, Bathynataliidae, Paravireiidae, Plakarthriidae, Serolidae, Sphaeromatidae, Tecticipitidae, new family, dichotomous keys

Introduction

Sphaeromatidea Wägele, 1989 have the pleonites fused to some degree and differ from the other large group of the former "Flabellifera" in having the uropodal rami lateral to the margin of the pleotelson and folding down alongside the branchial space, whereas in Cymothoidea the uropodal rami are ventral to the pleotelson and articulating from side to side along a vertical axis inside the branchial space.

Brandt and Poore (2003) separated superfamily Seroloidea (four families) from Sphaeromatoidea (three families) but the morphological criteria for doing so were weak. The small families Bathynataliidae and Basserolidae are similar to the larger Serolidae, and the small families Ancinidae and Tecticipitidae are similar to the much larger Sphaeromatidae. However, the relationships of Plakarthriidae and the enigmatic *Paravireia* (for which we erect Paravireiidae fam. nov.) are problematic. The superfamilies are not recognised here. The smaller families have diagnostic maxillula and maxilla being somewhat more reduced than in the Sphaeromatidae. These characters are not used in the key because of the difficulty of dissection – and are unnecessary.

Wetzer et al. (2013) provisionally found using molecular data (16S, 18S genes) that Sphaeromatidea was not monophyletic but part of a larger clade including Serolidae and Valvifera. Later, Wetzer et al. (2018) concluded that Sphaeromatidea (represented by Serolidae, Ancinidae, Plakarthriidae and many genera of Sphaeromatidae) was monophyletic. The largest family Sphaeromatidae is highly diverse, and the Plakarthriidae was doubtfully embedded within it.

Diagnosis. Head free from, or fused to pereonite 1. Pereopodal coxal dorsal plates present (secondarily reduced in some species); coxal dorsal plate of pereopod 1 fused to tergite, or free from tergite (*Plakarthrium*); coxal plate 7 present, or absent (coxal dorsal plate 6 and pleonal epimera 1 or 2 in contact); coxal ventral plates 1–7 (medial extension of coxa replacing sternite) obsolete (not distinguished from sternite), or extending to midpoint (well defined and separated by suture). Pleonites 1–5 variously fused, occasionally fused to pleotelson, pleonites 1–3 sometimes indicated by lateral sutures. Pleotelson underside vaulted, branchial chamber defined by ridges along mesial margin of lateral edge (except in Sphaeromatidae "Cassidiniinae"); ventrolateral margins of pleon and pleotelson narrow, or broad and flattened. Telsonic region of pleotelson elongate, anus situated anteriorly on pleotelson. Penial processes mesial, closer to midpoint than to pereopods. Mandibular lacinia mobilis present on both sides, or present on left side, reduced and fused with spine row on right, or absent; molar usually a cylindrical process with triturative flat end, or absent; palp present, or absent (*Plakarthrium*). Maxilla trilobed. Maxillipedal endite reaching at least distal margin of palp article 2, usually distally truncate and setose. Pereopods 1–3 usually ambulatory (pereopod 1 sometimes subchelate or subprehensible), directed anteriorly; pereopods 4–7 directed posteriorly. Pleopods 1 and 2 biramous. Uropod attached anterolaterally on pleotelson or on posterior margin of pleotelson; peduncle not operculate; rami lateral to margin of pleotelson, articulating in longitudinal axis and folding alongside branchial chamber.

This is contribution number 1045 from the Water Research Group, North-West University, South Africa.

Key to families of Sphaeromatidea

1. Pereopod 1 ambulatory, propodus not expanded or ovate 2
– Pereopod 1 subprehensible or subchelate, propodus dilated, ovate 4
2. Uropod absent. Body vaulted. Coxal dorsal plates and pleonal epimera with setal fringe (fig. 9.5) ..... Paravireiidae fam. nov. ... p. 370
– Uropod present. Body vaulted or flat. Coxal dorsal plates and pleonal epimera rarely with setal fringe 3
3. Coxal dorsal plate 1 free from pereonite, separated by suture. Pleon and pleotelson completely surrounded, laterally by coxal plates 7 and posteriorly by uropods (fig. 9.4) ..... Plakarthriidae ... p. 369
– Coxal dorsal plate 1 fused to pereonite, without visible suture. Pleon and pleotelson not completely surrounded laterally by coxal dorsal plates 7; pleotelson sometimes enclosed by lateral uropods (figs 9.9–9.21) ..... Sphaeromatidae ... p. 382
4. Pereonite 7 not visible dorsally, submerged, without coxal dorsal plates (short segment following pereonite 6 is pleonite 1) (figs 9.2, 9.6, 9.7) 5
– Pereonites 1–7 visible, separate dorsally (figs 9.1, 9.3, 9.22) 6
5. Pleopods 1–3 with rectangular peduncles, with terminal rami. Maxillipedal palp of 1 article (fig. 9.2) ..... Basserolidae ... p. 366
– Pleopods 1–3 narrow, tapering, directed laterally, rami distal and subdistal. Maxillipedal palp of 3 articles, second more or less cordiform (rarely 2-articled) (fig. 9.8a, e, f) ..... Serolidae ... p. 371
6. Pleon rectangular over most of length. Uropods attached on posterior margin of pleotelson (fig. 9.3) ..... Bathynataliidae ... p. 367
– Pleotelson more or less triangular or pentagonal. Uropods attached anterolaterally to pleotelson 7
7. Head fused medially to pereonite 1. Uropod without endopod; exopod long (fig. 9.1) ..... Ancinidae ... p.365
– Head free from pereonite 1. Uropod biramous (fig. 9.22) ..... Tecticipitidae ... p. 430

Contributions of the authors

NLB was the leading author for Sphaeromatidae while GCBP was the leading author for all other families.

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Credits

Most line illustrations in this chapter are tracings of figures assembled from the literature, all more or less simplified, undertaken by GCBP using Adobe Illustrator®. Others, listed below, are reprinted directly with permission of the publisher and/or author or are in the public domain. The references cited can be found in sections dealing with relevant families.

Fig. 9.1a, Poore (1990). Fig. 9.2a, Guedes-Silva et al. (2019); b, c, Shimomura (2008). Fig. 9.3a, Kensley (1978); b, Poore (2005); c, Kensley (1979). Fig. 9.4, Poore and Brandt (2001). Fig. 9.5, Brokeland et al. (2001). Fig. 9.6a, Moreira (1971); b, Kussakin (1967); c, j, Menzies (1962); d, Moreira (1976); e, Storey and Poore (2009); f, Kensley (1978); g, Vanhöffen (1914); h, Wägele (1994); i, Brandt (1992); k, Harrison and Poore (1984); l, Sheppard (1933). Fig. 9.7a, Bruce (2009); b, Moreira (1974); c, Wägele (1994); d, Bruce (2009); e, f, j, k, Wägele (1994); g–i, Poore (1987); l, Moreira (1971). Fig. 9.9a, Müller (1995); b, d, e, Bruce (1994c); c, Harrison (1984); f, Wetser and Bruce (1999); g, h, Bruce (2003); i, k, l, Bruce (1994a); j, Richardson (1910); m, n, Harrison and Holdich (1984); o, p, Bruce and Holdich (2002); q, Bruce (1994). Fig. 9.10a, Khalaji-Pirbalouty and Bruce (2021); b, Brandt (1998); c, d, Bruce (1994b); e, f, Harrison and Holdich (1982b); g, h, Bruce (1994a); i, j, Holdich and Harrison (1981); k, l, Kussakin and Malyutina (1993); m, n, Harrison and Holdich (1984); o, Kussakin (1979). Fig. 9.11a, b, Harrison and Holdich (1984); c, d, Holdich and Harrison (1983); e, Brandt and Wägele (1989); f, Baker (1926); g, h, Schotte and Kensley (2005); i, j, Bruce (1994c); k, l, Holdich and Harrison (1980); m, n, Harrison and Holdich (1982a); o, p, Kensley and Bruce (2001). Fig. 9.12a, Hurley and Jansen (1977); b, c, Harrison and Holdich (1982a); d, e, Messana (1990); f, g, Bruce (1994b); h, i, Holdich and Harrison (1983); j, Brandt and Wägele (1989); k, l, Menzies and Glynn (1968); m, n, Harrison and Holdich (1982b); o, p, Baker (1926). Fig. 9.13a, Khalaji-Pirbalouty and Bruce (2014); b, c, Menzies and Miller (1955); d, e, Harrison and Holdich (1982a); f, Hurley and Jansen (1977); g, h, Bruce (1993); i, j, n, o, Bruce (2003); k, l, Bruce (1992); m, Nishimura (1976). Fig. 9.14a, b, Harrison (1984); c, d, k, l, o, p, Harrison

and Holdich (1982b); e, f, m n, Harrison and Holdich (1984); g, h, Bruce (2004c); i, j, Müller (1991); q, r, Javed and Ahmed (1988). Fig. 9.15a, Buss and Iverson (1981); b, c, Bruce (2001); d, Kensley (1978); e, f, Bruce (2003); g, h, Harrison and Holdich (1982b); i, Harrison and Holdich (1984); j, k, Harrison (1984); l, m, Holdich and Harrison (1981b). Fig. 9.16a, b, Bruce (2009); c, d, Bruce and Wetzer (2008); e, f, k, l, Harrison and Holdich (1984); g, h, Holdich and Harrison (1983); i, j, Loyola e Silva (1966); m, n, Holdich and Harrison (1981a); o, Bruce (2001); p, Glynn (1968). Fig. 9.17a, b, Holdich and Harrison (1981b); c, d, Eleftheriou et al. (1980); e, f, Harrison (1984); g, Bruce (1994a); h, i, Harrison and Holdich (1984). Fig. 9.22a, Kussakin (1979).

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Ancinidae Dana, 1852

Figure 9.1

Ancinidae comprise two small genera from quite different habitats: *Ancinus* from sand beaches of the New World and *Bathycopea* from shelf and bathyal environments (Loyola e Silva, 1971). Their family status was confirmed by Bruce (1993). Iverson (1982) provided a more extensive diagnosis but treated the group as a subfamily of Sphaeromatidae.

Because of the homology of the uropod to that of some Sphaeromatidae and because the absence of the exopod in this family is rare, we treat the only ramus of the uropod as its exopod.

Diagnosis. Body oval, vaulted; head medially fused with pereonite 1; pereonites 1–7 visible dorsally, separated by sutures. Coxal dorsal plates 2–7 delimited from tergite by suture; plate 7 similar to dorsal coxal plate 6. Pleon with pleonite 1 almost hidden dorsally, pleonites 2–5 fused, indicated laterally by none or one suture. Pleotelson broad, triangular. Antennular and antennal peduncles cylindrical, not part of margin of body. Mandibular incisor cultrate, with or without cusps. Maxillula mesial endite small, with 1 simple seta; lateral endite with 7–12 spines, some serrate. Maxilla mesial endite small; second and lateral endites with long setae. Maxillipedal palp of 5 free articles. Pereopod 1 subchelate, propodus swollen, palm with row of close-set robust setae. Pereopod 2 subchelate in males only. Pleopods 1–3 peduncles subquadrate, with terminal rami. Uropods attached anterolaterally to pleotelson; uniramous (exopod only), attached to anterolateral pleotelson.

Key to genera of Ancinidae

1. Uropodal exopod styliform, acute. Pleopod 1 uniramous (fig. 9.1a) ..... *Ancinus*
– Uropodal exopod laminar. Pleopod 1 biramous (fig. 9.1b, c) ..... *Bathycopea*

Ancinus H. Milne Edwards, 1840

Diagnosis. Mandibular molar process absent. Maxilla with 2 endites. Pleopod 1 uniramous (exopod only). Pleopod 3 without transverse suture. Uropod styliform.

Intertidal, subtidal. Tropical Atlantic, Western Indo-Pacific, Tropical Eastern Pacific. 10 species (Kensley and Schotte, 1987; Rocha-Ramírez et al., 2010; Guedes-Silva et al., 2019: rediagnosis, key to species).

Bathycopea Tattersall, 1905

Diagnosis. Mandibular molar process present. Maxilla with 3 endites. Pleopod 1 biramous. Pleopod 3 with transverse suture. Uropod laminar.

Shelf–abyssal (17–4070 m). Temperate Northern Atlantic, Tropical Atlantic, Temperate Northern W Pacific, Tropical Eastern Pacific, Temperate Southern Africa, Temperate Australasia. 6 species (Shimomura, 2008: rediagnosis, key to species).

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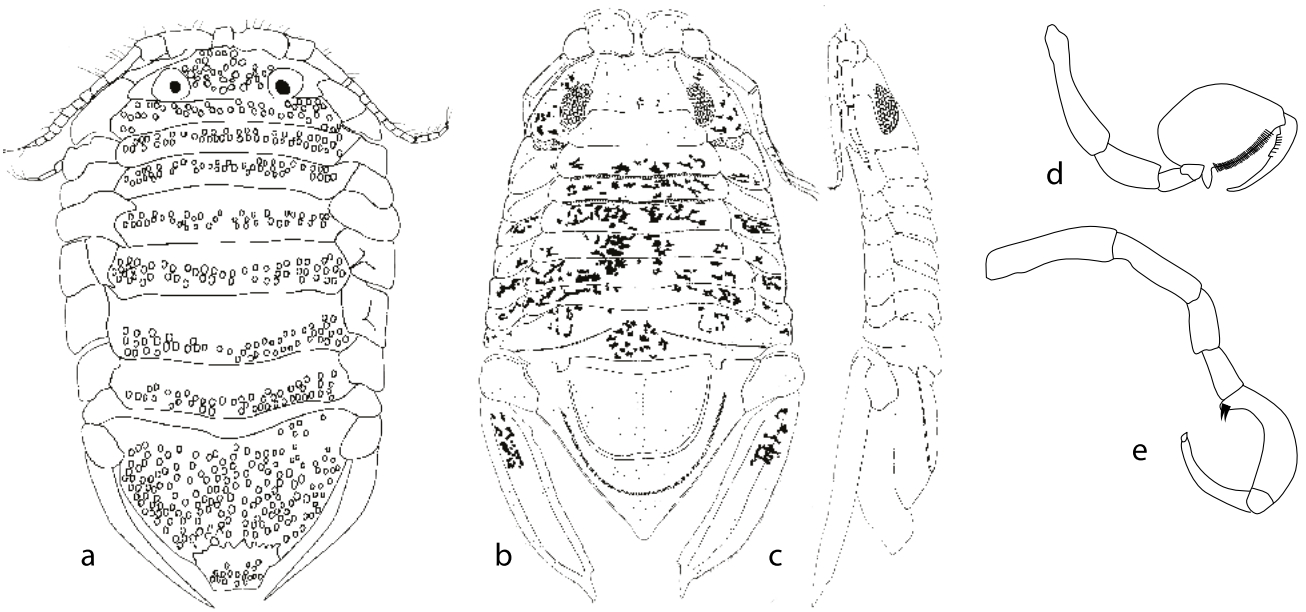


Figure 9.1. Ancinidae. a, *Ancinus velella* Guedes-Silva, Paiva, Maida and Souza-Filho, 2019; b, c, *Bathycopea oculata* Shimomura, 2008; d, e, *Ancinus*, pereopods 1, 2 (male).

Basserolidae Brandt and Poore, 2003

Figure 9.2

Pereopod 1 lacks the complex robust setae along the propodal palm seen in serolids, and pleopods 1–3 have a quadrate peduncle, not the transverse triangular form seen in serolids. Brandt and Poore (2003) removed the only genus from Serolidae.

Diagnosis. Body almost evenly oval, flat, margin defined by head, coxal plates and pleon, slight interruptions between coxal plates and pleon; head fused medially with pereonite 1; pereonite 7 not visible dorsally, submerged; pereonites 5–7 ventral coxal plates meeting in midline. Coxal dorsal plates 2–6 delimited from tergite by suture, 4–6 weakly so; plate 7 not visible dorsally. Pleon with pleonite 1 visible dorsally, without epimera; pleonites 2 and 3 free, with prominent epimera; pleonal sternites 1–3 present. Pleotelson broad, laterally oval. Antennular and antennal peduncles flattened, not part of margin of body. Maxillula mesial endite short, with 1 seta, lateral endite with 5 or 6 distal setae. Maxilla mesial endite obscure, without setae, second endite with 1 simple seta, lateral endite with 2 simple setae. Mandibular incisor triangular; molar process absent. Maxillipedal palp of 1 short article. Pereopod 1 subchelate, propodus barely tapering, palm straight with row of well-spaced robust setae. Pereopod 2 not sexually dimorphic. Pleopods 1–3 peduncles subquadrate, with terminal rami. Uropods attached on posterior margin of pleotelson; biramous, with mesially expanded peduncle.

Basserolis Poore, 1985

Shelf (115–200 m). Temperate SE Australia. 2 species (Poore, 1985, 1990).

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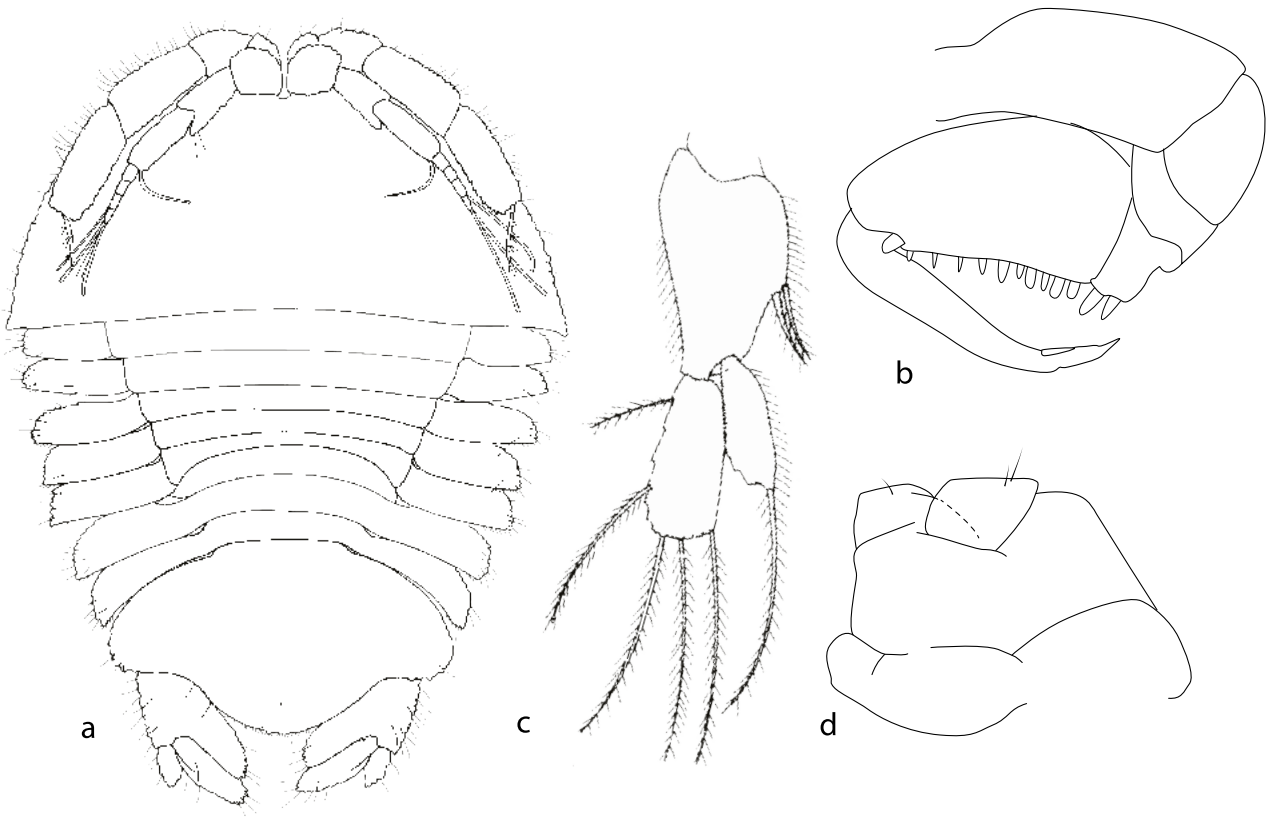


Figure 9.2. Basserolidae. a, *Basserolis franklinae* Poore, 1990; b, pereopod 1; c, pleopod 1; d, maxilliped.

Bathynataliidae Kensley, 1978

Figure 9.3

Bathynataliids are a diverse family of four Southern Hemisphere species in three genera. The head embedded in the surrounding pereonite 1 resembles that of serolids, but the two families differ in the number of free pleonites.

Diagnosis. Body elongate–oval, flat or vaulted, with rectangular pleotelson; head fused medially with pereonite 1; pereonites 1–7 visible dorsally, separated by sutures; pereonites 5–7 sternites and ventral coxal plates fused together at midline. Coxal dorsal plates 2–7 delimited from tergite by suture; plate 7 visible but shorter than coxal plate 6, or not visible dorsally. Pleon of 4 free pleonites (or pleonites 1, 2 fused dorsally) and fused pleonite 5–pleotelson, or of 5 free pleonites (with slight movement) and pleotelson; pleonal sternites 1–3 absent. Pleotelson scarcely tapering, uropods attached posteriorly. Antennular and antennal peduncles cylindrical, not part of margin of body. Mandibular incisor multicuspid; molar process absent. Maxillula mesial endite minute, with 1 short simple seta; lateral endite usually with 11 large setae. Maxilla mesial endite with few plumose setae; second and lateral endites each with 2 long setae or lateral endite absent. Maxillipedal palp of 3 articles, fused articles 2–3 oval. Pereopod 1 subchelate, propodus barely tapering, palm straight with row of well-spaced robust setae, or subchelate, propodus about as wide as long, palm straight with few robust setae. Pereopod 2 not sexually dimorphic. Pleopods 1–3 peduncles subquadrate, with terminal rami. Uropods attached on posterior margin of pleotelson; biramous, or with knob-like rami fused to peduncle.

Key to genera of Bathynataliidae

1. Body deeply vaulted; middorsal pereonites and coxae with blunt projections (fig. 9.3a) ..... *Bathynatalia*
– Body almost evenly oval, margin defined by head, coxal plates and pleon; without projections 3
2. Eyes absent. Pleon comprising 5 free pleonites and pleotelson (fig. 9.3c). Pereopod 7 absent ..... *Brianaudea*
– Eyes minute. Pleon comprising 4 free pleonites and fused pleonite 5–pleotelson (fig. 9.3b). Pereopod 7 present ..... *Biremia*

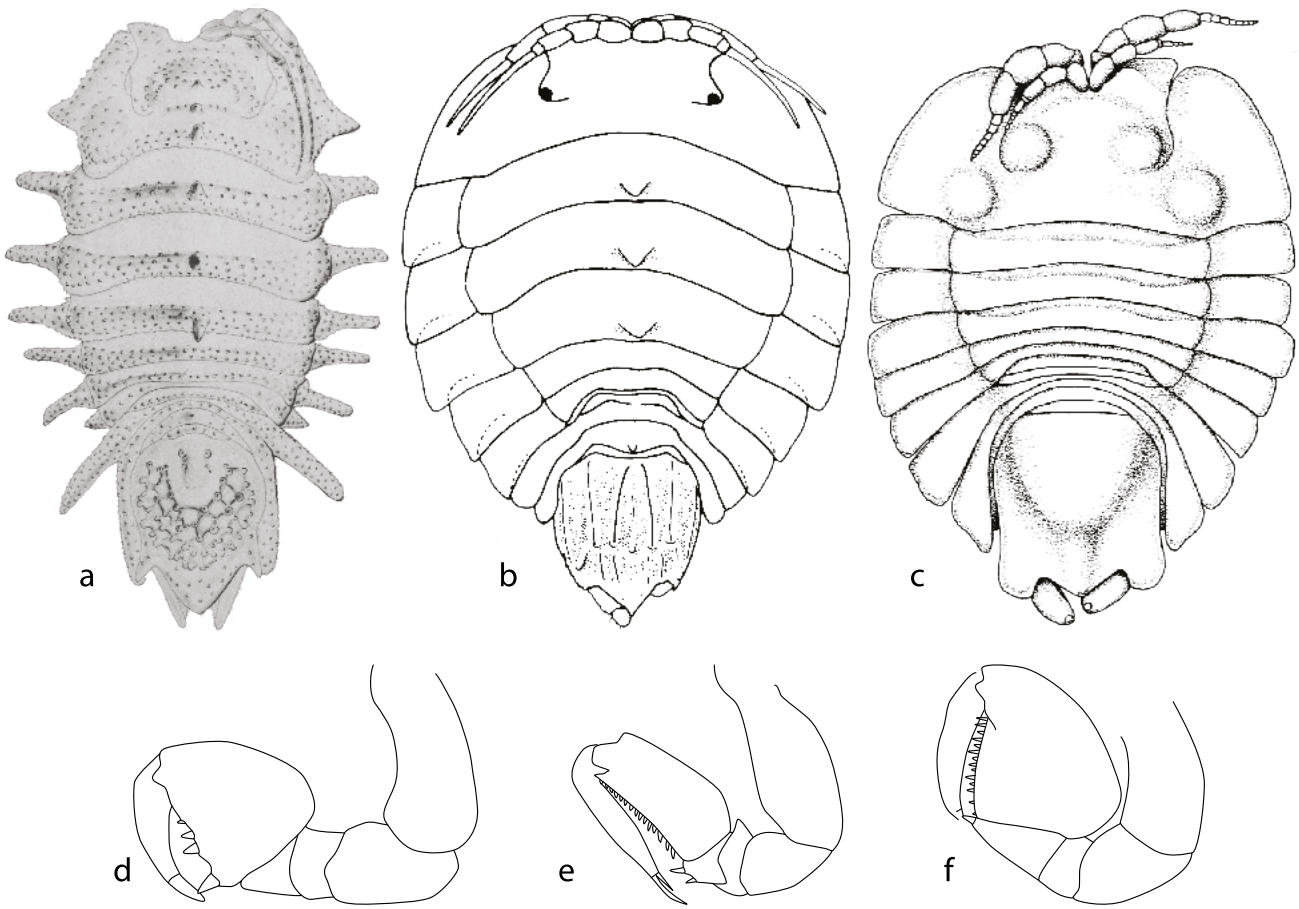


Figure 9.3. Bathynataliidae. a, *Bathynatalia gilchristi* Barnard, 1957; b, *Biremia kensleyi* Poore, 2005; c, *Brianaudea louwae* (Kensley, 1979). Pereopod 1: d, *Bathynatalia*; e, *Biremia*; f *Brianaudea*.

Bathynatalia Barnard, 1957

Diagnosis. Body elongate–oval, with blunt lateral coxal spines; middorsal line of head and pereonites 1–4 with middorsal erect spines. Coxal dorsal plate 7 visible but shorter than coxal plate 6. Pleon of 5 free pleonites (with slight movement) and pleotelson. Eyes absent. Maxillipedal palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus about as broad as long, palm straight, with few simple robust setae. Pereopod 7 present; of male not sexually differentiated. Pleopod 1 operculate, indurate. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached sublaterally at about midlength of pleotelson, with knob-like rami fused to peduncle.

Slope (840–850 m). Western Indo-Pacific, Temperate Southern Africa (Coast of South Africa). 1 species (Barnard, 1957: species description; Kensley, 1978: redescription, family diagnosis).

Biremia Bruce, 1985

Diagnosis. Body almost evenly oval, margin defined by head, coxal plates and pleon, slight interruptions between coxal plates

and pleon; middorsal line with short triangular middorsal processes on posterior margin of pereonites 2–4. Coxal dorsal plate 7 not visible dorsally. Pleon of 4 free pleonites (or pleonites 1, 2 fused dorsally) and fused pleonite 5–pleotelson. Eyes minute. Maxillipedal palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus barely tapering, palm straight, with few simple robust setae. Pereopod 7 present; of male not sexually differentiated. Pleopod 1 laminar, like pleopod 2. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached sublaterally at about midlength of pleotelson; biramous (small rami present).

Shelf, slope (150–458 m). Central Indo-Pacific (Great Barrier Reef, Qld, Australia). 2 species (Bruce, 1985: description; Poore, 2005: second species).

Brianaudea Boyko, 2021

Diagnosis. Body almost evenly oval, margin defined by head, coxal plates and pleon, slight interruptions between coxal plates and pleon; middorsal line smooth in lateral view. Coxal dorsal plate 7 not visible dorsally. Pleon of 5 free pleonites (with slight movement) and pleotelson. Eyes absent. Maxillipedal palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus about as broad as long, palm straight, with few simple robust setae. Pereopod 7 absent in adult; of male not sexually differentiated. Pleopod 1 operculate, indurate. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached sublaterally at about midlength of pleotelson; cylindrical (with minute exopod).

Slope (850 m). Western Indo-Pacific (KwaZulu-Natal, South Africa). 1 species (Kensley, 1979: species description; Boyko, 2021: replacement name for *Naudea* Kensley, 1979).

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Plakarthriidae Hansen, 1905

Figure 9.4

Isopods of the single genus *Plakarthrium*, with three species in cool temperate Southern Hemisphere locations, are flattened, almost limpet-like inhabitants of shallow macroalgal communities. They are unique in that the margin of the body is defined entirely by flattened limbs, antennulae, antennae, pereopodal coxae and uropods. The head is free from pereonite 1 and, unlike most isopods, the first coxal plate is free from the pereonal tergite.

Diagnosis. Body oval, flat, margin defined by plates of antennulae, antennae, coxae and uropods; head free from pereonite 1; pereonites 1–7 visible dorsally, separated by sutures. Coxal dorsal plates 1–7 delimited from tergite by suture; plate 7 expanded posteriorly, similar to coxal plate 6, visible dorsally. Pleotelson rectangular, flattened, pleonites 1, 2 fully or laterally demarcated, enclosed by coxae 7 laterally, uropods attached posteriorly. Antennular and antennal peduncles laminar, defining margin of body. Mandibular incisor with 2 blunt teeth; molar process absent. Maxillula with single endite, with 7 terminal stout setae. Maxilla with single endite, with 8 terminal stout setae. Maxillipedal palp of 5 free articles. Pereopod 1 ambulatory, palm with few setae. Pereopod 2 not sexually dimorphic. Pleopods 1–3 peduncles subquadrate, with terminal rami. Uropods attached on posterior margin of pleotelson; biramous, contiguous, terminal.

Plakarthrium Chilton, 1883

Subtidal (6–49 m). Temperate South America, Temperate Australasia, Southern Ocean (subantarctic islands, Antarctic Peninsula). 3 species (Wilson et al., 1976: rediagnosis of family, family placement; Poore and Brandt, 2001: description of third species).

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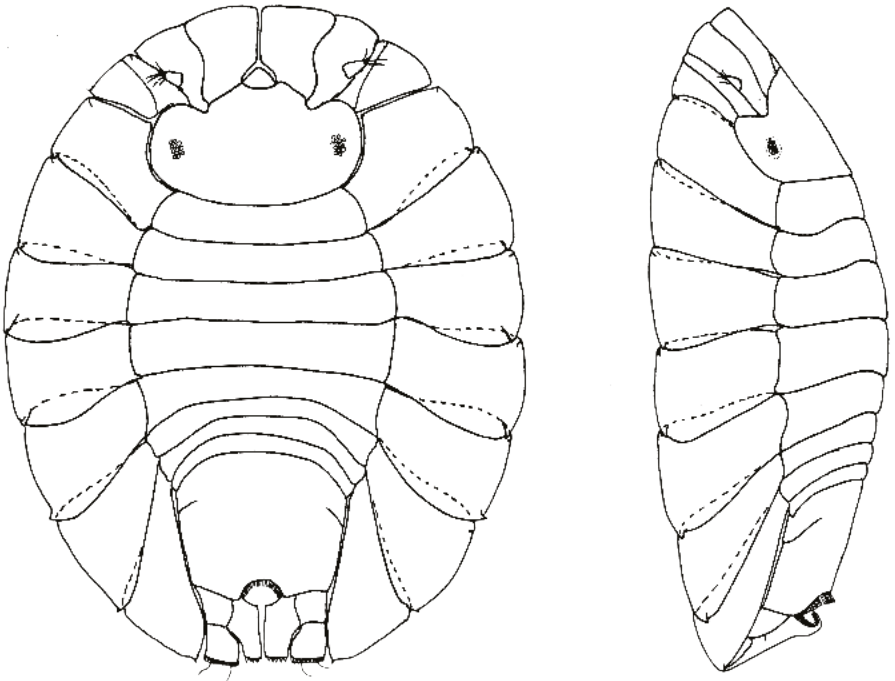


Figure 9.4. Plakarthriidae. *Plakarthrium australiense* Poore and Brandt, 2001.

Paravireiidae fam. nov.

Figure 9.5

The enigmatic genus *Paravireia* Chilton, 1925 long been recognised as similar to Sphaeromatidae but has not been placed in any of the families of Sphaeromatidea. Brökeland et al. (2001) described a third species and discussed relationships of the genus but left *Paravireia* as *incertae sedis*. In their morphological cladistic analysis, Brandt and Poore (2003) found the genus to be on a separate clade from one including Ancinidae, Sphaeromatidae and Tecticipidae. We erect a new family for *Paravireia*, realising that Wetzer et al. (2013) provisionally found (using molecular data) that Sphaeromatidea was not monophyletic but part of a larger clade including Serolidae and Valvifera. The new family differs from other sphaeromatoids in having four free pleonites (plesiomorphic), lacking uropods (apomorphic), and the maxilla consisting of a simple lobe with a distally attached small endite, wholly unlike that of any other Sphaeromatidea and of similar form (homoplasious) to that seen in Aegidae and Cymothoidae.

(http://zoobank.org/urn:lsid:zoobank.org:act:7E22261E-0DA9-41F4-ACB5-E6C0451A4A6A)

Type genus. *Paravireia* Chilton, 1925 by present designation.

Diagnosis. Body oval, vaulted; head free from pereonite 1; pereonites 1–7 visible dorsally, separated by sutures. Coxal dorsal plates 1–7 not delimited from tergite by suture; plate 7 similar to dorsal coxal plate 6. Pleon with 4 free pleonites dorsally. Pleotelson broad, laterally oval. Antennular and antennal peduncles cylindrical, not part of margin of body. Mandibular incisor tricuspid; molar process present. Maxillula mesial endite with 3 simple seta; lateral endite with 5 large and 1 small spines, 4 serrate setae. Maxilla simple, with mesial endite smaller than lateral endite, neither with long setae. Maxillipedal palp of 5 partly fused articles. Pereopod 1 ambulatory, palm with few setae. Pereopod 2 ambulatory. Pleopods 1–3 peduncles subquadrate, with terminal rami. Uropods absent. (fig. 9.5).

Paravireia Chilton, 1925

Estuarine, marine, intertidal, supratidal in empty barnacle shells. Temperate Northern Atlantic (Canary Islands), Temperate Australasia (New Zealand). 3 species (Chilton, 1925; Jansen, 1973: second species from New Zealand; Brökeland et al., 2001: rediagnosis, third species from Canary Islands, discussion of relationships).

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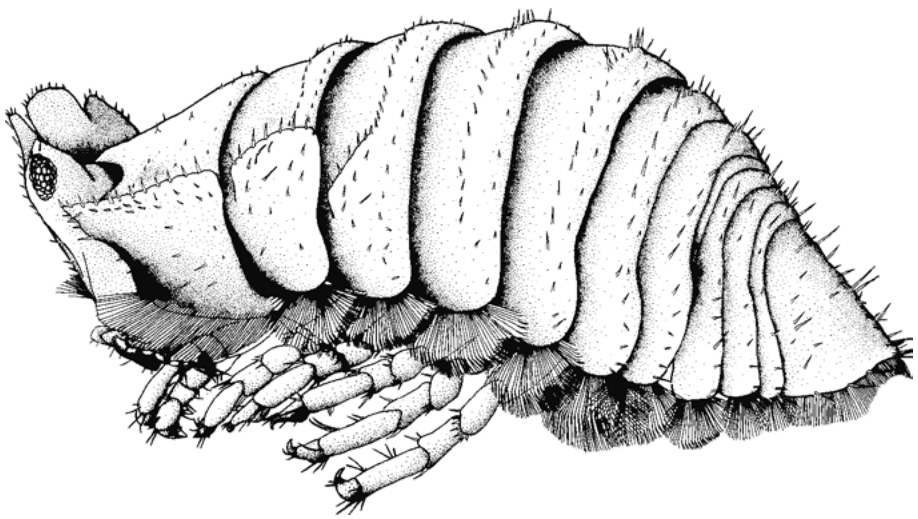


Figure 9.5. Paravireiidae. *Paravireia holdichi* Brökeland, Wägele and Bruce, 2001. Habitus.

Serolidae Dana, 1852

Figures 9.6–9.8

Serolids are flattened benthic isopods with greatest diversity in the Southern Hemisphere but extending into equatorial regions in deep water (Brandt, 1991; Wägele, 1994). Serolids are distinguished from other sphaeromatideans by having the peduncles of pleopods 1–3 directed laterally from midventral sternites and often triangular or tapering. Many species, especially from deep water, have spectacular acute extensions of the coxal plates and pleonal epimera. Two foundation studies (Nordenstam, 1933; Sheppard, 1933) reviewed the anatomy and taxonomy of the family, then comprising one genus. Sheppard (1933) provided a key to the 37 species then known. Bastida and Torti (1973) reviewed and provided a key to the 27 species from Argentina. Several additional genera were diagnosed in two major reviews (Brandt, 1988; Wägele, 1994); Held (2000) provided partial molecular support for their classification. Bruce (2009) discussed relationships between some genera and provided a key to seven genera from the Indo-West Pacific. Two attempts at phylogenies of Serolidae based on morphological characters are only partly resolved, the first of 14 genera (Brandt, 1991) and another of 20 genera (Wägele, 1994). In a PhD thesis, Costa (2017) reviewed 15 genera and 53 species from the Atlantic. She recognised but did not name new species and a new genus.

Identifying lateral extensions is critical in the taxonomy of serolid genera. The head of serolids is deeply embedded in pereonite 1 and fused to it medially. Viewed dorsally, pereonites 1–6 and pleonites 2 and 3 are variously produced laterally or posterolaterally as coxal dorsal plates and as pleonal epimera. Pereonite 7 is invisible dorsally and does not have a coxal dorsal plate; the most posterior coxal dorsal plate is the sixth. The tergite of pleonite 1 is visible dorsally, usually as a narrow segment, and lacks epimera; pleonites 2 and 3 are free, their epimera sometimes produced posteriorly to enclose the anterior pleotelson. Posterior pereonites (5–7) and pleonite 1 are variously fused middorsally (figs 9.6, 9.7). In ventral view (fig. 9.8a), pereonal sternites are variously fused and coxal plate 7 is absent. The sternites of pleonites 1–3 have a midventral plate, sometimes with a medial keel, separating the peduncles of pleopods 1–3. Pleopod 4 has an operculiform endopod.

Serolids are sexually dimorphic, the male being relatively broader than the female; pereopod 2 is modified as a subchelate clasping limb and the dactylus of pereopod 7 is also sometimes modified from the typical linear shape (see Poore, 1987 for examples).

Diagnosis. Body more or less oval, flat, margin defined by flattened dorsal coxal plates 1–6 and pleonal epimera 2, 3; head medially fused with pereonite 1; pereonite 7 tergite not visible dorsally. Coxal dorsal plates 2–4 or more delimited from tergite by suture, 5 and 6 weakly so if at all, or 1–6 not delimited from tergite by suture (rare); coxal plate 7 absent. Pleon with pleonite

1 visible dorsally, without epimera; pleonites 2 and 3 free, with epimera, sometimes prominent; pleonal sternites 1–3 present. Pleotelson usually more or less triangular or semicircular or pentagonal, uropods usually attached anterolaterally. Antennular and antennal peduncles flattened, not part of margin of body. Mandibular incisor with obsolete teeth; molar process absent. Maxillula mesial endite minute, with 1 short simple seta; lateral endite usually with 11 large setae. Maxilla with prominent mesial endite with plumose setae; second and lateral endites with 2 or 3 long serrate setae (rarely lateral endite absent). Maxillipedal palp of 3 articles, fused articles 2–3 cordiform, or of 1 short and 1 oval article (rare). Pereopod 1 subchelate, propodus oval, palm convex, with row of close-set robust setae. Pereopod 2 sexually dimorphic, subchelate in male. Pleopods 1–3 peduncles narrow, tapering, directed laterally, rami distal and subdistal. Uropods attached anterolaterally to pleotelson, or on posterior margin of pleotelson; endopod fused to peduncle (laminar, sometimes reduced or absent), exopod usually laminar (sometimes absent or styliform).

Key to genera of Serolidae

1. Uropods on posterolateral angle of pleotelson, uropods and pleonites forming part of continuous oval body outline (fig. 9.7l) ..... *Thysanoserolis*

– Uropods mediolateral or anterolateral, not forming part of body outline 2

2. Coxal dorsal plate 6 far exceeding posteriorly pleonal epimera 2 and 3 (e.g., fig. 9.6b, g); sometimes pleonites 2, 3 without epimera visible in dorsal view (fig. 9.6j, l) 3

– Coxal dorsal plate 6 not exceeding or almost level posteriorly with pleonites 2 and 3 and their epimera (e.g., fig. 9.7c, d) 13

3. Coxal dorsal plates 1–6 with distinct attenuated projections, directed laterally on anterior pereonites, directed posteriorly on posterior pereonites; coxal dorsal plate 6 reaching or well exceeding posterior margin of pleotelson. Pleonal epimera 2, 3 similarly attenuated (figs 9.6b, e, g) 4

– Coxal dorsal plates 1–6 squarish or triangular, without distinct projections; pereopod 6 coxal dorsal plate not or barely exceeding posterior margin of pleotelson. Pleonal epimera 2, 3 triangular or not visible in dorsal view (e.g., fig. 9.6j) 6

4. Pereonites smooth in lateral view. Head sculptured between eyes. Pleotelson middorsal keel with prominent teeth, sometimes attenuated posteriorly, dentate laterally (fig. 9.6g) ..... *Ceratoserolis*

– Pereonites with medial spines visible in lateral view. Head with spine or smooth in lateral view. Pleotelson middorsal keel smooth, posterior margin truncate 5

5. Coxal dorsal plates 1–5 interacting only by means of key-like lobes, coxal plate 6 exceeding pleotelson by at least pleotelson length. Middorsal spines absent or obscure. Pleotelson without ridges and keels (fig. 9.6e) ..... *Brucerolis*

– Coxal dorsal plates 1–5 coxal dorsal plates slot into each other without aperture between, coxal plate 6 exceeding pleotelson by less than pleotelson length. Middorsal spines prominent. Pleotelson with ridges or keels (fig. 9.6b) ..... *Acutiserolis*

6. Body with continuous oval margin. Antennal peduncle articles 4, 5 each about twice as long as wide. Eyes absent. Pereopod 7 absent in adult (fig. 9.6j). Uropod with endopod only (fig. 9.8g) ..... *Glabroserolis*

– Body with at least coxal plate 6 projecting from margin. Antennal peduncle articles 4, 5 each at least 4 times as long as wide. Eyes present. Pereopod 7 present in adult. Uropod with 2 rami 7

7. Pleotelson with concave posterolateral margin and narrow triangular apex 8

– Pleotelson with convex posterolateral margin and broad triangular apex or apical notch 9

8. Pleotelson with sublateral ridges over anterior half ending in small tooth. Coxal dorsal plate 6 not reaching base of uropod. Pleonal epimera 1, 2 short, square. Uropod not visible in dorsal view (fig. 9.6h) ..... *Cristaserolis*

– Pleotelson with flattened plate-like ridges laterally. Coxal dorsal plate 6 exceeding base of uropod. Pleonal epimera 2, 3 acute, overlapping pleotelson. Uropod visible in dorsal view (fig. 9.6i) ..... *Frontoserolis*

9. Uropod peduncle as long or longer than rami (fig. 9.8h). Pleonal epimera 2, 3 not or scarcely visible in dorsal view. Pleotelson with obsolete dorsolateral carinae (fig. 9.6l) ..... *Leptoserolis*

– Uropod peduncle much shorter than half length of rami (fig. 9.8i). Pleonal epimera 2, 3 usually clearly visible in dorsal view. Pleotelson usually with prominent dorsolateral sculpture 10

10. Pleonites 1, 2 and pleotelson as long as head plus pereon in midline; pereonites 5–pleonite 1 fused middorsally. Eyes minute, oval. Pereopods 1–6 coxal plates margins contiguous. Pleotelson with obsolete sublateral ridges (fig. 9.7a) ..... *Myopiarolis*

– Pleonites 1, 2 and pleotelson as long as pereonites 2–6 in midline; pereonites 5, 6 free middorsally. Eyes half as long as head, reniform. Pereopods 1–6 coxal plates apices diverging, especially posteriorly. Pleotelson with sublateral plates and ridges 11

11. Pereonites with middorsal spines on posterior margins. Pleotelson with 2 pairs of lateral plates, first with rounded margin, second with submedial tooth. Pleonal epimeron 2 much longer than epimeron 3 (fig. 9.6a) ..... *Acanthoserolis*

– Pereonites without middorsal spines on posterior margins. Pleotelson with submarginal carinae or plates. Pleonal epimera 2, 3 of similar lengths 12

12. Pleotelson with flattened plate-like ridges laterally. Pleonal epimera 2, 3 extending posteriorly, enclosing anterior half of pleotelson. Uropod attached near midpoint of pleotelson lateral margin (fig. 9.7f) ..... *Serolella*

– Pleotelson with oblique ridges laterally. Pleonal epimera 2, 3 not extending posteriorly, not enclosing anterior half of pleotelson. Uropod attached well posterior to midpoint of pleotelson lateral margin (fig. 9.7j) ..... *Serolis*

13. Uropodal endopod fused to peduncle. Pleonites 2, 3 without epimera. Pleotelson with sharp epimeral tooth (fig. 9.7k) ..... *Spinoserolis*

– Uropodal endopod free from peduncle. Pleonites 2, 3 with epimera reaching body margin. Pleotelson without epimeral tooth 14

14. Eyes absent 15

– Eyes present 17

15. Pleotelson with broad truncate posterior margin. Uropod attached anteriorly, its mesial margin in dorsal groove on pleotelson lateral margin (fig. 9.7d) ..... *Sedorolis*

– Pleotelson tapering to rounded or narrow apex. Uropod attached near midlength of pleotelson lateral margin, visible or not 16

16. Coxal dorsal plate 6 and pleonal epimera 2, 3 reaching to midlength of pleotelson. Uropodal rami of similar lengths (fig. 9.6f) ..... *Caecoserolis*

– Coxal dorsal plate 6 and pleonal epimera 2, 3 reaching slightly along sides of pleotelson. Uropodal exopod minute (figs 9.6c, 9.8j) ..... *Atlantoserolis*

17. Pleonites 2, 3 with small epimera, usually exceeded posteriorly by coxal dorsal plate 6 18

– Pleonites 2, 3 with posteriorly directed epimera, usually extending more posteriorly than coxal dorsal plate 6 19

18. Maxillipedal palp of 1 short and 1 oval article (fig. 9.8e). Pleotelson tapering from base to narrow rounded apex. Eye oval. Uropod not visible in dorsal view (fig. 9.6d) ..... *Brazilserolis*

– Maxillipedal palp of 3 segments, fused articles 2–3 cordiform (fig. 9.8f). Pleotelson tapering from parallel-sided anterior half to narrow truncate apex. Eye reniform. Uropod visible in dorsal view (fig. 9.6k) ..... *Heteroserolis*

19. Coxal dorsal plate 6 and pleonal epimera 2, 3 similar, each considerably more produced than the one before. Head with 3 similar prominent lobes along posterior margin. Pleotelson with 2 pairs of triangular dorsal plates (fig. 9.7c) ..... *Paraserolis*

– Coxal dorsal plate 6 and pleonal epimera 2, 3 similar or dissimilar, similarly produced posteriorly. Head without or with 1 prominent lobe on posterior margin. Pleotelson smooth or without 2 pairs of triangular dorsal plates 20

20. Pleotelson with 3–7 longitudinal carinae. Uropod reaching halfway along posterolateral margin of pleotelson (fig. 9.7e) ..... *Septemserolis*

– Pleotelson without longitudinal carinae. Uropod reaching nearly to apex of pleotelson 21

21. Head with median tubercle on posterior margin. Coxal dorsal plate 6 completely overlapping pleonal epimera 2, 3 in male, partially in female (fig. 9.7g–i). Pereopod 1 propodus with alternating complex bifid setae and scales, both flagellate, along margin (fig. 9.8d) ..... *Serolina*

– Head without median tubercle on posterior margin. Coxal dorsal plate 6 not overlapping pleonal epimera 2, 3 (fig. 9.7b). Pereopod 1 propodus with flagellate robust setae and simple setae along margin (fig. 9.8c) ..... *Neoserolis*

Acanthoserolis Brandt, 1988

Diagnosis. Body oval, increasingly incised between triangular posteriorly directed coxal plates 2–6; middorsal line with short triangular middorsal processes on posterior margin of head, pereonites 2–4 and pleonites 1–3, evident in lateral view. Coxal dorsal plates 2–5 delimited from tergite by suture; 1–6 increasingly produced posteriorly; plate 6 reaching almost as far posteriorly as pleonal epimeron 2 and posterior margin of pleotelson. Pleonal epimeron 2 longer than coxal dorsal plate 6; epimeron 3 short. Pleotelson posterior margin broadly rounded; with 2 middorsal triangular keels, one behind other; dorsal surface with 2 pairs of lateral plates, first with rounded margin, second with submedial tooth. Eyes reniform. Mandible left lacinia mobilis slender. Maxillipedal epipod fused to basis; palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with alternating flagellate cylindrical setae and flagellate plate-like setae. Pereopod 2 of male subchelate; palm of propodus with robust setae surrounding an oval palm. Pereopod 7 of male not sexually differentiated. Male pleopod 2 endopod without distal stem supporting appendix masculina. Pleopod 4 endopod bilobed. Uropod attached posterolaterally, pair almost meeting in midline; biramous, rami of similar lengths or exopod shorter.

Shelf (36–136 m). Temperate South America (Atlantic). 2 species (Moreira, 1971: figures of type species; Brandt, 1988). Costa (2017) synonymised *Acanthoserolis* with *Serolis*, a decision not followed here.

Acutiserolis Brandt, 1988

Diagnosis. Body deeply incised between extremely long, attenuating, posteriorly directed coxal and epimeral plates; middorsal line dominated by strong middorsal spine (prominent in lateral view) on posterior margin of head, pereonites 2–4 and pleonites 1–3. Coxal dorsal plates 2–5 with proximal anterior margins straight, slotting into grooves on preceding coxae, with no aperture between; plate 6 extending posterior to pleotelson by about half its length; plate 6 with blunt process on anterior margin slotting into groove on coxa 5 and isolating an oval aperture. Coxal ventral plates 2–4 meeting in midline, with pair of contiguous teeth on anteromesial corners of sternites 2, smaller pair on sternites 3. Pleonal epimera 2, 3 smaller than extension of pereonite 6 coxal dorsal plate, extending posteriorly along pleotelson lateral margins. Pleotelson posterior margin truncate; with sharp middorsal keel, upturned posteriorly; dorsal surface with sublateral sharply defined longitudinal keels ending acutely, and obscure irregularities along a submarginal posterolateral ridge. Eyes contiguous with head margin posteriorly, 3 times as long as wide, with concave mesial margin. Mandible left lacinia mobilis expanded, half as wide as mandibular incisor. Maxillula inner lobe a simple expanded plate, outer lobe with ~11 robust terminal setae. Maxillipedal palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with alternating flagellate cylindrical setae and flagellate plate-like setae. Pereopod 2 of male subchelate; palm of propodus with robust setae surrounding an oval palm. Pereopod 7 of male sexually differentiated, propodus broader than in female, with felt of fine scale setae, dactylus simple, curved. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached sublaterally at about midlength of pleotelson; biramous, rami of similar lengths or exopod shorter.

Slope, bathyal (400–2267 m). Southern Ocean 7 species (Kussakin, 1967: type species; Poore and Storey, 2009: figures of type species).

Atlantoserolis Wägele, 1994

Diagnosis. Body almost evenly oval, margin defined by head, coxal plates and pleon, slight interruptions between coxal plates and pleon; middorsal line smooth in lateral view. Coxal dorsal plates 2–4 or 2–5 delimited from tergite by suture; 2–5 contiguous; plate 6 overlapping but not extending posteriorly far beyond pleonal epimera 2, 3. Pleonal epimera 2, 3 smaller than extension of pereonite 6 coxal dorsal plate, not extending posteriorly along pleotelson lateral margins. Pleotelson posterior margin narrowly rounded; with short median carina; dorsal surface smooth. Eyes absent. Maxillipedal palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with few simple robust setae. Pereopod 2 of male subchelate; heel indistinct, palm straight, with few robust setae. Pereopod 7 of male not sexually differentiated. Male pleopod 2 endopod with distal stem supporting appendix masculina. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached sublaterally at about midlength of pleotelson; biramous, peduncle longer than endopod; exopod minute.

Slope–abyssal (834–5024 m). Temperate Northern and Tropical W Atlantic, Temperate South America. 4 species (Menzies, 1962: figures of type species; Wägele, 1994; Brandt et al., 2014).

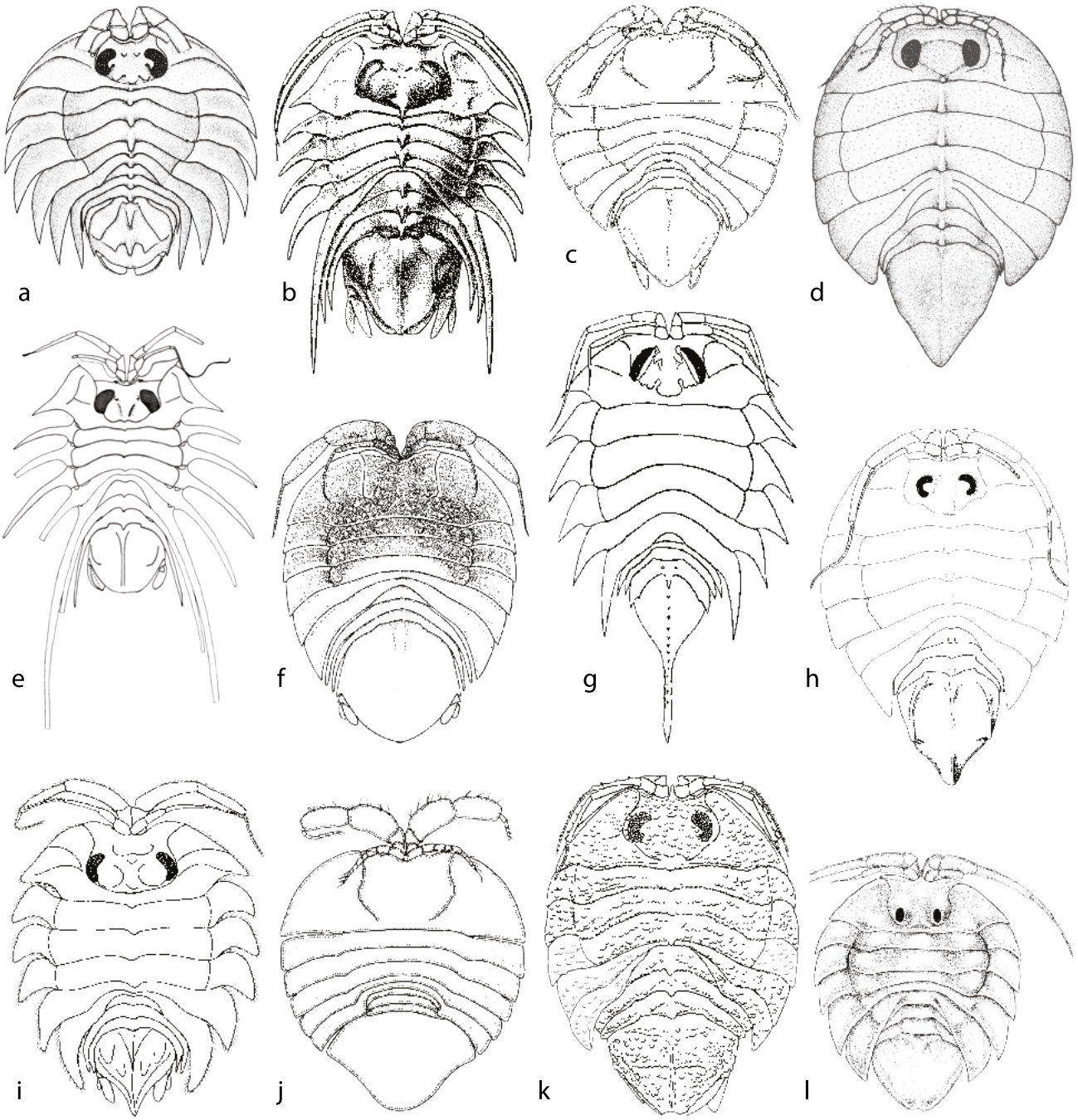


Figure 9.6. Serolidae. a, *Acanthoserolis polaris* (Richardson, 1911); b, *Acutiserolis spinosa* (Kussakin, 1967); c, *Atlantoserolis vemae* (Menzies, 1962); d, *Brazilserolis mirabilis* (Moreira, 1976); e, *Brucerolis brandtae* Storey and Poore; f, *Caecoserolis brinki* (Kensley, 1978); g, *Ceratoserolis meridionalis* (Vanhöffen, 1914); h, *Cristaserolis convexa* (Cunningham, 1871); i, *Frontoserolis waegelei* (Brandt, 1988); j, *Glabroserolis specialis* Menzies, 1962; k, *Heteroserolis australiensis* (Beddard, 1884); l, *Leptoserolis orbiculata* (Sheppard, 1933).

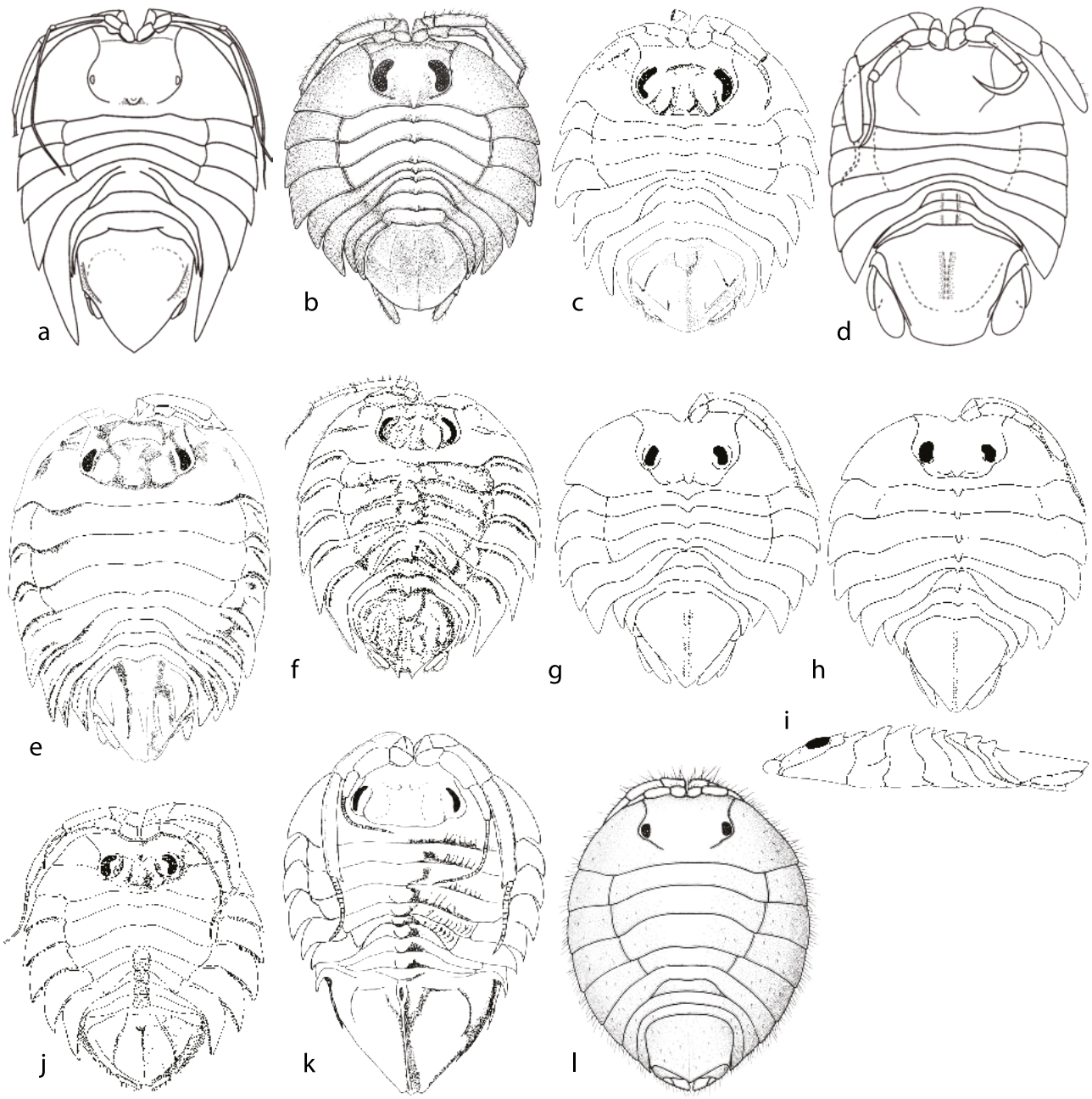


Figure 9.7. Serolidae. a, *Myopiarolis systir* Bruce, 2009; b, *Neoserolis exigua* (Nordenstam, 1933); c, *Paraserolis polita* (Pfeffer, 1887); d, *Sedorolis simplex* Bruce, 2009; e, *Septemserolis septemcarinata* (Miers, 1875) ; f, *Serolella pagenstecheri* (Pfeffer, 1887); g–i, *Serolina acaste* Poore, 1987 (male, female, lateral); j, *Serolis paradoxa* (Fabricius, 1775); k, *Spinoserolis latifrons* (White, 1847); l, *Thysanoserolis completa* (Moreira, 1971).

Brazilserolis Wägele, 1994

Diagnosis. Body almost evenly oval, margin defined by head, coxal plates and pleon, slight interruptions between coxal plates and pleon; middorsal line smooth in lateral view. Coxal dorsal plates contiguous, without intermediate gaps; plate 6 overlapping and extending well posterior of pleonal epimera 2 and 3. Pereonites 5–7 fused middorsally. Pleonal epimera 2, 3 smaller than extension of pereonite 6 coxal dorsal plate, not extending posteriorly along pleotelson lateral margins. Pleotelson posterior margin narrowly rounded; with short median carina; dorsal surface smooth. Eyes oval. Maxillipedal palp of 1 short and 1 oval article. Pereopod 1 propodus with alternating flagellate cylindrical setae and flagellate plate-like setae. Pereopod 2 of male subchelate; heel indistinct, palm straight, with few robust setae. Pereopod 7 of male not sexually

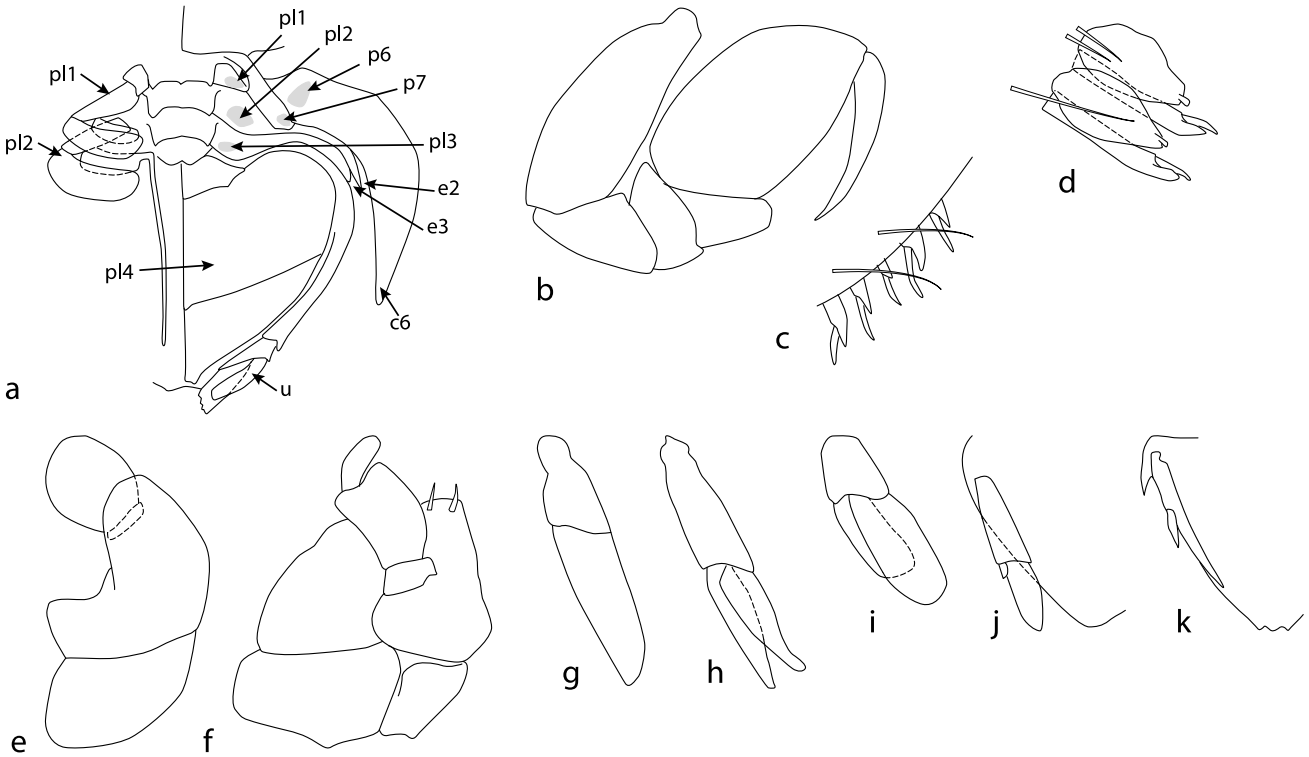


Figure 9.8. Serolidae. a, ventral view of posterior pereon and pleotelson, right pleopods 1, 2 (pleopod 2 with appendix masculina), left pleopod 4, *Serolis*; b, pereopod 1 (generic). Pereopod 1 palm marginal setae: c, *Neoserolis*; d, *Serolis*. Maxilliped: e, *Brazilserolis*; f, *Heteroserolis*. Left uropod: g, *Glabroserolis*; h, *Leptoserolis*; i, *Myopiarolis*. Right uropod, pleotelson margin (ventral view): j, *Atlantoserolis*; k, *Spinoserolis*. c6, coxal dorsal plate 6 extension; e2, e3, pleonal epimera 2, 3; p6, p7, attachment of bases of pereopods 6, 7; pl1–pl4, pleopods 1–4 or sites of attachment; u, uropod.

differentiated. Male pleopod 2 endopod with distal stem supporting appendix masculina. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached ventrally, not visible in dorsal view; biramous, exopod half as long as endopod.

Shelf (136 m). Tropical Atlantic. 2 species (Bastida and Torti, 1970: second species; Moreira, 1976: type species; Wägele, 1994).

Brucerolis Poore and Storey, 2009

Diagnosis. Body deeply incised between extremely long, attenuating, posteriorly directed coxal and epimeral plates; middorsal line with short triangular middorsal processes on posterior margin of head, pereonites 2–4 and pleonites 1–3, evident in lateral view. Coxal dorsal plates 2–6 with anterior blunt process slotting into groove on preceding coxae, isolating an oval aperture between coxae, coxal plate 5 with an intermediate anterior process meeting a similar posterior process on coxal plate 4, so subdividing intercoxal aperture; plate 6 extending posterior to pleotelson by more than twice its length. Coxal ventral plates 2–4 meeting in midline, with transverse ridges on mesial, anterior and posterior margins outlining a transverse depression. Pleonal epimera 2, 3 smaller than extension of pereonite 6 coxal dorsal plate, extending posteriorly along pleotelson lateral margins. Pleotelson posterior margin truncate; with horizontal obscure middorsal keel; dorsal surface with flattened plate-like ridges laterally. Eyes contiguous with head margin posteriorly, twice as long as wide, reniform. Mandible left lacinia mobilis expanded, half as wide as mandibular incisor. Maxillula inner lobe a simple expanded plate, outer lobe with ~11 robust terminal setae. Maxillipedal palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with alternating flagellate cylindrical setae and flagellate plate-like setae. Pereopod 2 of male subchelate; palm of propodus with U-shaped row of robust setae. Pereopod 7 of male sexually differentiated, propodus broader than in female, with felt of fine scale setae, dactylus simple, curved. Male pleopod 2 endopod without distal stem supporting appendix masculina. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached sublaterally at about midlength of pleotelson; biramous, rami of similar lengths or exopod shorter.

Slope–abyssal (315–3839 m). Central Indo-Pacific, Temperate Australasia, Southern Ocean (S Indian Ocean east to S Atlantic). 10 species (Poore and Storey, 2009: type species; Storey and Poore, 2009: key to species).

Caecoserolis Wägele, 1994

Diagnosis. Body almost evenly oval, margin defined by head, coxal plates and pleon, slight interruptions between coxal

plates and pleon; middorsal line smooth in lateral view. Coxal dorsal plates contiguous, without intermediate gaps; plate 6 overlapping but not extending posteriorly far beyond pleonal epimera 2, 3. Pleonal epimera 2, 3 smaller than extension of pereonite 6 coxal dorsal plate, extending posteriorly along pleotelson lateral margins. Pleotelson posterior margin broadly rounded; without middorsal keel; dorsal surface smooth. Eyes absent. Mandible left lacinia mobilis two thirds as wide as incisor. Maxillipedal palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with alternating flagellate cylindrical setae and flagellate plate-like setae. Pereopod 2 of male subchelate; palm of propodus with U-shaped row of robust setae. Pereopod 7 of male not sexually differentiated. Male pleopod 2 endopod without distal stem supporting appendix masculina. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached sublaterally at about midlength of pleotelson; biramous, rami of similar lengths or exopod shorter.

Slope (680 m). Temperate Southern Africa. 1 species (Kensley, 1978: figure of type species; Wägele, 1994; Bruce, 2009: rediagnosis, figures of type species).

Ceratoserolis Brandt, 1988

Diagnosis. Body oval, incised between triangular posteriorly directed coxal and epimeral plates; middorsal line smooth in lateral view; head sculptured between eyes. Coxal dorsal plates 1–3 or more with posterior lobe keying into groove on following plate; plate 6 overlapping and extending well posterior of pleonal epimera 2 and 3. Pleonal epimera 2, 3 smaller than extension of pereonite 6 coxal dorsal plate, extending posteriorly along pleotelson lateral margins. Pleotelson apex acute, sometimes attenuated; with middorsal toothed keel; dorsal surface with flattened plate-like ridges laterally. Eyes reniform, narrow. Maxillipedal palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with alternating flagellate cylindrical setae and flagellate plate-like setae. Pereopod 2 of male subchelate; palm of propodus with U-shaped row of robust setae. Pereopod 7 of male not sexually differentiated. Male pleopod 2 endopod without distal stem supporting appendix masculina. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached sublaterally at about midlength of pleotelson; biramous, rami of similar lengths or exopod shorter.

Shelf–bathyal (20–3017 m). Southern Ocean. 4 species (Wägele, 1986: polymorphism of type species; Brandt, 1988: validation of name; Held, 2003: cryptic species).

Cristaserolis Brandt, 1988

Diagnosis. Body almost evenly oval, margin defined by head, coxal plates and pleon, slight interruptions between coxal plates and pleon; middorsal line smooth in lateral view. Coxal dorsal plates 2–4 delimited from tergite by suture; contiguous, without intermediate gaps; plate 6 overlapping and extending well posterior of pleonal epimera 2 and 3. Pleonal epimera 2, 3 smaller than extension of pereonite 6 coxal dorsal plate, not extending posteriorly along pleotelson lateral margins. Pleotelson with concave posterolateral margin and narrow triangular apex; with obsolete middorsal keel; dorsal surface with sublateral ridges over anterior half ending in small tooth. Eyes reniform. Mandible left lacinia mobilis expanded, half as wide as mandibular incisor. Maxillipedal palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with alternating flagellate cylindrical setae and flagellate plate-like setae; carpus of male with dense field of setae. Pereopod 2 of male subchelate; palm of propodus with robust setae surrounding an oval palm. Pereopod 7 of male not sexually differentiated. Male pleopod 2 endopod with distal stem supporting appendix masculina. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached ventrally, not visible in dorsal view; biramous, exopod half as long as endopod.

Shelf–bathyal (12–3017 m). Temperate South America, Southern Ocean (Atlantic). 6 species (Bastida and Torti, 1970: figure of type species; Brandt, 1988; Wägele, 1994: figures).

Frontoserolis Brandt, 1991

Diagnosis. Body incised between triangular posteriorly directed coxal plates; middorsal line with short triangular middorsal processes on posterior margin of head, pereonites 2–4 and pleonites 1–3, evident in lateral view. Coxal dorsal plates not contiguous; plate 6 overlapping and extending well posterior of pleonal epimera 2 and 3. Pleonal epimera 2, 3 smaller than extension of pereonite 6 coxal dorsal plate, extending posteriorly along pleotelson lateral margins. Pleotelson with concave posterolateral margin and narrow triangular apex; with middorsal keel; dorsal surface with flattened plate-like ridges laterally. Eyes reniform. Maxillipedal palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with alternating flagellate cylindrical setae and flagellate plate-like setae. Pereopod 2 of male subchelate; heel prominent, palm concave, with few robust setae. Male pleopod 2 endopod without distal stem supporting appendix masculina. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached sublaterally at about midlength of pleotelson; biramous, exopod half as long as endopod.

Slope, bathyal. Southern Ocean. 6 species (Brandt, 1991; 1992: figure of type species; Wägele, 1994: rediagnosis; Brandt, 2003: sixth species).

Glabroserolis Menzies, 1962

Diagnosis. Body almost evenly oval, margin defined by head, coxal plates and pleon, slight interruptions between coxal plates and pleon; middorsal line smooth in lateral view. Coxal dorsal plates not delimited from tergite by suture; contiguous, without intermediate gaps; plate 6 contiguous with pleotelson. Pleonites 2, 3 without epimera. Pleotelson posterior margin broadly rounded; without middorsal keel; dorsal surface smooth. Eyes absent. Antenna articles 4 and 5 each about twice as wide as long as wide. Maxillipedal epipod fused to basis; palp of 3 articles, fused articles 2–3 cordiform; palp article 2 rectangular. Pereopod 1 propodus with alternating flagellate cylindrical setae and flagellate plate-like setae. Pereopod 7 absent in adult; of male not sexually differentiated. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached ventrally, not visible in dorsal view; with knob-like rami fused to peduncle.

Abyssal (4885 m). Temperate Southern Africa. 2 species (Menzies, 1962: figure of type species; Brandt et al., 2014: figures of 2 species).

Heteroserolis Brandt, 1991

Diagnosis. Body almost evenly oval, margin defined by head, coxal plates and pleon, slight interruptions between coxal plates and pleon; middorsal line smooth in lateral view, or with posteriorly directed tubercles on head and most pereonites. Coxal dorsal plates contiguous, without intermediate gaps; plate 6 overlapping but not extending posteriorly far beyond or not overlapping pleonal epimera 2, 3. Pereonites 5–7 fused middorsally. Pleonal epimera 2, 3 smaller than extension of pereonite 6 coxal dorsal plate, not extending posteriorly along pleotelson lateral margins. Pleotelson posterior margin narrow, excavate; with middorsal keel; dorsal surface sometimes tuberculate. Eyes reniform. Maxillipedal palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with alternating flagellate cylindrical setae and flagellate plate-like setae. Pereopod 2 of male subchelate; palm of propodus with U-shaped row of robust setae. Pereopod 7 of male not sexually differentiated. Male pleopod 2 endopod with distal stem supporting appendix masculina. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached sublaterally at about midlength of pleotelson; biramous, rami of similar lengths or exopod shorter.

Shelf, slope (18–792 m). Temperate Northern Atlantic, Temperate Northern Pacific (N American coasts), Central Indo-Pacific, Temperate Australasia. 10 species (Harrison and Poore, 1984: key to 6 species; Brandt, 1992: comparison of 3 genera; 1999: description of *H. mcgrayi*; Bruce, 2009: description of *H. pellucida*). Two species from E and W coast of USA (Menzies and Frankenberg, 1966; Richardson, 1905; Hessler, 1972).

Leptoserolis Brandt, 1988

Diagnosis. Body almost evenly oval, margin defined by head, coxal plates and pleon, slight interruptions between coxal plates and pleon; middorsal line smooth in lateral view. Coxal dorsal plates contiguous, without intermediate gaps; plate 6 overlapping but not extending posteriorly far beyond pleonal epimera 2, 3. Pleonal epimera 2, 3 not visible in dorsal view. Pleotelson triangular, with acute or excavate apex; with middorsal keel; dorsal surface with sublateral carinae. Eyes reniform. Mandible left lacinia mobilis slender. Maxillipedal epipod fused to basis; palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with alternating flagellate cylindrical setae and flagellate plate-like setae. Pereopod 2 of male subchelate; palm of propodus with U-shaped row of robust setae. Pereopod 7 of male not sexually differentiated. Male pleopod 2 endopod with or without distal stem supporting appendix masculina. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached sublaterally at about midlength of pleotelson; biramous, peduncle as long or longer than rami.

Intertidal, shelf (0–162 m). Temperate South America, Southern Ocean (Atlantic coasts). 5 species (Sheppard, 1933: figure of type species; Brandt, 1988; Wägele, 1994: figures).

Myopiarolis Bruce, 2009

Diagnosis. Body almost evenly oval, margin defined by head, coxal plates and pleon, slight interruptions between coxal plates and pleon; middorsal line smooth in lateral view. Coxal dorsal plates margins contiguous, without intermediate gaps; plate 6 overlapping but not extending posteriorly far beyond pleonal epimera 2, 3. Pleonal epimera 2, 3 not visible in dorsal view. Pleotelson triangular, with acute or excavate apex; with middorsal keel; dorsal surface with sublateral carinae. Eyes reniform. Mandible left lacinia mobilis slender. Maxillipedal epipod fused to basis; palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with alternating flagellate cylindrical setae and flagellate plate-like setae. Pereopod 2 of male subchelate; palm of propodus with U-shaped row of robust setae. Pereopod 7 of male not sexually differentiated. Male pleopod 2 endopod with or without distal stem supporting appendix masculina. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached sublaterally at about midlength of pleotelson; biramous, peduncle as long or longer than rami.

Slope, bathyal (700–3184 m). Western and Central Indo-Pacific, Southern Ocean. 9 species (Bruce, 2009: diagnosis, key to 5 species; Spong and Bruce, 2015: new species).

Neoserolis Wägele, 1994

Diagnosis. Body almost evenly oval, margin defined by head, coxal plates and pleon, slight interruptions between coxal plates and pleon; middorsal line with short triangular middorsal processes on posterior margin of pereonites 1–6, pleonites 2, 3. Coxal dorsal plates contiguous, without intermediate gaps; plate 6 not overlapping pleonal epimera 2, 3. Pleonal epimera 2, 3 slightly smaller than coxal dorsal plate 6, extending posteriorly along pleotelson lateral margins. Pleotelson posterior margin broadly rounded; with middorsal keel; dorsal surface with flattened plate-like ridges laterally, or smooth. Eyes reniform. Mandible left lacinia mobilis slender. Maxillipedal epipod fused to basis; palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with setae similar, slender, bifid. Pereopod 2 of male propodus rectangular. Pereopod 7 of male not sexually differentiated. Male pleopod 2 endopod without distal stem supporting appendix masculina. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached sublaterally at about midlength of pleotelson; biramous, rami of similar lengths or exopod shorter.

Shelf (1–545 m). Temperate South America, Southern Ocean (Atlantic coasts). 4 species (Moreira, 1974: figures of type species; Wägele, 1994).

Paraserolis Wägele, 1994

Diagnosis. Body incised between triangular posteriorly directed coxal plates; middorsal line smooth in lateral view; head with row of 3 lobes. Coxal dorsal plates not contiguous; plate 6 not overlapping pleonal epimera 2, 3. Pleonal epimera 2, 3 similar to extension of pereonite 6 coxal dorsal plate, extending posteriorly along pleotelson lateral margins. Pleotelson posterior margin broadly rounded; with middorsal keel; dorsal surface with flattened plate-like ridges laterally. Eyes reniform. Maxillipedal epipod free; palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with alternating flagellate cylindrical setae and flagellate plate-like setae. Pereopod 2 of male subchelate; palm of propodus with U-shaped row of robust setae. Pereopod 7 of male not sexually

differentiated. Male pleopod 2 endopod without distal stem supporting appendix masculina. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached sublaterally at about midlength of pleotelson; biramous, rami of similar lengths or exopod shorter.

Intertidal–slope (0–700 m). Temperate South America, Southern Ocean (Atlantic Sector). 1 species (Wägele, 1994).

Sedorolis Bruce, 2009

Diagnosis. Body almost evenly oval, margin defined by head, coxal plates and pleon, slight interruptions between coxal plates and pleon; middorsal line smooth in lateral view. Coxal dorsal plates contiguous, without intermediate gaps; plate 6 overlapping and extending well posterior of pleonal epimera 2 and 3. Pleonal epimera 2, 3 smaller than extension of pereonite 6 coxal dorsal plate, not extending posteriorly along pleotelson lateral margins. Pleotelson rectangular, posterior margin broadly convex; without middorsal keel; dorsal surface smooth. Eyes absent. Mandible left lacinia mobilis two thirds as wide as incisor. Maxillula inner lobe a simple expanded plate, outer lobe with ~11 robust terminal setae. Maxillipedal palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with setae similar, slender, bifid. Pereopod 2 of male subchelate; heel indistinct, palm straight, with few robust setae. Pereopod 7 of male not sexually differentiated. Male pleopod 2 endopod with distal stem supporting appendix masculina. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached anteriorly, mesial margin in dorsal groove on pleotelson lateral margin; biramous, exopod half as long as endopod.

Slope (440–570 m). Central Indo-Pacific (New Caledonia). 1 species (Bruce, 2009).

Septemserolis Wägele, 1994

Diagnosis. Body almost evenly oval, margin defined by head, coxal plates and pleon, slight interruptions between coxal plates and pleon; middorsal line smooth in lateral view. Coxal dorsal plates 2–5 contiguous; plate 6 not overlapping pleonal epimera 2, 3. Pleonal epimera 2, 3 similar to coxal dorsal plate 6, scarcely extending posteriorly beyond base of uropod. Pleotelson posterior margin narrow, excavate; with short median carina; dorsal surface with 3 pairs of sublateral carinae. Eyes reniform. Mandible left lacinia mobilis two thirds as wide as incisor. Maxillipedal epipod fused to basis; palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with alternating flagellate cylindrical setae and flagellate plate-like setae. Pereopod 2 of male subchelate; heel prominent, palm concave, with few robust setae. Pereopod 7 of male sexually differentiated, propodus broader than in female, with felt of fine scale setae, dactylus simple, curved. Male pleopod 2 endopod without distal stem supporting appendix masculina. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached sublaterally at about midlength of pleotelson; biramous, rami of similar lengths or exopod shorter.

Intertidal–shelf (0–700 m). Southern Ocean. 3 species (Wägele, 1994; Leese et al., 2010: distribution).

Serolella Pfeffer, 1891

Diagnosis. Body oval, increasingly incised between triangular posteriorly directed coxal plates 2–6; middorsal line smooth in lateral view. Coxal dorsal plates contiguous, without intermediate gaps; plate 6 overlapping but not extending posteriorly far beyond pleonal epimera 2, 3. Pleonal epimera 2, 3 smaller than extension of pereonite 6 coxal dorsal plate, extending posteriorly along pleotelson lateral margins. Pleotelson posterior margin narrowly rounded, or posterior margin narrow, excavate; with short median carina; dorsal surface with flattened plate-like ridges laterally. Eyes reniform, narrow. Maxillipedal palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with alternating flagellate cylindrical setae and flagellate plate-like setae. Pereopod 2 of male subchelate; palm of propodus with U-shaped row of robust setae. Pereopod 7 of male sexually differentiated, propodus broader than in female, with felt of fine scale setae, dactylus simple, curved. Male pleopod 2 endopod without distal stem supporting appendix masculina. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached sublaterally at about midlength of pleotelson; biramous, rami of similar lengths or exopod shorter, or with knob-like rami fused to peduncle.

Shelf, slope (26–970 m). Southern Ocean. 4 species (Wägele, 1994: rediagnosis, figures).

Serolina Poore, 1987

Diagnosis. Body oval, increasingly incised between triangular posteriorly directed coxal plates 2–6; middorsal line smooth in lateral view, or with posteriorly directed tubercles on head and most pereonites. Coxal dorsal plates not contiguous, or 2–5 contiguous; plate 6 completely overlapping pleonal epimera 2, 3 in male, partially in female. Pereonites 5–7 fused middorsally. Pleonal epimera 2, 3 smaller than extension of pereonite 6 coxal dorsal plate, not extending posteriorly along pleotelson lateral margins. Pleotelson posterior margin narrowly rounded; with middorsal keel; dorsal surface smooth, or with sublateral carinae. Eyes reniform. Mandible left lacinia mobilis two thirds as wide as incisor. Maxillipedal epipod fused to basis; palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with alternating flagellate cylindrical setae and flagellate plate-like setae. Pereopod 2 of male subchelate; palm of propodus with U-shaped row of robust setae. Pereopod 7 of male sexually differentiated, propodus broader than in female, with felt of fine scale setae, dactylus simple, curved. Male pleopod 2 endopod with distal stem supporting appendix masculina. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached anterolaterally on pleotelson; biramous, rami of similar lengths or exopod shorter.

Subtidal, shelf (1–200 m). Central Indo-Pacific, Temperate Australasia. 12 species (Poore, 1987: diagnosis, key to species).

Serolis Leach, 1818

Diagnosis. Body oval, increasingly incised between triangular posteriorly directed coxal plates 2–6; middorsal line smooth in lateral view. Coxal dorsal plates 2–5 delimited from tergite by suture; 1–6 increasingly produced posteriorly; plate 6

overlapping and extending well posterior of pleonal epimera 2 and 3. Pleonal epimera 2, 3 smaller than extension of pereonite 6 coxal dorsal plate, not extending posteriorly along pleotelson lateral margins. Pleotelson posterior margin broadly rounded; with middorsal keel; dorsal surface with sublateral carinae. Eyes reniform. Mandible left lacinia mobilis two thirds as wide as incisor. Maxillipedal epipod fused to basis; palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with alternating flagellate cylindrical setae and flagellate plate-like setae. Pereopod 2 of male subchelate; palm of propodus with U-shaped row of robust setae. Pereopod 7 of male sexually differentiated, propodus broader than in female, with felt of fine scale setae, dactylus simple, curved. Male pleopod 2 endopod without distal stem supporting appendix masculina. Pleopod 4 endopod bilobed. Uropod attached posterolaterally, pair almost meeting in midline; biramous, rami of similar lengths or exopod shorter.

Shelf–bathyal (64–2930 m). Tropical Atlantic, Temperate South America, Southern Ocean. 11 species (Brandt, 1988: rediagnosis, redescriptions; 2003; Leese et al., 2008: distribution).

Spinoserolis Brandt, 1988

Diagnosis. Body oval, increasingly incised between triangular posteriorly directed coxal plates 2–6; middorsal line with posteriorly directed tubercles on head and most pereonites. Coxal dorsal plates not contiguous; plate 6 shorter than coxal plate 5. Pleonal epimera 2, 3 extensions absent. Pleotelson posterior margin narrow, excavate; with middorsal keel; dorsal surface smooth. Eyes reniform. Mandible left lacinia mobilis two thirds as wide as incisor. Maxillipedal palp of 3 articles, fused articles 2–3 cordiform. Pereopod 1 propodus with alternating flagellate cylindrical setae and flagellate plate-like setae. Pereopod 2 of male subchelate; palm of propodus with U-shaped row of robust setae. Pereopod 7 of male not sexually differentiated. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached anterolaterally on pleotelson; peduncle and endopod fused, exopod minute.

Subtidal–slope (1–400 m). Temperate Southern Africa. 2 species (Brandt, 1988; Wägele, 1994: description of type species).

Thysanoserolis Brandt, 1991

Diagnosis. Body almost evenly oval, margin defined by head, coxal plates and pleon, slight interruptions between coxal plates and pleon; middorsal line smooth in lateral view. Coxal dorsal plates 2–4 or 2–5 delimited from tergite by suture; contiguous, without intermediate gaps; plate 6 overlapping and extending well posterior of pleonal epimera 2 and 3. Pleonal epimera 2, 3 similar to extension of pereonite 6 coxal dorsal plate, extending posteriorly along pleotelson lateral margins. Pleotelson rectangular, posterior margin broadly convex; with short median carina; dorsal surface smooth. Eyes minute. Mandible left lacinia mobilis two thirds as wide as incisor. Maxillipedal palp of 3 articles, fused articles 2–3 cordiform; article 2 ovate, with distomesial setae. Pereopod 1 propodus with setae similar, slender, bifid. Pereopod 7 of male not sexually differentiated. Male pleopod 2 endopod with distal stem supporting appendix masculina. Pleopod 4 endopod simply triangular, not bilobed. Uropod attached on posterolateral angle of pleotelson, uropods and pleonites forming part of continuous body outline; biramous, exopod half as long as endopod.

Shelf, slope (33–430 m). Central Indo-Pacific, Temperate South America, Southern Ocean. 3 species (Brandt, 1991; 1992: commentary; Bruce, 2009: commentary, third species).

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Sphaeromatidae Latreille, 1828

Figures 9.9–9.21

The family Sphaeromatidae is commonly encountered in shallow-water marine environments. While morphologically diverse they are easily recognised, often by the compact shape but more reliably by the fusion of the pleonites and relatively simple walking legs. They are often brightly coloured and somewhat calcified, unlike cirolanid 'sea lice', for example. Few species attain lengths greater than 10 mm – many are smaller than this, 3–5 mm long, and about 30 mm is the greatest length found. The males of many species are ornately sculptured, showing considerable sexual dimorphism. Others can be smooth, even quite flat. Family diagnoses can be found in Bruce (1993) and Wetzer et al. (2018) and form the basis of the diagnosis here.

Sphaeromatidae are the largest family of free-living isopods, with 99 genera, of which six are exclusively freshwater (Wetzer et al., 2013, 2018). Species number almost 700, and numerous genera and countless species remain undescribed. Sphaeromatids are primarily shallow-water, with most species found on the continental shelf. Only 22 species of Sphaeromatidae have been recorded from depths of 400 metres or more (Bruce, 1994a, 1997; Calderon-López and Doti, 2025) and of these six extend to depths greater than 1000 metres, a number that remains unchanged to date. Sphaeromatidae are predominately found on hard substrata such as rocky shores and coral reefs, as well as sedimentary sea-floor habitats. Hard substrata are rarely sampled in deep water, but museum collections indicate that there is diverse sphaeromatid fauna on such habitats in deep water that is, as yet, unreported.

Wetzer et al. (2013) showed that the family is monophyletic based on an analysis based on an 18S rDNA dataset. Attempts to divide Sphaeromatidae into groups started with Hansen (1905), who recognised what he termed the platybranchiate,

hemibranchiate and eubranchiate genera, the three groups later raised to subfamilies by Hurley and Jansen (1977). "Platybranchiatinae" were characterised by the endopods and exopods of pleopods 4 and 5 lacking thickened transverse ridges, pleopods 3 and 4 without a transverse suture, and pleopod 5 exopod with a partial suture. "Hemibranchiatinae" were characterised by the endopods of pleopods 4 and 5 with thickened transverse ridges, pleopods 3–5 exopods usually with a transverse suture. "Eubranchiatinae" have endopods and exopods of pleopods 4 and 5 with thickened transverse ridges, pleopods 3 and 4 exopods usually without a transverse suture, and pleopod 5 exopod with partial or complete suture. Because these subfamily names are not based on a genus name, Iverson (1982) replaced them with Cassidininae Iverson, 1982, Sphaeromatinae Latreille, 1825 and Dynameninae Bowman, 1981 respectively. He listed 20, 20 and 31 genera in each subfamily respectively. Harrison (1984a) discussed the importance of the marsupium in sphaeromatid classification, but because generic identification depends almost entirely on adult male features, the number of oostegites and anterior and posterior brood pouches contribute little to generic diagnoses and nothing to the diagnoses here.

After discussion of the validity of these subfamilies (Bruce, 1995, 1997, 2003; Kussakin and Malyutina, 1993), Wetzer et al. (2018) used a 16S and 18S rDNA dataset from 44 species in 33 genera to show that the subfamilies are artificial. They recognised only two subfamilies, Sphaeromatinae (comprising three subclades) and Dynameninae (also comprising three subclades plus *Campecopea*), and a third *Gnorimosphaeroma* clade. The morphology of each clade and subclade were diagnosed, paraphrased here in the boxed text. Few of the clades and subclades can be diagnosed well from each other and do not help in providing key characters for identification of genera. In addition, three other "groups" of genera were morphologically characterised but not included in the analysis because there were no available sequences. Twelve genera could not placed in any of Wetzer et al.'s (2018: 23) proposed genus-groups.

Care, as always, is needed with dichotomous keys, on two counts. This key relies on having mature male specimens. Individuals with brood pouches are certainly not males but those with ornate sculpture almost certainly are; however, not all males are sculptured. Males can be confidently identified by the presence of paired penial processes or a fused penial process on the posterior ventral margin of pereonite 7 between the last pereopods and the presence of a pair of appendices masculinae, narrow rods attached to the mesial margins of the endopods of pleopod 2.

Further caution is needed because the generic diagnoses given adhere to the characterisation of the type species. It is widely recognised among isopod taxonomists brave enough to tackle Sphaeromatidae that several of the larger genera include species that should be elsewhere. Some relatively large genera such as *Cerceis* H. Milne Edwards, 1840, *Oxinasphaera* Bruce, 1997, *Paracassidina* Baker, 1911 and *Sphaeroma* Bosc, 1802 display either perceivable apomorphic characters or a uniform appearance and can be assumed to be monophyletic. Other genera, notably *Cymodoce* Leach, 1814, the group of genera *Cilicaea* Leach, 1818–*Cilicaeopsis* Hansen, 1905–*Paracilicaea* Stebbing, 1910, *Exosphaeroma* Stebbing, 1900, *Cymodopsis* Baker, 1926 and *Ischyromene* Racovitza, 1908, all contain species so dissimilar from the type species that they would be better housed in new genera. Further, many undescribed species cannot be placed in any existing genus. For all these reasons, caution must be taken in making a generic identification; ideally the keyed specimen/s should be checked against the generic diagnoses, and if possible detailed description of the genera in the literature cited. Splitting into more genera is inevitable in the future when revisions are undertaken (Wetzer et al., 2013).

The key to males of marine and estuarine genera below started from that of Harrison and Ellis (1991) but has been much modified. Their illustrated key relied on males of 81 genera. Some generic names have been updated and 18 more recent names added here. Six genera found only in fresh water are not included in the key but are appended below. Some estuarine genera can be found in coastal freshwater streams. *Ischyromene* appears twice in the key.

Pleonite 1 is usually free from the remaining pleon (fused pleonites 2–5) but is sometimes visible only laterally, hidden under the posterior margin on pereonite 7 and revealed only when the animal is more curled than flat. Partial sutures, lateral or posterior, on the pleon refer to those between pleonites 2–5. Pleonite 6 is part of the pleotelson, as in all isopods. Coxal dorsal plates refer to the lateral expansion of the coxae covering the bases (first mobile article) of pereopods 1–7 that are more or less fused to the pereonal tergite (a non-hinging suture may be visible dorsally or laterally between the tergite of pereonites 2–7 and the coxal dorsal plate).

Diagnosis. Body oval, vaulted, or flat; head free from pereonite 1; pereonites 1–7 visible dorsally. Coxal dorsal plates 2–7 delimited from tergite by weak non-articulating suture (sometimes not); dorsal coxal plate 7 similar, usually smaller, to dorsal coxal plate 6. Pleon with pleonite 1 usually present, often hidden dorsally; pleonites 2–5 fused mesially, indicated laterally by 0–3 sutures, occasionally fused to pleotelson. Antennular and antennal peduncles cylindrical, not part of margin of body, or flattened, defining anterior margin of body. Mandibular incisor process multicuspid; left incisor mobilis short, wide. Maxillipedal palp of 5 free articles. Pereopod 1 usually ambulatory. Pereopods 2–7 ambulatory. Uropodal endopod fused to peduncle (lamellar, sometimes reduced or absent), exopod usually lamellar (sometimes absent, cylindricalor styliform).

Implicit generic characters. Body vaulted, without setae, coxal and other margins smooth. Head with rostrum visible dorsally, rostrum simple, separating antennular bases; with anterior margin simple, not produced. Eyes lateral. Pereonite 6 simple, without bosses, processes or marginal extensions. Pereonite 7 as wide as pereonite 6, forming part of body outline, without dorsal bosses, processes or marginal extensions. Coxal dorsal plates tapering, rounded, coxal plates 2–6 overlapping the one behind. Pleonite 1 entire, free from pleonite 2, posterior margin even; pleon with 2 partial sutures visible on fused part; sutures (except first) running to posterior or posterolateral margin, all separate, sutures long; dorsal surface smooth; posterior margin without process; pleon posterior margin entire. Pleotelson vaulted, anteriorly as wide or almost as wide as pleon, without

Subfamilies and genus-groups proposed by Wetzer et al. (2018)

Sphaeromatinae. Pleon consisting of pleonites 1–3 fused medially segments (2 sutures visible on fused part). Epistome extended prominently anteriorly and elongate. Pleopod 1 rami not operculate. Pleopods 4 and 5 exopods and endopods with thickened transverse ridges.

Sphaeroma subclade. Body dorsal surfaces smooth or nodular, without setae, able to conglobate. Pleotelson posterior margin rounded broadly, without exit channel. Maxillipedal palp articles 2–4 mesial margins not or weakly lobate. Penial processes set apart basally. Uropodal rami lamellar, subequal.

Exosphaeroma subclade. Body dorsal surfaces smooth, without setae, able to conglobate. Pleotelson posterior margin rounded broadly, without exit channel. Maxillipedal palp articles 2–4 mesial margins not lobate. Penial processes set apart basally. Pleopods 4 and 5 exopods and endopods with or without thickened transverse ridges. Uropodal rami lamellar, subequal.

Cymodoce subclade. Body dorsal surfaces of males with nodular ornamentation or granular or with ridges or tubercles, densely setose. Maxillipedal palp articles 2–4 mesial margins extended, forming finger-like lobes. Penial processes in contact basally, long (extending to pleopod rami). Pleopod 2 appendix masculina elongate. Uropod with either endopod or exopod reduced.

Dynameninae. Pleotelson posterior margin complex, with sinuses, excisions, upturned, tubular; rarely simple. Maxillipedal palp articles 2–4 mesial margins lobate. Penial processes in contact basally. Pleopods 4 and 5 exopods and endopods with thickened transverse ridges.

Campecopea. Strongly sexually dimorphic. Pleonal sutures short. Maxillipedal palp articles 2–4 mesial margins weakly lobate. Pleopods 1–3 exopods lateral margins smooth. Pleopod 2 appendix masculina inserted basally or sub-basally. Uropodal exopod absent.

Ischyromene subclade. Not or weakly sexually dimorphic. Pleonal sutures short. Antennular peduncle article 2 longer than half article 1; article 3 as long as article 2. Pereopods secondary unguis with 2 accessory cusps. Pleopods 1–3 exopods lateral margins smooth. Pleopod 1 rami operculate, exopod and mesial margin of endopod indurate. Pleopod 2 appendix masculina inserted basally or sub-basally, longer than and extending beyond endopod. Pleopods 3 and 4 exopods without transverse suture.

Cerceis subclade. Pleonal sutures long. Antennular article 3 longer than article 2. Pleopods 1, 2 (sometimes 3) exopods lateral margins serrate, especially distally (usually). Pleopod 1 rami not operculate. Pleopod 2 appendix masculina inserted near midpoint of mesial margin or distally.

Dynamenella subclade. Pleonal sutures (except first) running to posterior margin. Antennular article 3 longer than article 2. Pleopods 1–3 exopods lateral margins smooth. Pleopod 1 rami not operculate.

Gnorimosphaeroma. Pleonal sutures running to lateral margin. Pleotelson posterior margin simple, arcuate, without exit channel. Pleopods 4 and 5 exopods and endopods without thickened transverse ridges. Uropodal rami lamellar, exopod shorter.

Three marine genus-groups lacked molecular data and therefore could not be assigned to any clade. These genera were characterised morphologically, and Wetzer et al. (2018) listed the included genera.

***Cassidina*-group**. Body margins expressed laterally (not ventrally) giving an overall flat appearance. Head lateral margins expanded, not set into pereonite 1. Epistome visible in dorsal view. Pereonites with coxal extensions. Pleonal sternite prominent. Pleon of 3 segments, laterally unfused. Antennular peduncle articles 1 and 2 flattened. Maxillipedal palp article 2 expanded, articles 3 and 4 finger-like medial lobes, article 5 elongate. Pereopod 1 modified, with 1 or more elongate articles and elongate dactylus; accessory unguis slender. Pleopod 1 rami subequal in width, distally rounded, usually collinear (from Bruce, 1994).

***Leptosphaeroma*-group**: Epistome not visible in dorsal view. Head set into pereonite 1, not laterally expanded. Pereonites without coxal extensions. Pleonal sternite absent. Pleonites all fused and pleon with a single segment, laterally unfused. Antennular peduncle articles 1 and 2 flattened, forming continuous outline. Maxillipedal palp articles with weak medial lobes. Pereopods all ambulatory. Penial processes partly or wholly fused. Pleopod 1 endopod subequal, more reduced than exopod; pleopod 2 appendix masculina basal (from Bruce, 1994).

***Moruloidea*-group**: Antenna with peduncular articles 4 and 5 robust, reflexed. Male pereopod 1 propodus with inferoproximal lobe (“heel”). Uropodal exopod reduced. Rugose and heavily calcified dorsum. Pereon folds “purse”-like at pereonite 5, with coxal plate 5 overlapping both anteriorly and posteriorly.

dorsal process. Antennular peduncle articles not flattened, with first articles not meeting medially; article 1 apices not produced, inferior margin without hard cuticular spines; article 2 without anterodistal lobe; with articles 2 and 3 colinear; longer than peduncle article 3. Antennal peduncle articles all colinear (or curving regularly), less robust than antennula, peduncle articles of similar thickness. Epistome anteriorly flush with head, not projecting. Mandibular incisor multicuspid; palp of 3 articles. Pereopod 1 ambulatory; propodus not club-shaped; merus simple, lower margin straight, not swollen. Pereopods 2 and 3 of similar proportions; pereopods 2, 3 propodal palm without proximal lobe. Pereopods 1–3 ischium upper margin without long stiff slender setae. Pereopod 5 of male similar to other pereopods. Penial processes entirely separate, tapering smoothly from base. Pleopods 1–3 exopods lateral margins smooth. Pleopod 1 rami not operculate; endopod usually of similar proportions to exopod. Pleopod 2 appendix masculina inserted basally or sub-basally, with straight margins, longer than and extending beyond endopod. Pleopod 3 exopod with transverse suture, endopod without transverse ridges. Uropodal rami flattened, not forming part of continuous body outline; peduncle-endopod lamellar, endopods not in contact posteriorly; exopod inserted laterally near anterolateral angle of peduncle-endopod, lamellar, similar in length to endopod, lateral margin finely serrate or smooth.

Key to adult males of marine and estuarine genera of Sphaeromatidae

1. Antennular peduncle article 1 or articles 1 and 2 flat, with expanded anterior and/or anterolateral lobes forming anterior margin of body 2
– Antennular peduncle articles 1 and 2 cylindrical or slightly flattened, without lobes forming anterior margin of body 15
2. Pereopod 1 carpus and dactylus scythe-shaped; merus with long setose lobe on upper margin (fig. 9.19o). ..... *Paracassidina*
– Pereopod 1 ambulatory or weakly prehensile; merus sometimes with a short lobe on upper margin (not as above) (fig. 9.19r) 3
3. Antennular peduncle article 1 alone expanded anteriorly as plate, meeting medially (fig. 9.19a) ..... *Amphoroidea*
– Antennular peduncle articles 1 and 2 flat, expanded as anterior and/or anterolateral lobes meeting medially or not (e.g. figs 9.9b, 9.15a) 4
4. Antennular peduncle articles 1 separated by epistome 5
– Antennular peduncle articles 1 in contact 8
5. Uropodal exopod minute, immobile, not obvious (fig. 9.17a, b) ..... *Syncassidina*
– Uropodal exopod mobile, obvious 6
6. Uropodal exopod almost as long as endopod. Pleotelson longer than uropod (fig. 9.16o) ..... *Stathmos*
– Uropodal exopod immersed in uropod body. Pleotelson about as long as uropod 7
7. Antennular peduncle article 1 longer than wide; epistome visible in dorsal view extending anteriorly beyond antennula (fig. 9.19d) ..... *Cassidina*
– Antennular peduncle articles 1 and 2 lobed anteriorly beyond epistome 8
8. Antennular peduncle articles 1 and 2 lobes truncate or subtruncate anteriorly. Uropodal exopod half as long as uropod body (fig. 9.10i) ..... *Chitonopsis*
– Antennular peduncle articles 1 and 2 lobes narrow, produced anteriorly. Uropodal exopod one quarter as long as uropod body (fig. 9.9b) ..... *Agostodina*
9. Pleon without sutures (fig. 9.15l) 10
– Pleon with 2 or more sutures running to lateral or posterior margin (figs 9.10k, 9.13m) 12
10. Uropodal endopods meeting or nearly so in midline posterior to pleotelson apex (fig. 9.15a) ..... *Paraleptosphaeroma*
– Uropodal endopods not meeting in midline posterior to pleotelson apex 11

11. Uropodal exopod triangular, lying anterior to endopod. Pleotelson without terminal foramen. Pereonite 1 enclosing head (fig. 9.15l, m) ..... *Platysphaera*

– Uropodal exopod lying alongside endopod. Pleotelson with terminal foramen. Pereonite 1 not enclosing head laterally (fig. 9.9f) ..... *Beatricesphaera*

12. Uropodal endopods meeting in midline posterior to pleotelson apex. Pleon with 2 sutures reaching lateral margin (fig. 9.13m) ..... *Leptosphaeroma*

– Uropodal endopods not meeting in midline posterior to pleotelson apex. Pleon without or with 1 suture reaching lateral margin, 1 or 2 reaching posterior margin 13

13. Pleon with first suture reaching lateral margin; second suture reaching posterior margin (fig. 9.10k, l). Appendix masculina spatulate, much longer than pleopod 2 endopod (fig. 9.20i) ..... *Chitonosphaera*

– Pleon with 1 or 2 pairs of sutures reaching posterior margin. Appendix masculina not spatulate 14

14. Pleon with 2 pairs of sutures reaching posterior margin (fig. 9.11i, j). Pleopods 4 and 5 rami lamellar, without transverse ridges (fig. 9.21g, h). Appendix masculina apex folded, distally forming groove (fig. 9.20l) ..... *Discidina*

– Pleon with 1 pair of sutures reaching posterior margin (fig. 9.9c). Pleopods 4 and 5 both rami with thickened transverse ridges (fig. 9.21e, f). Appendix masculina narrow ..... *Amphoroidella*

15. Dorsal surface of head with 2 long, slender, anterolateral processes, 1 each side of epistome in dorsal view. Epistome narrow, greatly extended anteriorly, about twice length of processes (fig. 9.10c, d) ..... *Ceratocephalus*

– Head without long anterior processes. Epistome not as above 16

16. Head produced into a substantial rounded cone about one third body length. Pereonites with transverse rows of conical projections. Pleotelson with 2 prominent domes, apex indistinctly trilobed, with indistinct ventral exit channel (fig. 9.9k, l) ..... *Bregmotypta*

– Characters not so combined 17

17. Pereopod 5 greatly enlarged, smooth, with swollen carpus and propodus, 1.5 times as long as other pereopods (fig. 9.19u). Body tuberculate dorsally (fig. 9.13k, l) ..... *Kranosphaera*

– Pereopod 5 similar to other pereopods. Body smooth or variously sculptured 18

18. Mandible with incisor process greatly elongate, flat, deeply bifid (fig. 9.19x) ..... *Hemisphaeroma*

– Mandible with incisor process short (fig. 9.19y, z) 19

19. Pleopod 1 endopod of male comprising basal part and long filamentous thread (about 5 times length of exopod) (figs 9.20e, 9.14i, j) ..... *Paracassidinopsis*

– Pleopod 1 endopod lamellar or indurate 20

20. Dorsal surface of body ornamented with small mushroom-headed tubercles each topped with a cluster of stemmed spheres. Epistome deeply bifid, projecting anteriorly beyond head in dorsal view (fig. 9.9j) ..... *Botryias*

– Body not covered with large, prominent, spherical, tuberculate processes (if tuberculate, tubercles not spherical). Epistome, if bifid, with rounded distal tips 21

21. Uropod a single broad plate alongside pleotelson, without exopod (fig. 9.18h) ..... *Scutuloidea*

– Uropod with exopod (may be minute, not obvious or housed in a notch on endopod external margin) 22

22. Antennular peduncle article 1 of male with anterodistal angle extended laterally as long, narrow, flat lobe (figs 9.9m, n, 9.19c) (incipient lobe in female) ..... *Calcipila*

– Antennular peduncle article 1 without anterodistal lateral lobe (usually cylindrical, sometimes a flat plate) 23

23. Pleopods 1 and 2 or 1–3 (especially pleopod 2, fig. 9.20a, f, s) exopods with lateral (obsolete on some pleopods in some genera) or few distolateral teeth. Appendix masculina attached at midpoint of pleopod 2 endopod (fig. 9.20s) 24

– Pleopods 1–3 exopods without lateral teeth. Appendix masculina usually attached basally to pleopod 2 endopod (fig. 9.20i, j, l, m) 32

24. Pereonite 7 with pronounced dorsal extension directed posteriorly, forming broad, finger-like process (fig. 9.12o, p) or flat, broad shield covering pleotelson (fig. 9.12, m, n) ..... *Haswellia*

– Pereonite 7 with posterior margin similar to preceding pereonites, without posterior extension 25

25. Body extremely flattened (c. 5 times as wide as deep), smooth 26

– Body not extremely flattened (less than 3 times as wide as deep). Pleotelson (at least) with 1 or more tubercles or ridges 27

26. Uropod with rami styliform, extending well beyond pleotelson apex (fig. 9.15i). Pleopods 1–3 exopods with lateral teeth (fig. 9.20r). Pleotelson deeply notched ..... *Platycerceis*

– Uropod with rami lamellar, extending just beyond pleotelson apex (fig. 9.9a). Pleopods 1 and 2 exopods with lateral teeth (fig. 9.20a) ..... *Afrocerceis*

27. Uropodal exopod narrow, usually cylindrical, not flattened, at least twice as long as reduced endopod; endopod not reaching level of pleotelson apex (figs 9.11g, h, 9.14k,l) 28

– Uropod with rami flattened; endopod not reduced, reaching level of pleotelson apex (fig. 9.12d) 29

28. Pleotelson apex with notch bearing pronounced median tooth extending posteriorly beyond level of notch opening (fig. 9.11g, h) ..... *Discerceis*

– Pleotelson apex with deep complex toothed notch which either lacks median tooth or has a median tooth that does not extend posteriorly beyond the level of notch opening (fig. 9.14k) ..... *Paracerceis*

29. Pleotelson bidomed, rectilinear in lateral view, without median ridge (fig. 9.12d, e) ..... *Eterocerceis*

– Pleotelson with 3 longitudinal ridges, or with median ridge or smooth or with pair of sublateral tubercles 30

30. Head anterior margin not extended. Median rostral process directed anteroventrally. Epistome visible in dorsal view when head is rotated dorsally to bring mouthparts forwards (fig. 9.19k) ..... *Pseudocerceis*

– Head anterior margin extended forwards. Median rostral process apex directed posteroventrally. Epistome never visible in dorsal view 31

31. Head anterior margin flattened dorsoventrally. Uropodal exopod acute (fig. 9.10e, f). Antennular peduncle article 1 with posterior angle elongate, acute (fig. 9.19e) ..... *Cerceis*

– Head anterior margin conical, blunt, not flattened dorsoventrally. Uropodal exopod distally serrate (fig. 9.12f, g). Antennular peduncle article 1 with posterior angle blunt (fig. 9.19h) ..... *Exocerceis*

32. Pereonite 6 with 1 median or pair of spine-like projections (figs. 9.9o, 9.11k, l) or if without projection, ischium of pereopods 5–7 elongate, 5–7 times as long as wide). Uropodal endopod minute or absent 33

– Pereonite 6 without posterior spine-like projection. Uropodal endopod usually well developed 34

33. Pereonite 6 without or with 1 median spine-like projection (fig. 9.9o, p). Ischium of pereopods 5–7 elongate, 5–7 times as long as wide. Pleopods 4, 5 with both rami without thickened transverse ridges ..... *Campecopea*

– Pereonite 6 with pair of spine-like projections (fig. 9.11k, l). Ischium of pereopods 5–7 not elongate. Pleopods 4, 5 with both rami with thickened transverse ridges (fig. 9.21e, f) ..... *Dynamene*

34. Pereonite 7 with dorsal posterior margin bearing 1 median, spine-like process directed posteriorly (fig. 9.17h, i) 35

– Pereonite 7 with posterior margin similar to that of preceding pereonites, or with 2 lobes or transverse ridges or 2 short acute processes, but not with 1 median spine 37

35. Pleotelson with subapical foramen connected to apex by narrow slit (fig. 9.15d) ..... *Parisocladus*

– Pleotelson without subapical foramen (may have an open notch) 36

36. Pleotelson apex entire, acute, or weakly emarginate; with a longitudinal ventral groove (fig. 9.13f) ..... *Isocladus*

– Pleotelson apex with terminal notch bearing median tooth (fig. 9.17h, i) ..... *Zuzara*

37. Uropodal peduncle cylindrical, endopod absent or stub-like; exopod cylindrical (rami not especially flattened) 38

– Uropod with peduncle-endopod and/or rami broadly flattened 47

38. Coxal plates 1, 2 triangular, directed laterally; coxal plates 2–5 and pleonite 2 with spine-like ventral process (fig. 9.11o, p) ..... *Dynameniscus*

– Coxal plates rounded or truncate, without spike-like process 39

39. Pleon with prominent median process (fig. 9.10m–p) 40

– Pleon without median process or with broad plate-like extension 42

40. Pleotelson posterior margin with median notch only (fig. 9.18k). Appendix masculina attached distally to pleopod 2 endopod (fig. 9.20g) ..... *Cassidias*

– Pleotelson posterior margin notch with or without median tooth (fig. 9.18k). Appendix masculina attached basally to pleopod 2 endopod (fig. 9.20j) 41

41. Pleotelson apical notch wide, with broad short median tooth (fig. 9.18l) ..... *Cilicaea*

– Pleotelson apical notch wide, smoothly rounded, without median tooth (fig. 9.18m) ..... *Cilicaeopsis*

42. Uropod attached at anterolateral angle of pleotelson, posterior margin of pleotelson extending well beyond peduncle (figs, 9.11a, 9.15g) 43

– Uropod attached at posterolateral angle of pleotelson, posterior margin of pleotelson almost transverse (e.g., fig. 9.18g) 44

43. Pleotelson apex with short tube directed dorsally, ventrally and posteriorly enclosed. Uropodal endopod stub-like; exopod, sinusoidal, blunt (fig. 9.15g, h) ..... *Pistorius*

– Pleotelson apex tapering, acute, without tube. Uropodal endopod absent; exopod straight, acute (fig. 9.11a, b) ..... *Cymodetta*

44. Pereonite 7 not reaching lateral margins in dorsal view. Uropodal exopod styliform, curved, twice length of peduncle in male (fig. 9.18g) (rami similar in female). Slope depths only ..... *Naesicopea*

– Pereonite 7 reaching lateral margins in dorsal view. Uropodal exopod cylindrical. Subtidal–slope depths 45

45. Pleon with tubercles on posterior margin. Pleotelson with pair of sublateral longitudinal curved triangular ridges (fig. 9.12k, l) ..... *Geocerceis*

– Pleon without tubercles on posterior margin. Pleotelson with or without bosses or ridges, none curved 46

46. Pleotelson with pair of sublateral longitudinal elongate bosses; posterior margin with small median notch and 2 small sublateral notches (figs 9.14c, d, 9.18q) ..... *Neonaesa*

– Pleotelson with pair of sublateral bosses; posterior margin with terminal notch with median tooth (fig. 9.14m, n) ..... *Paracilicaea*

47. Antennular peduncle article 1 with row of ventrally directed teeth, similar teeth on epistome (fig. 9.19i) ..... *Oxinasphaera*

– Antennular peduncle article 1 without row of ventrally directed teeth 48

48. Dorsal surface highly rugose, with angular tubercles. Pleotelson with solid tuberculate process, directed posteriorly. Pleon with pair of prominent dorsal elongate submedian keels (fig. 9.10g, h) ..... *Cercosphaera*

– Dorsal surface with distinct tubercles. Pleotelson without posteriorly directed solid tuberculate process. Pleon without pair of prominent dorsal elongate submedian keels 49

49. Pleon with broad medial plate-like extension. Uropodal exopod cylindrical, acute (fig. 9.16a, b) ... *Pooredoce*

– Pleon without broad medial plate-like extension. Uropodal exopod usually lamellar ... 50

50. Pleotelson posterior margin with broad, flat, triangular extension longer than main dome of pleotelson. Uropod with rami subequal, lamellar, distally expanded, with rounded, serrulate margins extending beyond pleotelson apex. Head with broad, dense, anterior patch of short setae (fig. 9.16g, h) ... *Ptyosphaera*

– Pleotelson posterior margin without flat acute extension or short extension. Uropod not so expanded. Head without dense, anterior patch of setae (may bear sparse setae over entire surface) ... 51

51. Pleotelson posterolateral margin curled ventrally to meet (or almost meet) in ventral midline, forming closed, cylindrical tube, directed posteriorly (fig. 9.11e). Uropodal rami lamellar; endopod well-formed ... 52

– Pleotelson apex either without enclosed foramen, or with foramen directed anterodorsally, dorsally or posterodorsally, but never with foramen directed posteriorly in the form of a tube. Uropods various ... 53

52. Antennular articles 1 and 2 robust; article 3 slender, articulating at right angles (fig. 9.19g). Pereopod 2 slender, narrower than pereopod 3 ... *Diclidocella*

– Antennular articles 1–3 colinear (figs 9.11e, 9.19f). Pereopod 2 as wide as pereopod 3 ... *Cymodocella*

53. Coxal dorsal plate 6 twice length of tergite, covering or almost covering pereopod 7 coxal plate in lateral view (fig. 9.12c). Uropodal rami subequal, lamellar (fig. 9.12b) ... 54

– Coxal dorsal plate 6 not covering coxal plate 7, at most overlapping it partially ... 55

54. Pleotelson apex with enclosed foramen directed posterodorsally. Coxal plate 6 overlapping pleon, not reaching ventral margin, pereonite 7 longer than pereonite 6 (fig. 9.12b, c) ... *Dynamenopsis*

– Pleotelson apex with deep, narrow, vertical slit. Coxal plates 6 and 7 both reaching ventral margin, pereonite 7 as long as pereonite 6 (fig. 9.14q, r) ... *Paraimene*

55. Body globular, highly domed, smooth. Pleonal epimeron 2 (first clearly visible) reaching ventrally well beyond epimera 3 and 4. Pleotelson highly domed. Uropodal exopod longer than endopod (fig. 9.17g) ... *Xynosphaera*

– Body not especially domed. Uropodal exopod rarely longer than endopod. Other characters not so combined ... 56

56. Uropod not visible in dorsal view; exopod minute (fig. 9.15e, f) ... *Pedinura*

– Uropod visible alongside pleotelson; exopod various ... 57

57. Pereonite 7 not reaching lateral margins of body. Pereonite 6 and pleon juxtaposed laterally (fig. 9.18a) ... *Artopoles*

– Pereonite 7 reaching lateral margins of body in dorsal view ... 58

58. Uropodal rami flattened, forming part of continuous body outline; exopod more or less embedded in peduncle (fig. 9.10i) ... 59

– Uropodal rami lamellar, not forming part of continuous body outline ... 60

59. Appendix masculina arising from long proximal lobe of pleopod 2 endopod, much longer than endopod, acute (fig. 9.20h) ... *Cassidinidea*

– Appendix masculina arising sub-basally on pleopod 2 endopod, as long or longer than endopod, spatulate (figs. 9.13a, 9.20o) ... *Heterodina*

60. Appendix masculina abruptly reflexed midlength (fig. 9.20n). Apex of pleotelson with narrow, deep, Y-shaped slit or foramen, usually lined with small teeth (fig. 9.18b) ... *Dynoides*

– Appendix masculina not reflexed midlength. Apex of pleotelson with or without foramen, not lined with small teeth ... 61

61. Penial processes proximally fused to midlength (fig. 9.19l). Appendix masculina with acute tip extending beyond endopod of pleopod 2 (fig. 9.20j). Apex of pleotelson with small elliptical foramen (fig. 9.10q) ..... *Cliamenella*

– These characters not combined 62

62. Pleotelson incorporating all pleonites (except sometimes pleonite 1), with at most 1 lateral suture (Figs 9.9g; 9.13p). Head produced as lobe in front of eyes, antennulae and antennae. Pleopod 1 semi-operculate, indurate (fig. 9.20d) 63

– Pleonite 1, pleon (usually with 2 lateral sutures) and pleotelson completely separated by dorsal sutures. Head rarely produced as lobe in front of eyes, antennulae and antennae. Pleopod 1 not operculate (except *Ischyromene*, indurate mesially) 66

63. Body extremely flat, scale-like. Uropodal endopods meeting posterior to pleotelson apex (fig. 9.13p, q) ..... *Maricoccus*

– Body flat or vaulted. Uropodal endopods not meeting posterior to pleotelson apex 64

64. All pleonites completely fused to pleotelson, with 1 lateral suture visble laterally (fig. 9.9g, h). Antennular peduncle article 2 extended distally so that article 3 articulates on posterior margin (fig. 9.19b) ..... *Austrasphaera*

– Pleon with free pleonite 1, remaining pleonites fused to pleotelson (1 lateral suture visible) 65

65. Pleotelson with distinct apical foramen (fig. 9.13n, o). Pereopods 2 and 3 propodus without basal heel ..... *Margueritta*

– Pleotelson apex entire, without apical foramen (fig. 9.13g, h). Pereopods 2 and 3 propodus with heel (fig. 9.19s) ..... *Juletta*

66. Body flattened or weakly vaulted; coxal plates directed laterally (fig. 9.9d, e). Estuarine ..... *Apemosphaera*

– Body not flattened, strongly vaulted; coxal plates directed ventrally 67

67. Pleotelson with median subapical foramen connected to apex by narrow slit (slit may be closed) (figs 9.12a, 9.16j) 68

– Pleotelson without subapical foramen (ventral groove in some) 72

68. Pereonite 6 twice as long as pereonite 5 in dorsal midline, with posterior margin bilobed. Pereonite 7 with pair of triangular submedial posterior projections (fig. 9.12a) ..... *Dynamenoides*

– Pereonite 6 subequal in length to pereonite 5 in dorsal midline, not posteriorly bilobed. Pereonite 7 without short, acute, posterior projections (fig. 9.13d, e) 69

69. Dorsal surface of entire body covered with large separate tubercles (fig. 9.16i, j). Pleopods 4 and 5 exopods flat, membranous; endopod with transverse ridges (fig. 9.21i, j) ..... *Sphaeramene*

– Entire body not covered with large separate tubercles (pleotelson may bear large tubercles). Pleopods 4 and 5 rami with thickened transverse ridges (fig. 9.21e, f) 70

70. Pleopod 1 operculate (covering other pleopods) with inner half of triangular endopod noticeably thickened (fig. 9.20c). Penial processes blunt, adjacent but separate from base (fig. 9.19m) ..... *Ischyromene* (part)

– Pleopod 1 endopod not obviously thickened (fig. 9.20b). Penial processes tapering, fused along half length (fig. 9.19l) 71

71. Pleotelson ventral margins with out-turned ridges not meeting posteriorly (pleotelson apices may meet) (fig. 9.14o, p; shaded in fig. 9.18s, t). Appendix masculina narrow, extending well beyond pleopod 2 endopod (fig. 9.20q) ..... *Paradella*

– Pleotelson ventral margins with out-turned ridges meeting posteriorly (fig. 9.11m, n; shaded in fig. 9.18o, p), or without out-turned ridges. Appendix masculina broad basally, tapering, extending to or beyond pleopod 2 endopod (fig. 9.20m) ..... *Dynamenella*

72. Antenna robust, peduncle article 5 reflexed. Coxal plate 5 larger than other coxal plates, appearing to overlap plates of both pereonite 4 and pereonite 6 when animal folded. Eyes obvious, dorsal (fig. 9.14a, b) ..... *Moruloidea*

– Antenna not robust, not reflexed. Coxal plate 5 not appearing to overlap those of both pereonites 4 and 6 when animal folded. Eyes various 73

73. Antennular peduncle article 1 with posterodistal angle extended as acute process (fig. 9.19j). Uropod with both rami styliform (fig. 9.15j, k) ..... *Platynympha*

– Antennular peduncle article 1 with distal angles blunt. Uropodal rami not styliform 74

74. Pereonite 7 with pair of posterior submedian lobes. Pleotelson apex with prominent median projection and basal short tubercle each side. Uropodal rami subequal, rounded (fig. 9.18e). Pleopods 4 and 5 rami with transverse ridges (fig. 9.21e, f) ..... *Holotelson*

– Pereonite 7 with posterior margin simple. Pleotelson apex without long, thick median process (if apex appears tridentate, pleopods 4 and 5 exopods without transverse ridges). Uropods various 75

75. Pereonites 2–7, pleon and pleotelson with dense dorsal mat of setae (fig. 9.13i, j) ..... *Koremasphaera*

– Pereonites 2–7, pleon and pleotelson without dense dorsal mat of setae 76

76. Pleotelson apex tridentate in dorsal view (sometimes weakly so; with notch bearing median tooth) (fig. 9.9q) 77

– Pleotelson apex not tridentate, with or without median tooth 79

77. Uropodal exopod half length of endopod; endopod not reaching pleotelson apex. All coxal plates acute, separate (fig. 9.9q) ..... *Cassidinella*

– Uropodal exopod longer than half length of endopod. Coxal plates not all acute and separate 78

78. Body smooth; pleon and pleotelson each with 1 boss each side of midline. Uropodal exopod twice length of endopod, scimitar-like, with acute, out-turned tip. Pereonite 1 lateral margin with truncate posteroventral lobe. Coxal plate 5 extending ventrally further than other coxal plates (fig. 9.13b, c) ..... *Heteruropus*

– Pleotelson, pleon and posterior region of pereon usually with tubercles, ridges and long setae. Uropodal exopod lanceolate, shorter than or extending just beyond endopod. Pereonite 1 lateral margin with acute or narrowly rounded posteroventral angle. Coxal plate 5 not extended ventrally more than other coxal plates (fig. 9.11c, d) ..... *Cymodoce*

79. Pereopod 2 heavily calcified, modified for clasping (i.e. subterminal articles broad, flattened, with pronounced inferior spines) (figs 9.15b, c, 9.19p, t). Pereopods 3–7 slender ..... *Parasphaeroma*

– Pereopod 2 not heavily calcified or modified for clasping, slender or flattened anterior to posterior. Pereopods 3–7 various 80

80. Uropodal exopod with prominent subterminal notch; endopod lateral margin not serrate (figs 9.14e, f, 9.18r). Pleopod 3 endopod with several transverse ridges (fig. 9.21b) ..... *Neosphaeroma*

– Uropodal exopod without prominent subterminal notch; endopod lateral margin serrate (fig.9.16k). Pleopod 3 endopod flat, without transverse ridges (fig. 9.21a) 81

81. Pereopods 1–3 each with ischium and merus (and propodus in *Sphaeroma*), superior margins each with dense row of long, stiff, setae (fig. 9.19q). Penial processes short 82

– Pereopods 1–3 each with ischium and merus superior margins each without dense row of long, stiff, setae (if pereopods bear many long setae over all surfaces, penial processes long) 83

82. Maxillipedal palp articles 3, 4 without mesial lobes, margins straight (figs 9.16k, l, 9.19w) ..... *Sphaeroma*

Maxillipedal palp articles 3, 4 with mesial lobes (fig. 9.19v) ..... *Lekanesphaera*

83. Pleotelson apex smoothly rounded, distal margin medially upturned, anterior surface with several prominent tubercles each side of midline (fig. 9.16c–f) ..... *Pseudosphaeroma*

– Pleotelson apex not upturned in lateral view, ornamentation various or absent 84

84. Pleopod 1 operculate (covering other pleopods) with inner of triangular endopod noticeably thickened (fig. 9.20c). Pleotelson with pronounced apical notch (fig. 9.13d, e). Pleopods 4 and 5 rami with thickened transverse ridges (fig. 9.21e, f) ..... *Ischyromene* (part)

– Pleopod 1 with inner half of endopod not noticeably thickened (fig. 9.20b). Pleotelson with or without apical notch. Pleopods 4 and 5 exopods with or without transverse ridges 85

85. Pleon with 1 or 2 suture lines reaching ventrolateral margins. Pleotelson apex smoothly rounded, without apical notch (fig. 9.18d) ..... *Gnorimosphaeroma*

– Pleon with suture lines reaching posterior or posterolateral margins (if lines reach posterolateral angles, pleotelson with vertical ventral apical notch not obvious in dorsal view) 86

86. Pleopods 4 and 5 rami both with transverse ridges. (fig. 21e, f). Pleotelson posterior margin almost truncate (figs 9.9b, 9.16m) 87

– Pleopods 4 and 5 exopods lamellar, without transverse ridges; endopods sometimes with transverse ridges (fig. 21a–d, g–j). Pleotelson posterior margin usually rounded or pointed (figs 9.12h, j, 9.16p), truncate in *Waiteolana* 88

87. Uropodal endopod broad, free mesial margin concave; exopod short, narrow, acute (fig. 9.10b) ..... *Cassidinopsis*

– Uropodal rami narrow, apically rounded, subequal or exopod slightly longer than endopod (figs 9.16m, n, 9.18i) ..... *Sphaeromopsis*

88. Eyes minute, not obvious. Pereopods 3–6 robust, hirsute (fig. 9.17c, d). Mandible without palp or with apical seta ..... *Tholozodium*

– Eyes obvious. Pereopods not especially robust. Mandible with 3-articled palp (fig. 9.19x–z), usually visible each side of epistome 89

89. Body flattened. Pleon with 2 short sutures converging on posterior margin (fig. 9.16p) ..... *Striella*

– Body vaulted. Pleon with 2 long sutures reaching posterolateral margin 90

90. Pleotelson with single or double median boss; with posteriorly produced lobe over ventrally directed groove (fig. 9.18n). Pleon dorsal surface smooth (fig. 9.11f) ..... *Cymodopsis*

– Pleotelson without dorsal ornamentation; without or with incomplete ventral exit channel. Pleon dorsal surface smooth or tuberculate 91

91. Body surface tuberculate. Uropodal endopod with distal notch (fig. 9.17e, f). Mandibular molar reduced to thin acute blade (fig. 9.19z) ..... *Waiteolana*

– Body surface smooth or setose. Uropodal endopod acute distally, rounded or truncate. Mandibular molar not reduced 92

92. Pleopods 4 and 5 with both rami flat, thick, without transverse ridges (figs 9.12h, i, 9.21g, h). Estuarine or freshwater ..... *Exosphaeroides*

– Pleopods 4 and 5 endopods usually with obvious transverse ridges; exopods flat (fig. 9.21c, d, i, j). Marine 93

93. Pleonite 1 with 2 submedian flat lobes (often concealed by pereonite 7), directed posteriorly (fig. 9.18c; not visible in fig. 9.12j). Without dense dorsal setae. Uropodal exopod simple ..... *Exosphaeroma*

– Pleonite 1 without 2 posteriorly directed submedian flat lobes. Usually densely setose dorsally. Uropodal exopod sometimes apically falcate (figs 9.9i, 9.18j) ..... *Benthosphaera*

Afrocerceis Müller, 1995

Diagnosis. Body flat, coxae without visible sutures, directed laterally, dorsal surfaces smooth, unable to conglobate; not or weakly sexually dimorphic. Head with ventral rostrum; with anterior margin produced, overriding antennules. Eyes more dorsal than lateral. Coxal plates truncate. Pleonite 1 narrower than remainder of pleon, not extending to pleon lateral margins. Pleotelson flat; posterior margin with shallow median indentation, with incomplete ventral groove or channel; ventrolateral margins simple. Antennular peduncle articles 1 and 2 robust, article 3 slender, with first articles meeting medially;

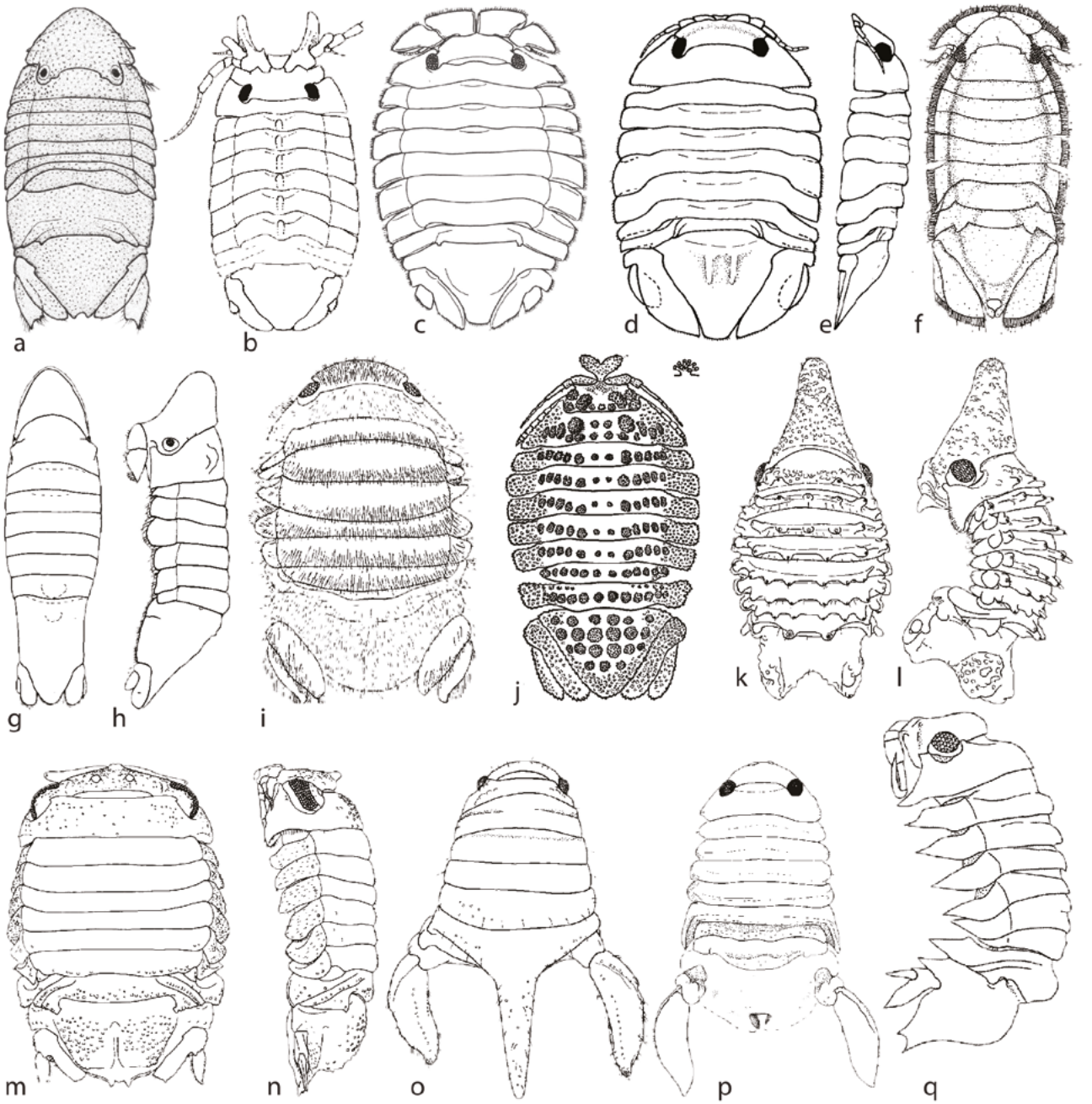


Figure 9.9. Sphaeromatidae. Dorsal and lateral views. a, *Afrocerceis kenyensis* Müller, 1995; b, *Agostodina munta* Bruce, 1994; c, *Amphoroidella elliptica* (Baker, 1908); d, e, *Apemosphaera naranagi* Bruce, 1994; f, *Beatricesphaera ruthae* Wetzer and Bruce, 1999; g, h, *Austrasphaera berentsae* Bruce, 2003; i, *Benthosphaera reburra* Bruce,1999; j, *Botryias fructiger* Richardson, 1910 (tubercle figured separately); k, l, *Bregmotypta pavicula* Bruce,1994; m, n, *Calcipila cornuta* Harrison and Holdich, 1984; o, *Campecopea hirsuta* (Montagu, 1804); p, *Campecopea lusitanica* (Nolting, Reboreda and Wägele, 1998); q, *Cassidinella incisa* Whitelegge, 1901.

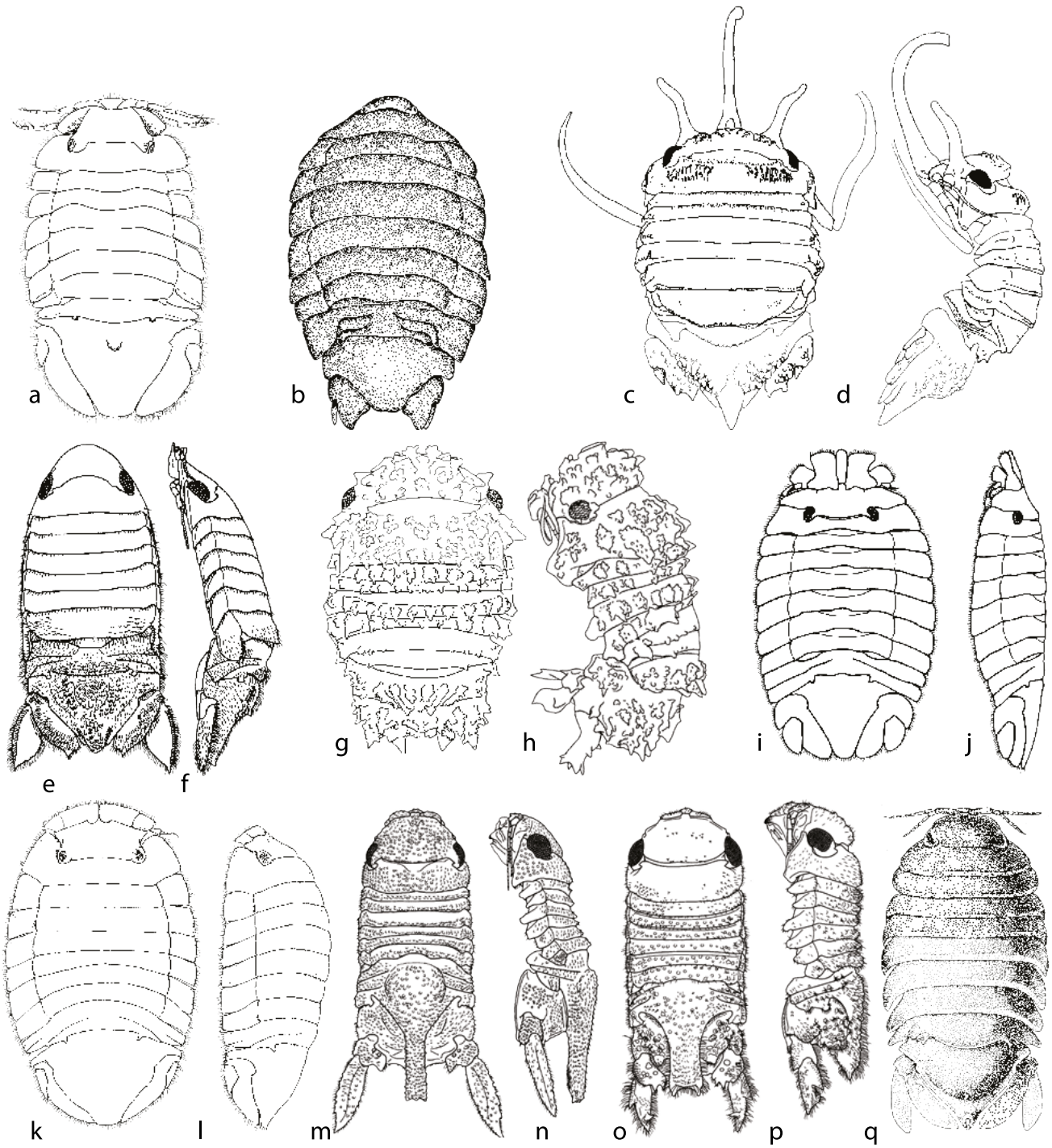


Figure 9.10. Sphaeromatidae. Dorsal and lateral views. a, *Cassidinidea ovalis* (Say, 1818); b, *Cassidinopsis emarginata* (Guérin-Méneville, 1843); c, d, *Ceratocephalus grayanus* Woodward, 1877; e, f, *Cerceis pustulosa* Harrison and Holdich, 1982; g, h, *Cercosphaera wirritin* Bruce, 1994; i, j, *Chitonopsis spatulifrons* Whitelegge, 1902; k, l, *Chitonosphaera lata* (Nishimura, 1968); m, n, *Cilicaea calcarifera* Harrison and Holdich, 1984; o, p, *Cilicaeopsis granulata* (Whitelegge, 1902); q, *Cliamenella fraudatrix* (Kussakin, 1962).

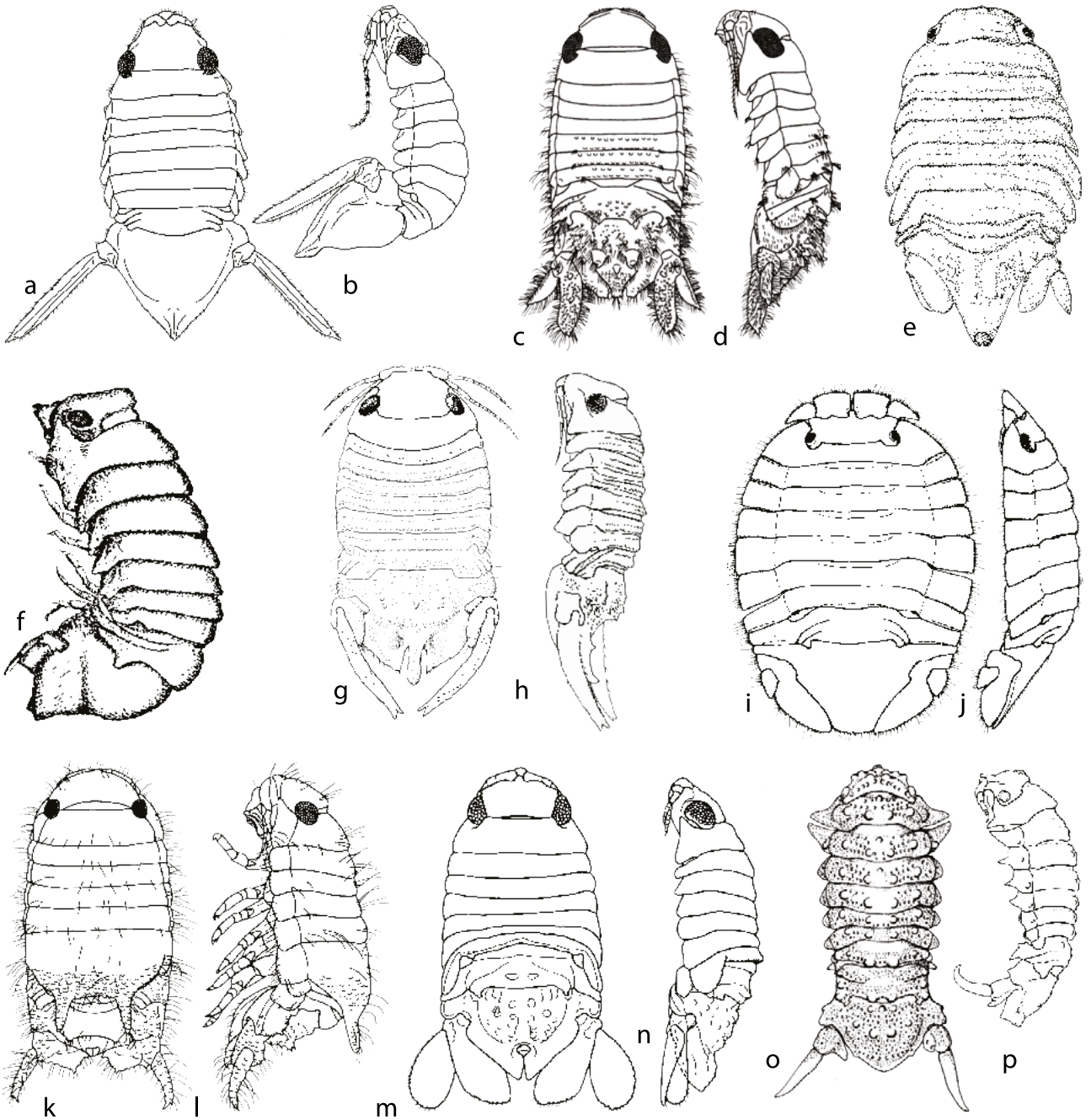


Figure 9.11. Sphaeromatidae. Dorsal and lateral views. a, b, *Cymodetta gracilipes* Holdich and Harrison, 1983; c, d, *Cymodoce bipapilla* Harrison and Holdich, 1984; e, *Cymodocella tubicauda* Pfeffer, 1887; f, *Cymodopsis latifrons* Baker, 1926; g, h, *Discerceis kensleyi* Schotte, 2005; i, j, *Discidina banawarra* Bruce, 1994; k, l, *Dynamene curalii* Holdich and Harrison, 1980; m, n, *Dynamenella trachydermata* Harrison and Holdich, 1982; o, p, *Dynameniscus carinatus* (Richardson, 1900).

article 2 with anterior and posterior acute processes; article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Epistome acute anteriorly. Mandibular molar process surface smooth, surrounded with basal fine setae. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes in contact basally, short (not extending beyond pleopod peduncles). Pleopods 1, 2 exopods lateral margins serrate, especially distally. Pleopod 2 appendix masculina inserted near midpoint of mesial margin, about as long as endopod. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with incomplete transverse suture, with thickened

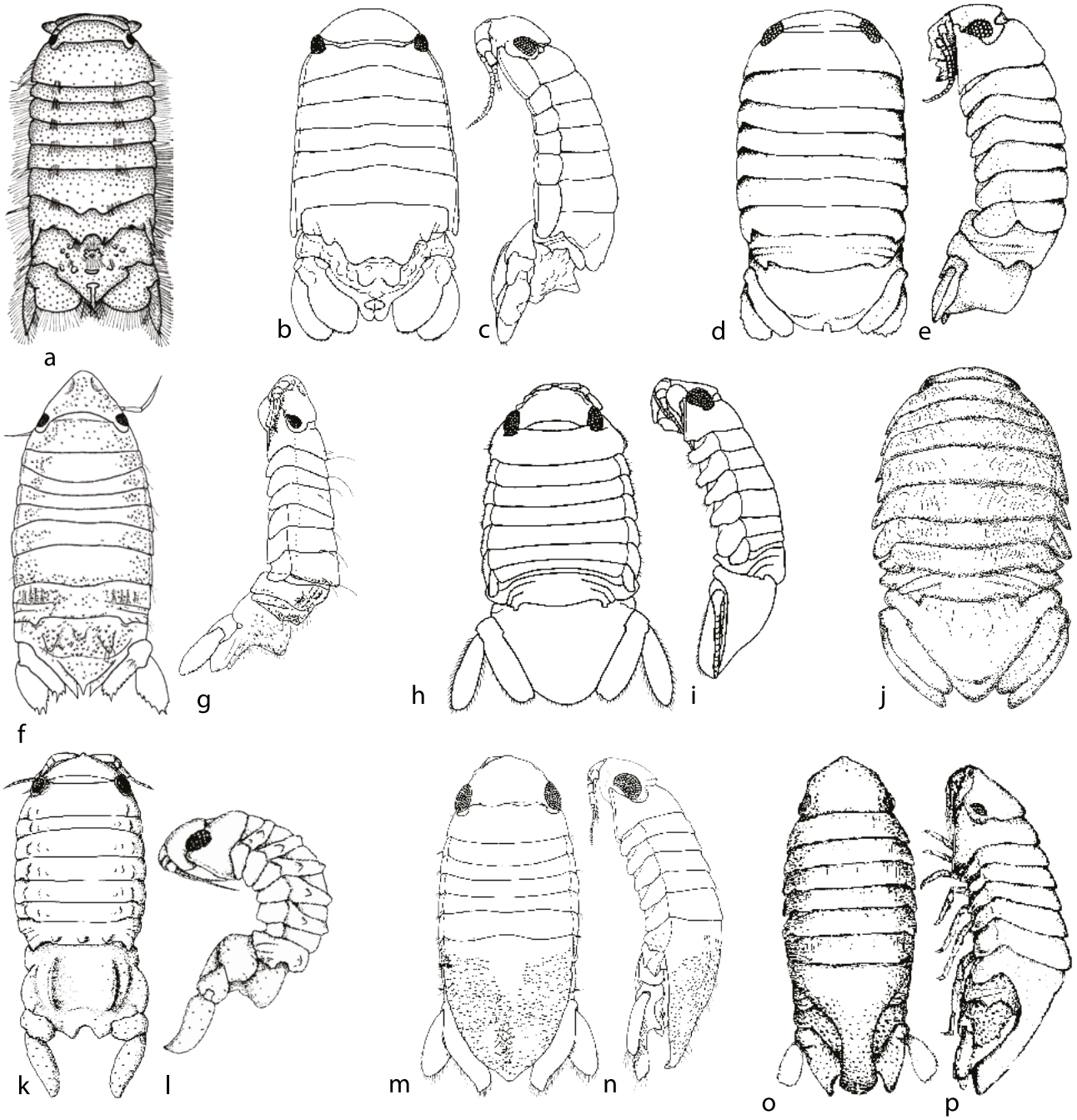


Figure 9.12. Sphaeromatidae. Dorsal and lateral views. a, *Dynamenoides vulcanata* Hurley and Jansen, 1977; b, c, *Dynamenopsis obtusa* Baker, 1908; d, e, *Eterocerceis somala* Messana, 1990; f, g, *Exocerceis nasuta* (Whitelegge, 1902); h, i, *Exosphaeroides fluvialis* Holdich and Harrison, 1983; j, *Exosphaeroma gigas* (Leach 1818); k, l, *Geocerceis barbarae* Menzies and Glynn, 1968; m, n, *Haswellia carnea* (Haswell, 1881); o, p, *Haswellia intermedia* Baker, 1926.

transverse ridges, with 2 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod broadly rounded distally; exopod with 2 or 3 distal teeth.

Intertidal, subtidal. Tropical East Africa (Kenya) and India (Dutta et al., 2019). 1 species (Müller, 1995).

Agostodina Bruce, 1994

Diagnosis. Body flat, coxae without visible sutures, directed laterally, dorsal surfaces smooth, coxal and other margins with fringe of short setae, unable to conglobate; not or weakly sexually dimorphic. Rostrum truncate, separating antennular

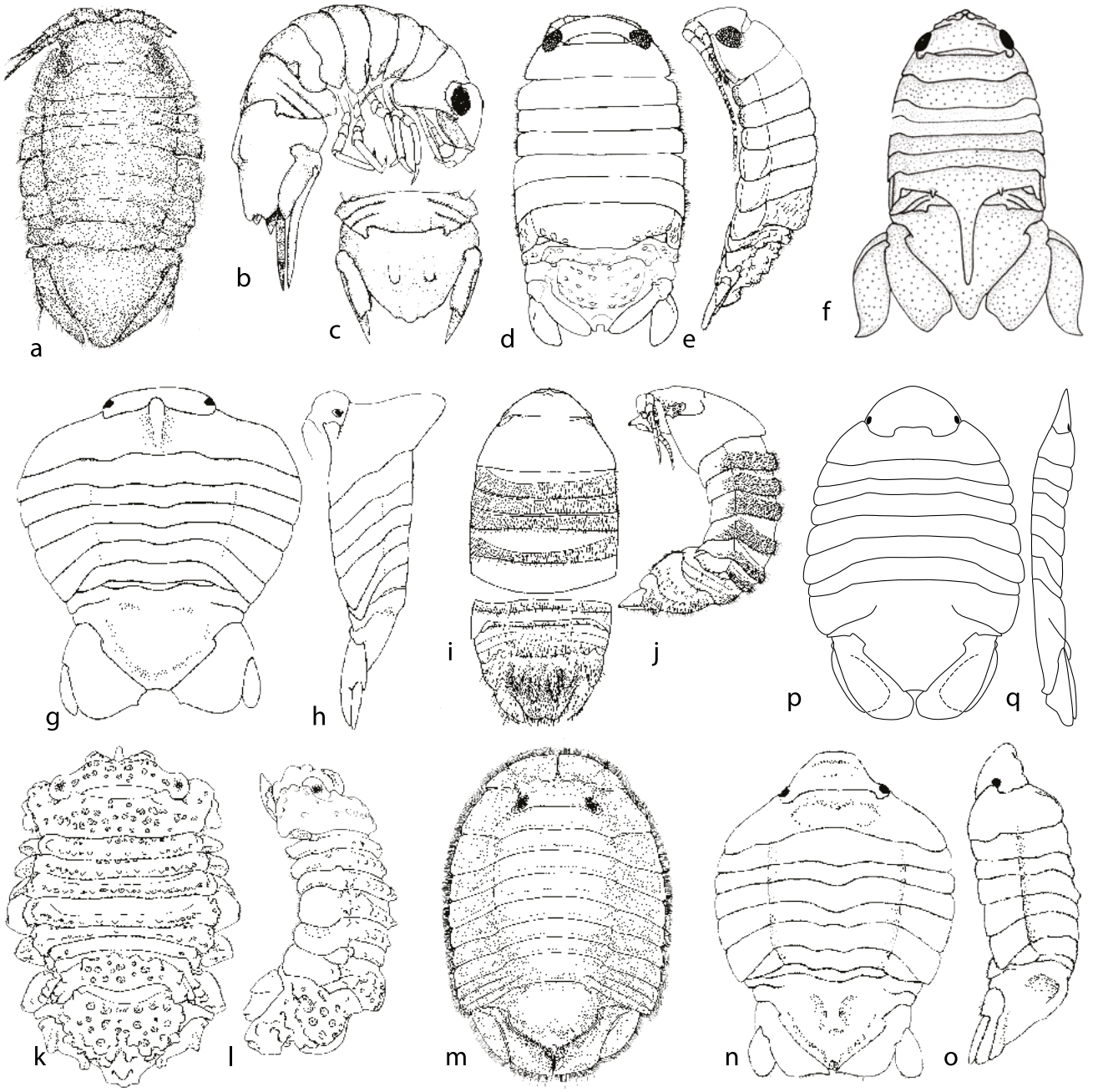


Figure 9.13. Sphaeromatidae. Dorsal and lateral views. a, *Heterodina qeshmensis* Khalaji-Pirbalouty and Bruce, 2014; b, c, *Heteruropus faxoni* (Richardson, 1905); d, e, *Ischyromene polytyla* Harrison and Holdich, 1982; f, *Isocladus armatus* (H. Milne Edwards, 1840); g, h, *Juletta miranda* Bruce, 1993; i, j, *Koremasphaera colonus* Bruce, 2003; k, l, *Kranosphaera haptomela* Bruce, 1992; m, *Leptosphaeroma gottschei* Hilgendorf, 1885; n, o, *Margueritta sylviae* Bruce, 1993; p, q, *Maricoccus brucei* Poore, 1994.

bases (with epistome). Eyes more dorsal than lateral. Coxal plates truncate. Pleonite 1 fused medially to pleonite 2, narrower than remainder of pleon, not extending to pleon lateral margins; pleon with 1 partial suture visible on fused part. Pleotelson flat, narrower anteriorly than pleon; posterior margin simple, arcuate, without exit channel; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 flat, expanded as anterior and/or anterolateral lobes, with first articles separated by prominent epistome; article 1 produced anteriorly; article 2 with distinct anterodistal lobe; article 3 much shorter than article 2; flagellum shorter than peduncle. Epistome extended prominently anteriorly and elongate, wide anteriorly. Mandibular

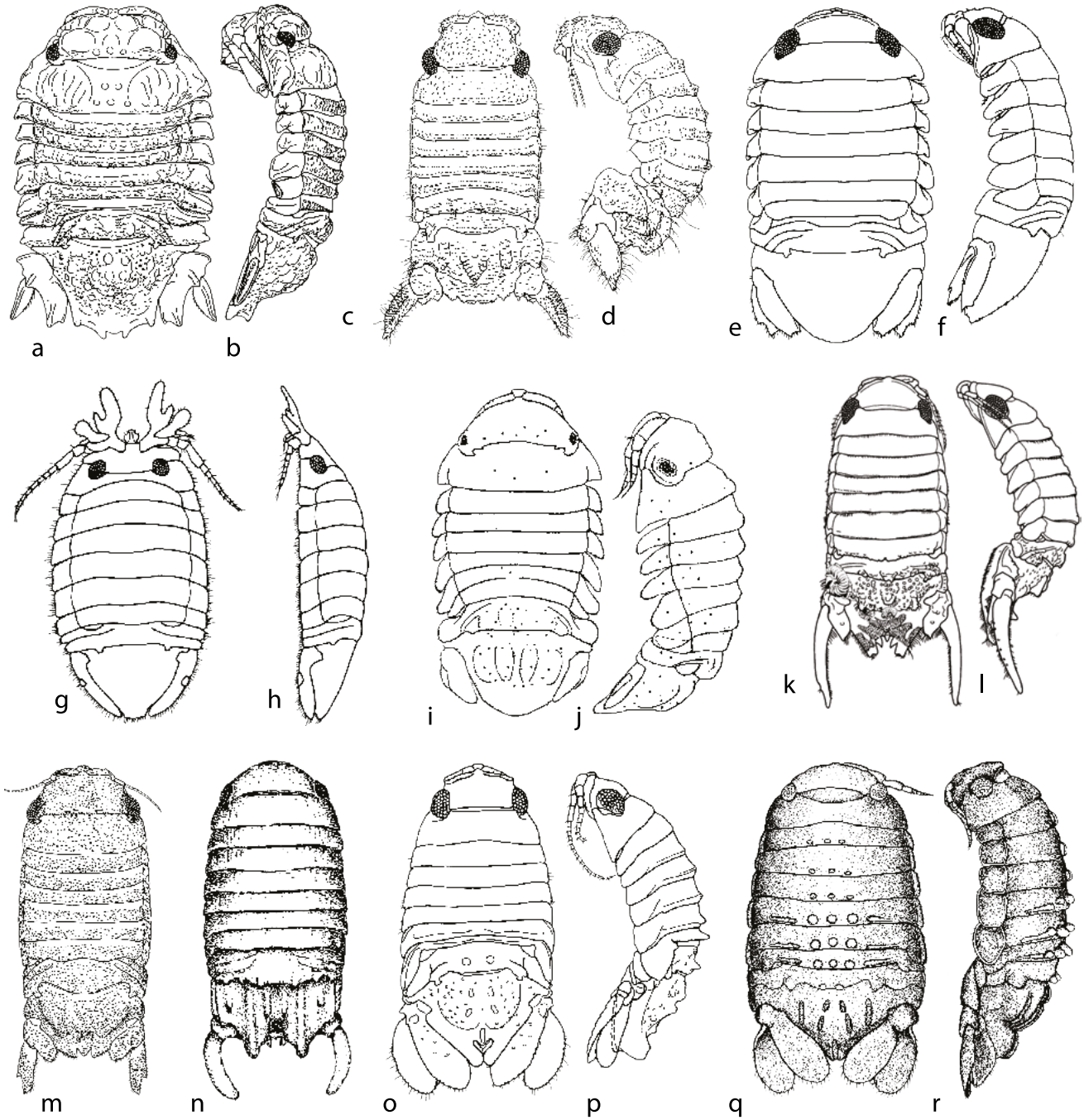


Figure 9.14. Sphaeromatidae. Dorsal and lateral views. a, b, *Moruloidea lacertosa* Baker, 1908; c, d, *Neonaesa rugosa* Harrison and Holdich, 1982; e, f, *Neosphaeroma australe* (Whitelegge, 1902); g, h, *Paracassidina pectinata* Baker, 1911; i, j, *Paracassidinopsis sculpta* Nobili, 1906; k, l, *Paracerceis sculpta* (Holmes, 1904); m, n, *Paracilicaea pubescens* (H. Milne Edwards, 1840); o, p, *Paradella dianae* (Menzies, 1962); q, r, *Paraimene tuberculata* Javed and Ahmed, 1988.

molar process surface smooth with palisade of spines on proximal margin. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 expanded. Pereopod with elongate propodus. Penial processes set apart basally, short (not extending beyond pleopod peduncles), straight. Pleopod 2 appendix masculina spatulate terminally. Pleopod 4 exopod without transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod with incomplete transverse suture, without thickened transverse ridges, with 3 discrete scale patches; endopod without thickened transverse

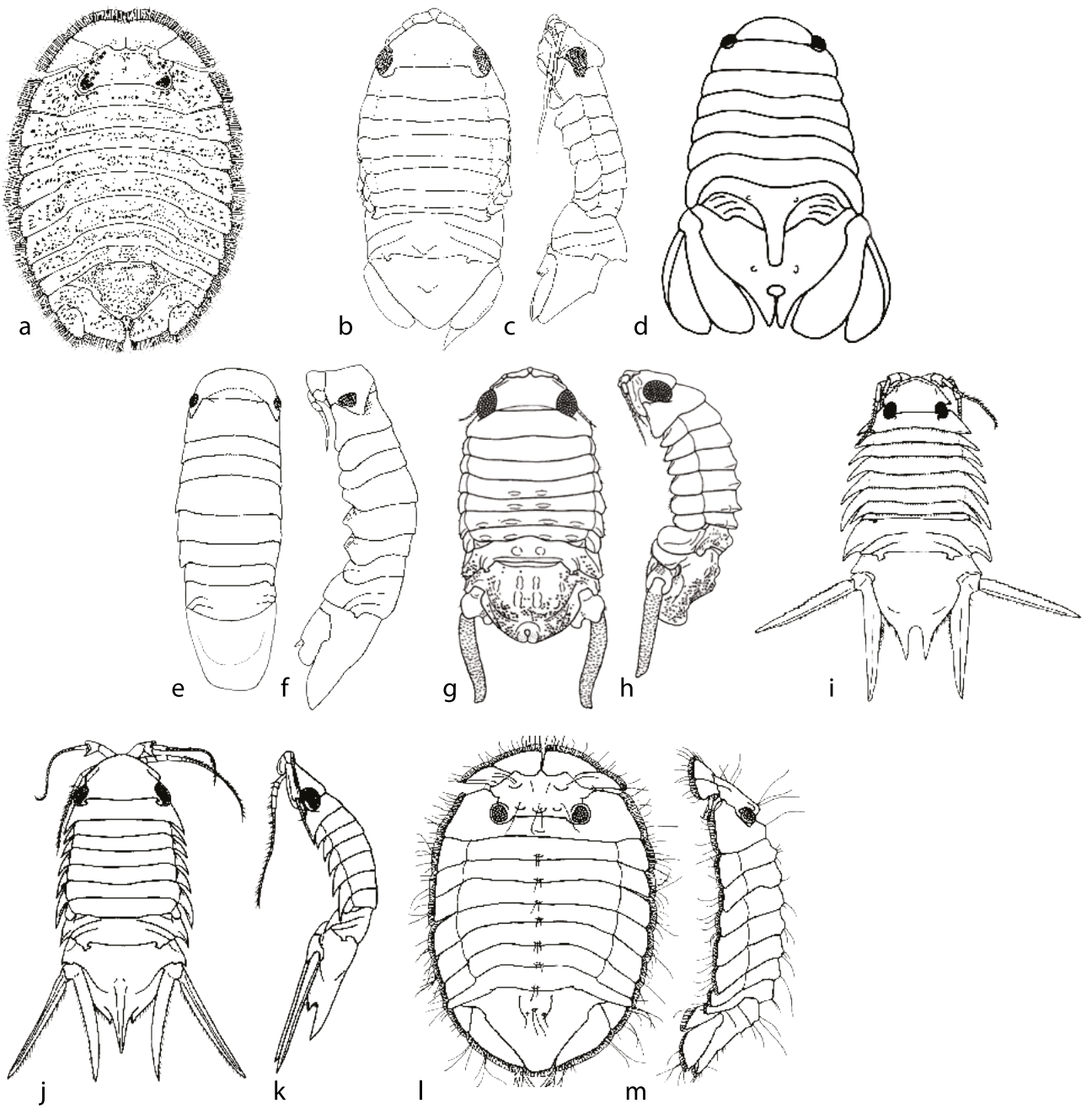


Figure 9.15. Sphaeromatidae. Dorsal and lateral views. a, *Paraleptosphaeroma glynni* Buss and Iverson, 1981; b, c, *Parasphaeroma prominens* Stebbing, 1902; d, *Parisocladus perforatus* (H. Milne Edwards, 1840); e, f, *Pedinura flindersia* Bruce, 2003; g, h, *Pistorius bidens* Harrison and Holdich, 1982; i, *Platycerceis hyalina* Baker, 1926; j, k, *Platynympha longicaudata* (Baker, 1908); l, m, *Platysphaera membranata* Holdich and Harrison, 1981.

ridges. Uropodal rami forming part of continuous body outline; uropodal endopod rounded broadly distally; exopod inserted near midpoint of lateral margin of peduncle-endopod, reduced, mobile, rounded broadly distally.

Shelf. Central Indo-Pacific (Australian NW shelf). 2 species (Bruce, 1994c).

Amphoroidea H. Milne Edwards, 1840

Diagnosis. Body vaulted weakly, dorsal surfaces smooth, unable to conglobate; not or weakly sexually dimorphic. Rostrum acute, not separating antennular bases. Coxal plates truncate. Pleonite 1 narrower than remainder of pleon, not extending to pleon lateral margins. Pleotelson flat; posterior

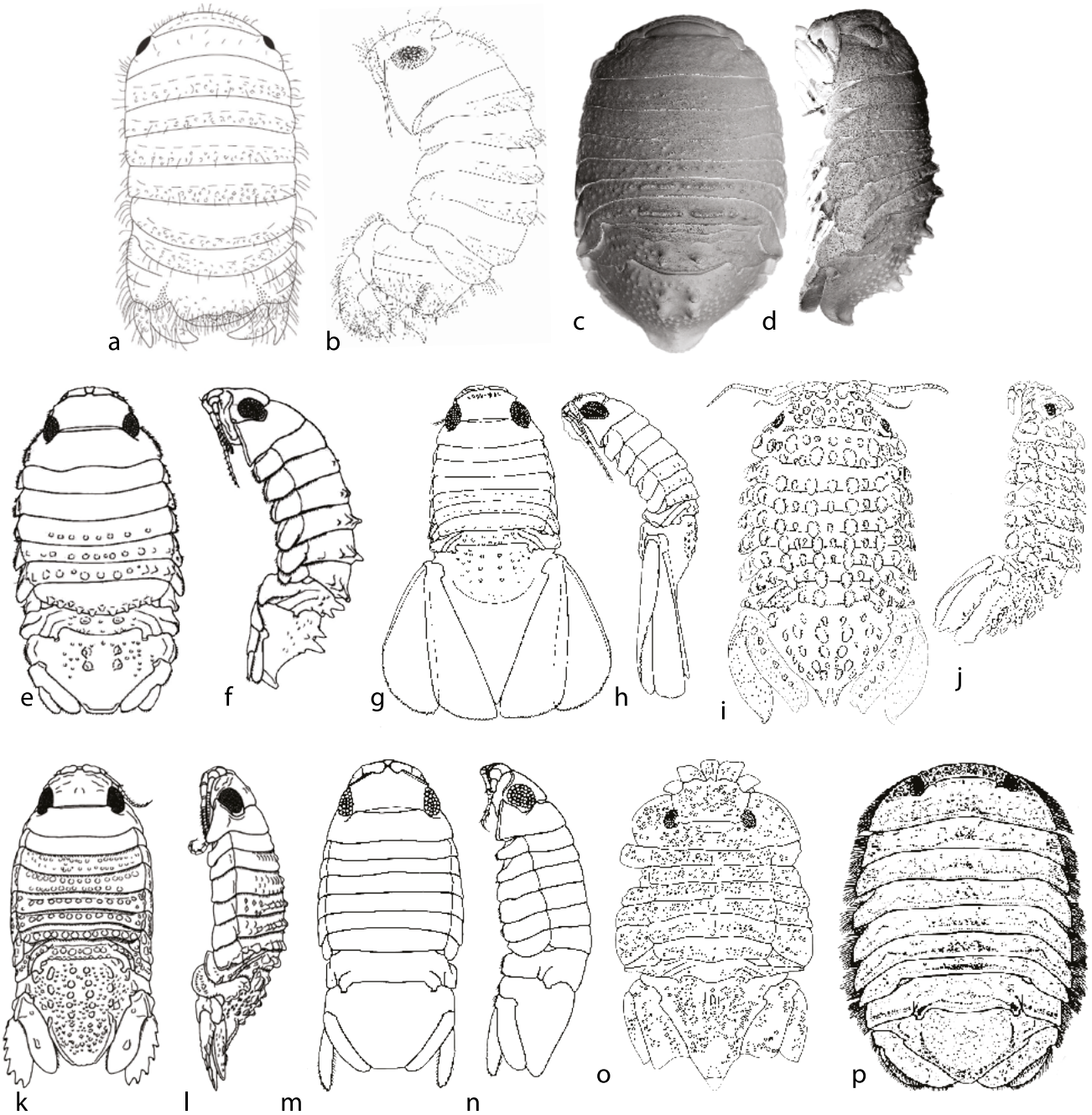


Figure 9.16. Sphaeromatidae. Dorsal and lateral views. a, b, *Pooredoce garyi* Bruce, 2009; c–f, *Pseudosphaeroma* sp.; g, h, *Ptyosphaera alata* (Baker, 1926); i, j, *Sphaeramene flausinae* Loyola e Silva, 1966; k, l, *Sphaeroma walkeri* Stebbing, 1905; m, n, *Sphaeromopsis amathitis* Holdich and Jones, 1973; o, *Stathmos coronatus* Barnard, 1940; p, *Striella balani* Glynn, 1968.

margin with shallow median indentation, with incomplete ventral groove or channel or with small triangular (widest posteriorly) notch; ventrolateral margins simple. Antennular peduncle article 1 expanded anteriorly as part of anterior margin, with first articles meeting medially; article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Epistome wide anteriorly. Mandibular molar process surface with transverse ridges or smooth, surrounded with basal fine setae. Maxillipedal palp articles 2–4 mesial margins not lobate, article 2 not expanded. Pereopod 2 more slender and longer than pereopods 1 and 3. Penial processes in contact basally, short (not extending beyond pleopod peduncles), straight. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, with thickened transverse ridges;

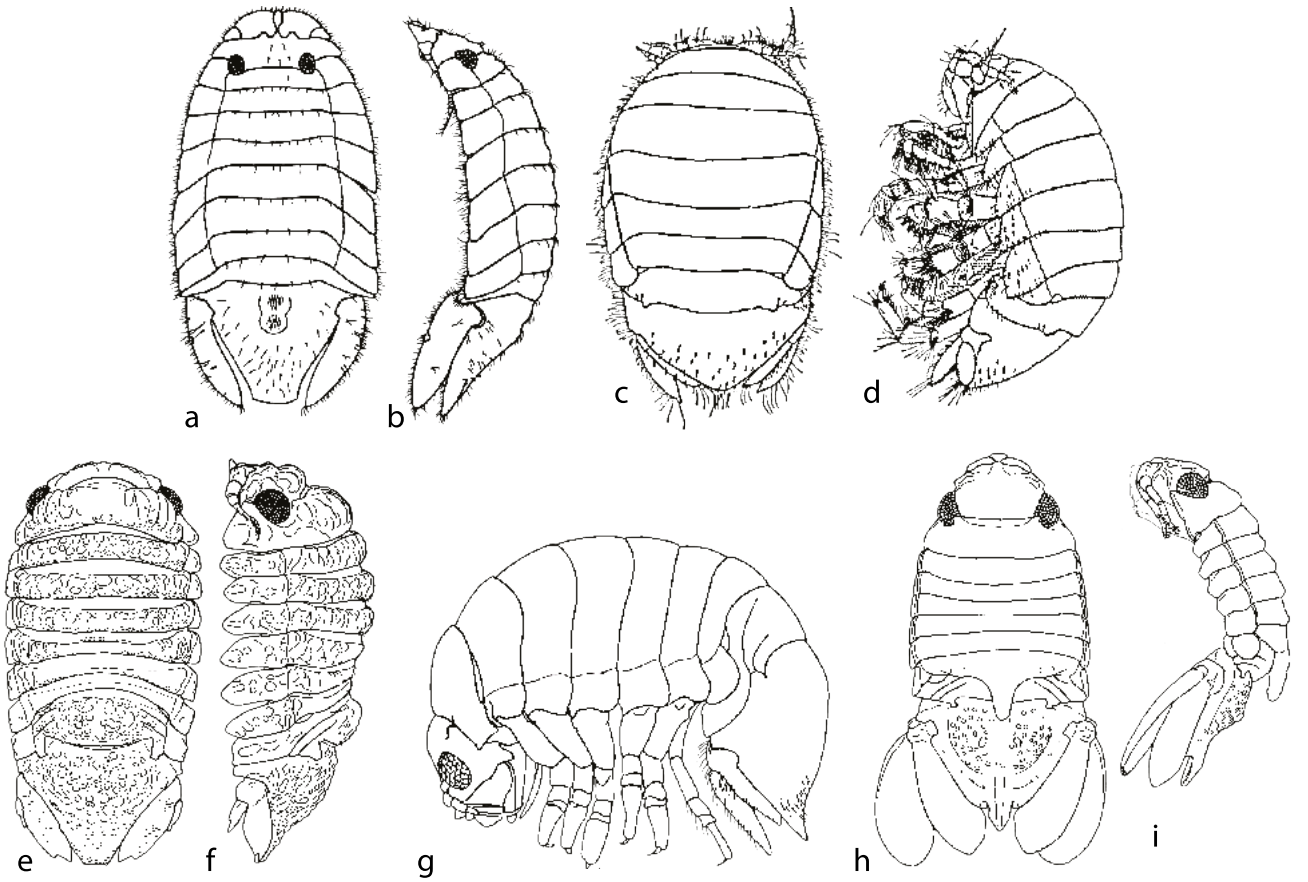


Figure 9.17. Sphaeromatidae. Dorsal and lateral views. a, b, *Syncassidina aestuaria* Baker, 1928; c, d, *Tholozodium ocellatum* Eleftheriou, Holdich and Harrison, 1980; e, f, *Waiteolana gibbera* Harrison, 1984; g, *Xynosphaera colemani* Bruce, 1994; h, i, *Zuzara curtispina* Harrison and Holdich, 1984.

endopod with thickened transverse ridges. Pleopod 5 exopod without transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod truncate distally; exopod acute distally.

Intertidal, subtidal. Temperate South America, Temperate Australasia (Australia, New Zealand, Chile). 7 species (Baker, 1911: figure of *Amphoroidea elegans* Baker, 1911; Hale, 1929: key to 2 Australian species; Menzies, 1962: rediagnosis, figure of type species; Hurley and Jansen, 1977: rediagnosis, key to 3 New Zealand species).

Amphoroidella Baker, 1908

Diagnosis. Body weakly vaulted, dorsal surfaces smooth, unable to conglobate; not or weakly sexually dimorphic. Rostrum not separating antennular bases. Eyes more dorsal than lateral. Coxal plates truncate. Pleon with 1 partial suture visible on fused part. Pleotelson flat; posterior margin simple, arcuate, without exit channel. Antennular peduncle articles 1 and 2 flat, expanded as anterior and/or anterolateral lobes, with first articles meeting medially; article 3 as long as or shorter than article 2. Epistome wide anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate. Pleopod 2 appendix masculina inserted basally or sub-basally. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, with thickened transverse ridges, with 2 discrete scale patches; endopod with thickened transverse ridges. Uropodal rami forming part of continuous body outline; endopod distally acute; exopod embedded and flush with margin of endopod.

Intertidal, subtidal. Temperate Australia. 1 species (Baker, 1908; Harrison, 1984b: rediagnosis).

Apemosphaera Bruce, 1994

Diagnosis. Body flat, coxae without visible sutures, directed laterally, dorsal surfaces smooth, unable to conglobate. Head with rostrum (small) visible dorsally, not separating antennular bases. Eyes more dorsal than lateral. Coxal plates truncate, coxal plate 5 overlapping coxal plates 4 and 6 when folded. Pleonite 1 fused medially to pleonite 2, narrower than remainder of pleon, not extending to pleon lateral margins; sutures (except

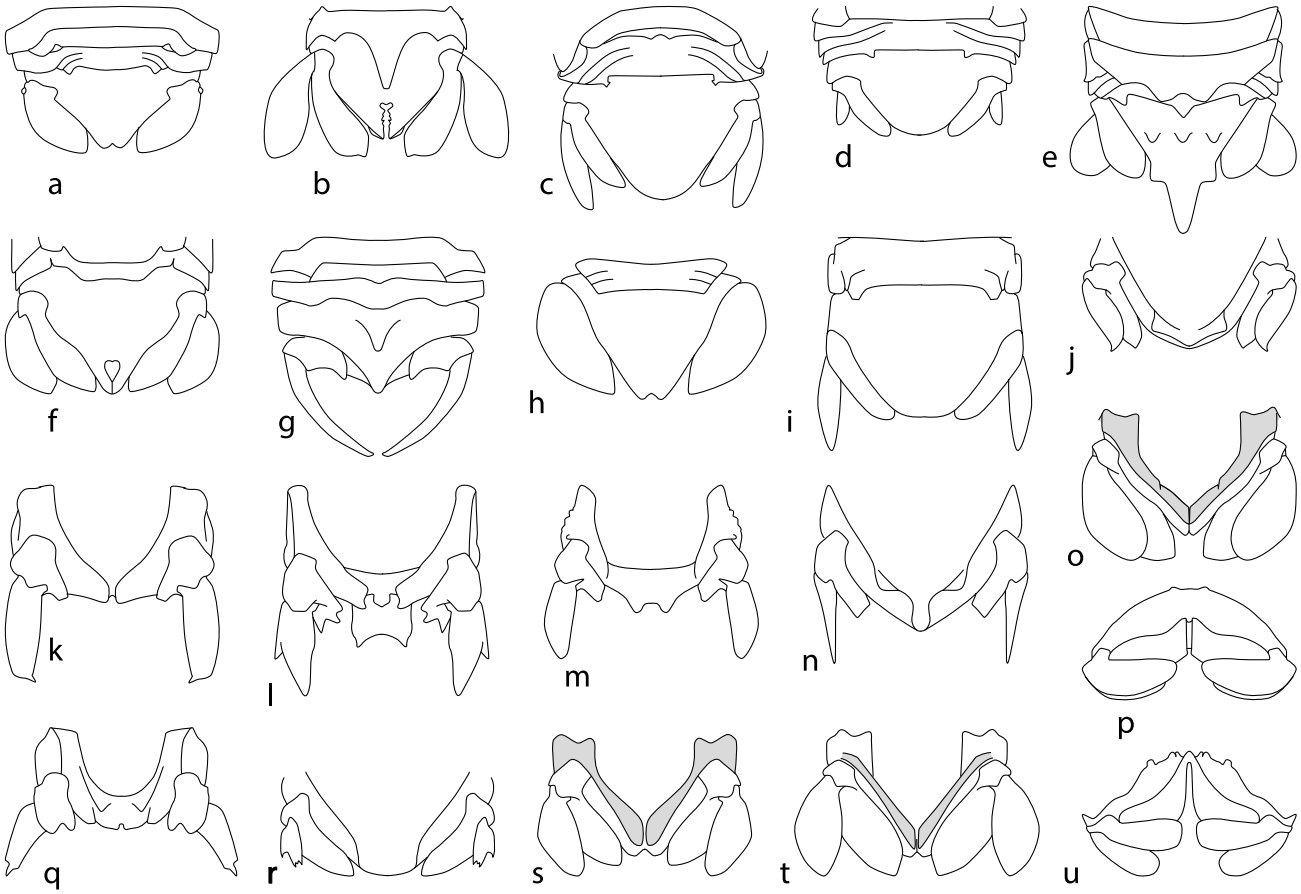


Figure 9.18. Sphaeromatidae. Pleon, pleotelson, uropods (dorsal views). a, *Artopoles* (with pereonites 6, 7); b, *Dynoides*; c, *Exosphaeroma* (with pereonite 7, pleonite 1 visible); d, *Gnorimosphaeroma*; e, *Holotelson* (with pereonites 6, 7); f, *Ischyromene*; g, *Naesicopea* (with pereonite 7); h, *Scutuloidea*; i, *Sphaeromopsis*. Pleotelson, uropods (ventral views). j, *Benthosphaera*; k, *Cassidias*; l, *Cilicaea*; m, *Cilicaeopsis*; n, *Cymodopsis*; o, p, *Dynamenella* (plus posterior view); q, *Neonaesa*; r, *Neosphaeroma*; s, t, *Paradella* (2 spp.). Pleotelson, uropods (posterior view). u, *Paraimene*.

first) running to posterior or posterolateral margin. Pleotelson flat, narrower anteriorly than pleon; posterior margin simple, arcuate, without exit channel; ventrolateral margins simple. Antennular peduncle articles articles 1, 2 robust, article 3 slender, longer than article 2; flagellum about as long as peduncle. Epistome extended prominently anteriorly and elongate, wide anteriorly. Mandibular molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes in contact basally, short (not extending beyond pleopod peduncles). Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges (4 very weak). Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 2 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod acute distally; exopod reduced, mobile, broadly rounded distally.

Estuarine. Central Indo-Pacific (NT, Australia). 1 species (Bruce, 1994c).

Artopoles Barnard, 1920

Diagnosis. Body flat, coxae without visible sutures, directed laterally, dorsal surfaces smooth, coxal and other margins with fringe of short setae, unable to conglobate. Head with rostrum visible dorsally or without rostrum, not separating antennular bases. Eyes more dorsal than lateral. Pereonite 7 narrower than pereonite 6, coxa 6 in contact with pleon. Coxal plates truncate. Pleonite 1 fused medially to pleonite 2, narrower than remainder of pleon, not extending to pleon lateral margins. Pleotelson flat; posterior margin narrowed posteriorly, without exit channel or with small triangular (widest posteriorly) notch; ventrolateral margins simple. Antennular peduncle articles 1 and 2 robust, flattened strongly (compressed dorsoventrally but not part of anterior margin), article 3 slender; article 1 with lower distal angle produced; article 2 with distinct anterodistal lobe; article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Epistome projecting anteriorly, not conspicuous dorsally, narrow anteriorly. Mandibular molar

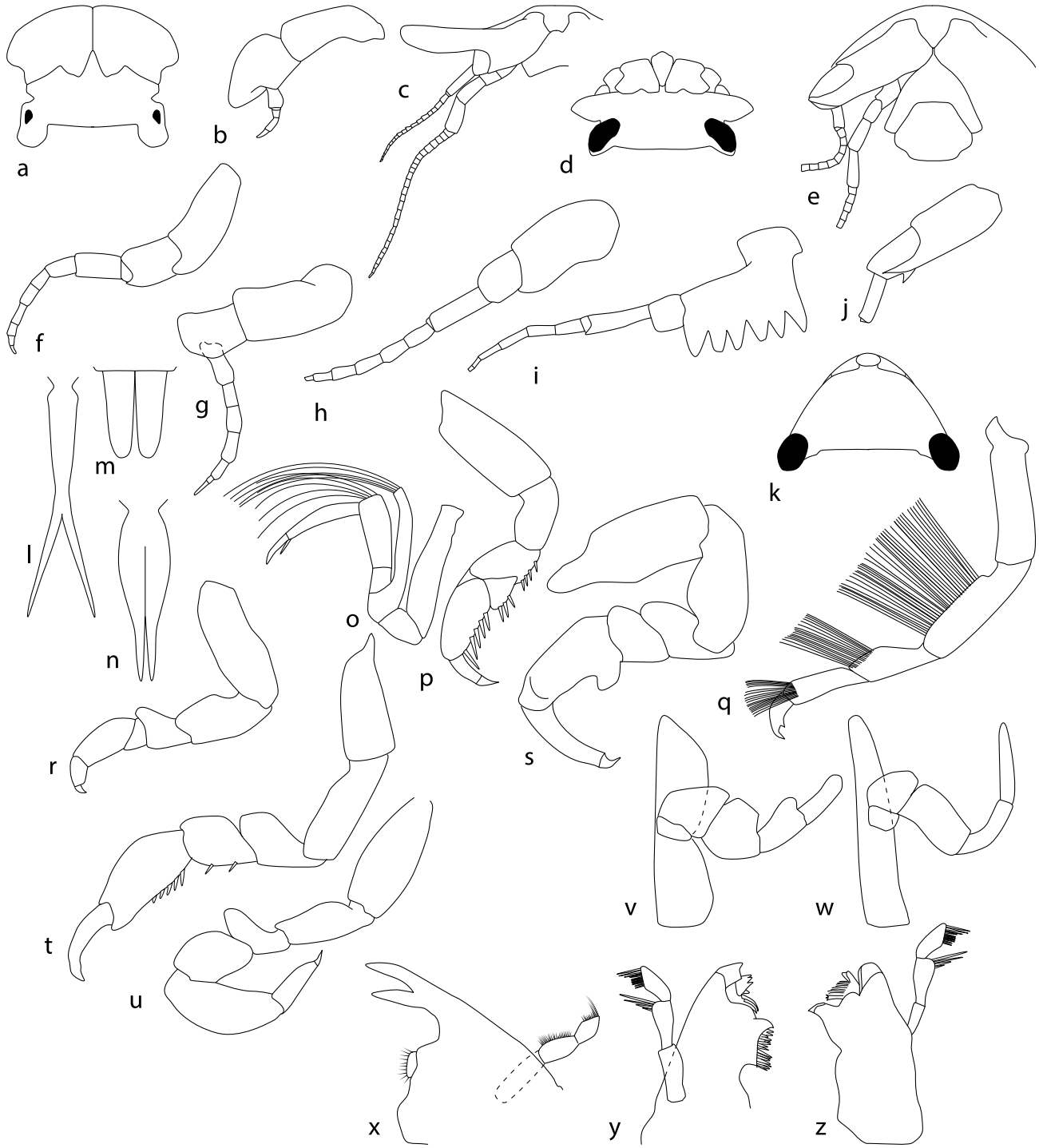


Figure 9.19. Sphaeromatidae. Antennula. a, *Amphoroidea* (articles 1, with head, dorsal view); b, *Austrasphaera*; c, *Calcipila* (male, with antenna, ventral view); d, *Cassidina* (with epistome, head, dorsal view); e, *Cerceis* (with antenna, rostrum, epistome, ventral view); f, *Cymodocella*; g, *Diclidocella*; h, *Exocerceis*; i, *Oxinasphaera*; j, *Platynympha*; k, *Pseudocerceis* (with head, rostrum, epistome, dorsal view). Penial processes. l, *Cliamenella*; m, *Ischyromene*; n, *Sphaeromopsis*. Pereopod 1. o, *Paracassidina*; p, *Parasphaeroma*; q, *Sphaeroma*; r, *Sphaeromopsis*. Pereopod 2. s, *Juletta*; t, *Parasphaeroma*. Pereopod 5. u, *Kranosphaera*. Maxilliped (setae not shown). v, *Lekanesphaera*; w, *Sphaeroma*. Mandible. x, *Hemisphaeroma*; y, *Pooredoce*; z, *Waiteolana*.

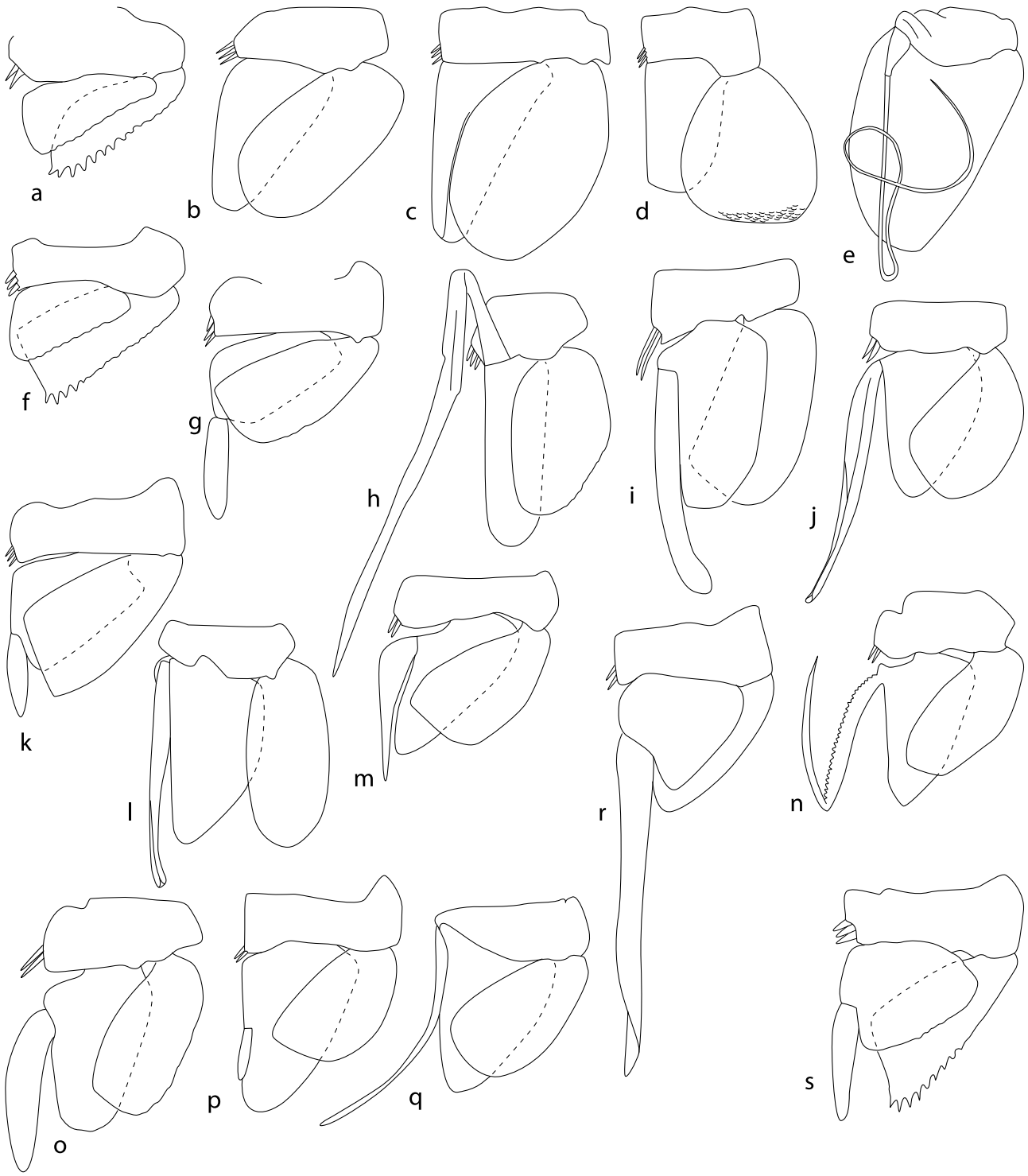


Figure 9.20. Sphaeromatidae. Pleopod 1 (marginal setae not shown). a, *Afrocerceis*; b, *Gnorimosphaeroma*; c, *Ischyromene*; d, *Maricoccus*; e, *Paracassidinopsis*; f, *Pseudocerceis*; Male pleopod 2 with appendix masculina (marginal setae not shown) g, *Cassidias*; h, *Cassidinidea*; i, *Chitonosphaera*; j, *Cliamenella*; k, *Discerceis*; l, *Discidina*; m, *Dynamenella*; n, *Dynoides*; o, *Heterodina*; p, *Neonaesa*; q, *Paradella*; r, *Platycerceis*; s, *Pseudocerceis*.

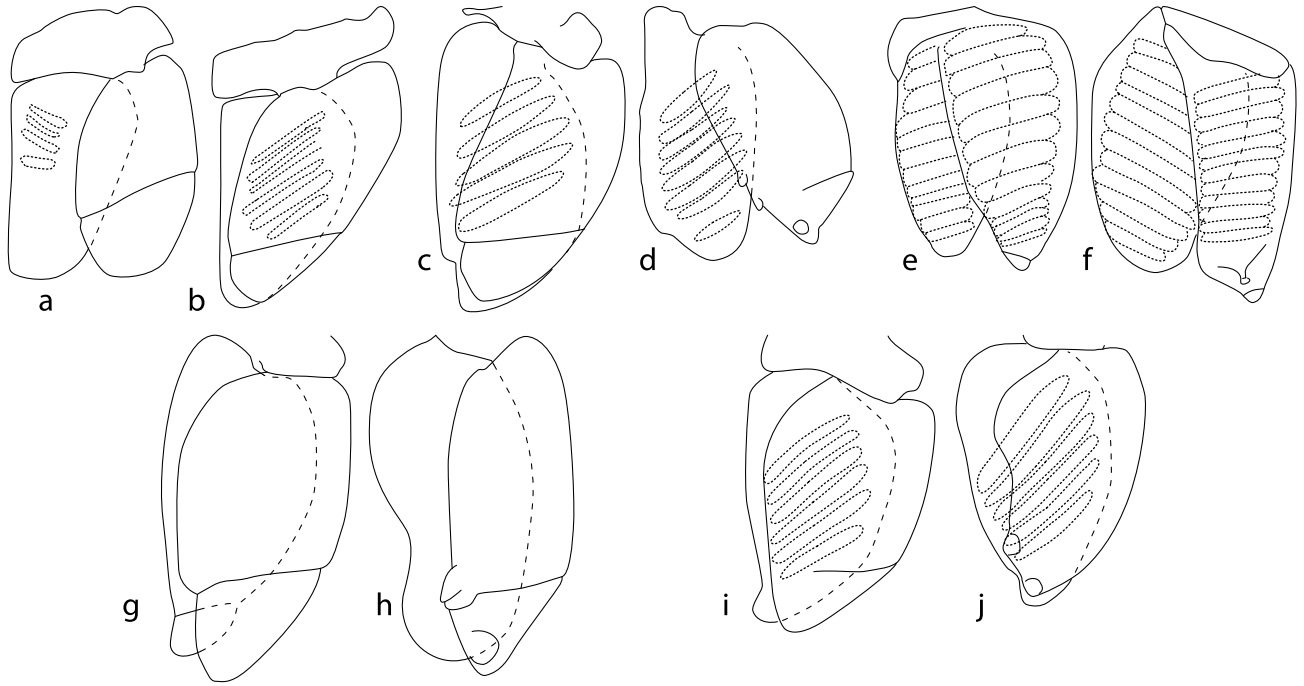


Figure 9.21. Sphaeromatidae. Pleopod 3 (marginal setae not shown). a, *Gnorimosphaeroma*; b, *Neosphaeroma*. Pleopods 4, 5 (marginal setae not shown). c, d, *Benthosphaera*; e, f, *Dynamene*; g, h, *Exosphaeroides*; i, j, *Exosphaeroma*.

process surface smooth, surrounded with basal fine setae. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 expanded. Pereopod 1 lower margin swollen. Penial processes close-set basally. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges, or with obsolete transverse ridges. Pleopod 5 exopod with transverse suture, with thickened transverse ridges, with 2 discrete scale patches; endopod with thickened transverse ridges, or with obsolete transverse ridges. Uropodal endopod broadly rounded or acute distally; exopod minute, immobile.

Shelf. Temperate Southern Africa. 2 species (Bruce, 2001).

Austrasphaera Bruce, 2003

Diagnosis. Body vaulted, narrow, 3–4 times as long as wide, dorsal surfaces smooth, unable to conglobate; not or weakly sexually dimorphic. Rostrum not separating antennular bases; head with anterior margin produced, overriding antennules, such that antennules are directed posteroventrally. Coxal plates tapering, rounded or coxal plates truncate. Pleon with all pleonites fused to pleotelson; sutures absent. Pleotelson posterior margin simple, arcuate, without exit channel or with incomplete ventral groove or channel; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, articles 1 and 2 flattened strongly (compressed dorsoventrally but not part of anterior margin); article 2 about as long as article 1, extended distally so that article 3 articulates on posterior margin; with article 3 offset posteriorly, article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Epistome narrow anteriorly. Mandibular incisor unicuspid; molar process surface smooth, surrounded with basal fine setae. Maxillipedal palp articles 2–4 mesial margins not lobate, article 2 not expanded. Pereopod 1 with elongate propodus. Penial processes set apart basally, short (not extending beyond pleopod peduncles). Pleopod 1 rami operculate, mesial margin of endopod and exopod indurate. Pleopod 2 appendix masculina massive, spatulate. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod distally broadly rounded ; exopod reduced, mobile, broadly rounded distally.

Subtidal (2–23 m). Temperate Australia. 2 species (Bruce, 2003).

Beatricesphaera Wetzer and Bruce, 1999

Diagnosis. Body vaulted weakly, dorsal surfaces smooth, with sparse setae, coxal and other margins with membrana cingula (membranous setose fringe), unable to conglobate; not or weakly sexually dimorphic. Head without rostrum, antennular bases not separated. Eyes more dorsal than lateral. Pereonite 7 narrower than pereonite 6, coxa not reaching as ventrally as coxa 6. Coxal plates truncate. Pleon comprising a single unit; sutures absent. Pleotelson with subapical circular foramen connected to posterior by narrow slit (female entire); ventrolateral margins simple. Antennular peduncle articles 1

and 2 flat, expanded as anterior and/or anterolateral lobes, with first articles meeting medially; article 3 as long as or shorter than article 2; flagellum shorter than peduncle, shorter than peduncular article 3. Epistome wide anteriorly. Mandibular incisor unicuspid; molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins not lobate, article 2 not expanded. Pereopod 2 more slender and longer than pereopods 1 and 3. Penial processes in contact basally, short (not extending beyond pleopod peduncles). Pleopod 2 appendix masculina tapering to point. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod with incomplete transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod without transverse suture, with thickened transverse ridges (weak and irregular), with 2 discrete scale patches; endopod without thickened transverse ridges. Uropodal rami forming part of continuous body outline; uropodal endopod broadly rounded distally; exopod reduced, mobile, broadly rounded distally.

Subtidal. Tropical Atlantic (Caribbean). 1 species (Wetzer and Bruce, 1999).

Botryias Richardson, 1910

Diagnosis. Body vaulted weakly, dorsal surfaces ornamented with small mushroom-headed tubercles each topped with a cluster of stemmed spheres, unable to conglobate. Head without rostrum. Eyes absent. Pereonite 7 narrower than pereonite 6, coxa not reaching as ventrally as coxa 6, without dorsal bosses, processes or marginal extensions. Coxal plates truncate, coxal plates 2–7 not overlapping. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins; pleon with 1 partial suture visible on fused part; dorsal surface tuberculate. Pleotelson tuberculate; posterior margin simple, arcuate, without exit channel; ventrolateral margins simple. Antennular peduncle articles 1 and 2 robust, article 3 slender; longer than article 2; flagellum shorter than peduncle. Epistome extended prominently anteriorly and bifid, wide anteriorly. Mandibular incisor unicuspid. Penial processes in contact basally, short (not extending beyond pleopod peduncles), straight. Uropodal endopod broadly rounded distally; exopod similar in length to endopod, broadly rounded distally.

Slope (330 m). Central Indo-Pacific (Philippines). 1 species (Richardson, 1910; Wetzer et al., 2018).

Bregmotypta Bruce, 1994

Diagnosis. Body dorsal surfaces with nodular ornamentation, unable to conglobate. Head with anterior margin produced into a substantial rounded cone about one third body length. Pereonite 6 with bosses. Pereonite 7 with dorsal bosses. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins. Pleotelson with paired submedial bosses; posterior margin with ventral thickened rim, with simple rectangular or rounded notch; ventrolateral margins simple. Antennular peduncle articles 1 and 2 robust, article 3 slender; longer than article 2; flagellum shorter than peduncle. Epistome narrow anteriorly. Mandibular incisor unicuspid; molar process surface smooth, surrounded with basal fine setae. Maxillipedal palp articles 2–4 mesial margins extended, forming finger-like lobes, article 2 not expanded. Penial processes in contact basally, long (extending to pleopod rami). Pleopod 2 appendix masculina swollen basally (flask-shaped). Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropod attached anterolaterally to pleotelson, cylindrical (not especially flattened); peduncle-endopod round in section, truncate distally; exopod cylindrical, reduced, mobile, truncate distally.

Subtidal (23 m). Temperate SE Australia. 1 species (Bruce, 1994a).

Benthosphaera Bruce, 1994

Diagnosis. Body dorsal surfaces smooth, without setae or densely setose, able to conglobate; not or weakly sexually dimorphic. Pereonite 7 narrower than pereonite 6, coxa not reaching as ventrally as coxa 6. Pleonite 1 narrower than remainder of pleon, not extending to pleon lateral margins. Pleotelson posterior margin simple, arcuate, without exit channel; ventrolateral margins simple. Antennular peduncle articles 1 and 2 robust, article 3 slender; article 3 longer than article 2; flagellum shorter than peduncle. Epistome projecting anteriorly, not conspicuous dorsally, wide anteriorly. Mandibular molar process surface smooth, surrounded with basal fine setae. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes in contact basally, long (extending to pleopod rami). Pleopod 2 appendix masculina narrowed abruptly distally. Pleopod 3 endopod with transverse ridges. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with weakly thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 3 discrete scale patches or with 4 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod truncate distally or broadly rounded or acute; exopod falcate distally.

Shelf, slope (150–1117 m). Central Indo-Pacific, Temperate E and NE Australia. 3 species (Bruce, 1994a: diagnosis, key to 4 species).

Calcipila Harrison and Holdich, 1984

Diagnosis. Body dorsal surfaces granular, unable to conglobate; adult female unknown. Head with anterior margin very steep. Pleon with 1 partial suture visible on fused part. Pleotelson tuberculate; with submedian tubercles and weak median tooth between; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender; article 1 of male with anterodistal angle extended as long, narrow, flat lobe longer than remaining antennular peduncle (incipient lobe in female). Maxillipedal palp articles 2–4 mesial margins extended, forming finger-like lobes. Penial processes set apart basally, short (not extending beyond pleopod peduncles).

Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod truncate distally; exopod shorter than endopod, acute distally.

Subtidal. Temperate SE Australia. 1 species (Harrison and Holdich, 1984).

Campecopea Leach, 1814

Diagnosis. Body dorsal surfaces granular, with sparse setae, coxal and other margins with fringe of short setae, able to conglobate; strongly sexually dimorphic. Rostrum not separating antennular bases. Pereonite 6 simple, without bosses, processes or marginal extensions, or with single process directed posteriorly. Pereonite 7 narrower than pereonite 6, coxa not reaching as ventrally as coxa 6. Pleonite 1 entire, free from pleonite 2 or wholly fused to pleonite 2, as wide as remainder of pleon, extending to pleon lateral margins; pleon comprising a single unit; sutures absent. Pleotelson posterior margin with ventral thickened rim, without exit channel and with incomplete ventral groove or channel or with triangular (widest anteriorly) foramen; ventrolateral margins forming ridge. Antennular peduncle article 1 robust, longer and more solid than 2 and 3 combined; article 3 longer than article 2; flagellum about as long as peduncle. Epistome narrow anteriorly. Mandibular molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins lobate (weakly), article 2 not expanded. Penial processes close-set basally, short (not extending beyond pleopod peduncles). Pleopod 4 exopod with incomplete transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod without transverse suture, without thickened transverse ridges, with 3 discrete scale patches; endopod without thickened transverse ridges. Uropod articulating at anterior dorsolateral position; peduncle without endopod; exopod curved laterally, exceeding telson apex, acute distally.

Intertidal. Temperate Northern NE Atlantic. 4 species (Bruce and Holdich, 2002: rediagnosis, key to 4 species).

Cassidias Richardson, 1906

Diagnosis. Body dorsal surfaces granular, with sparse setae, unable to conglobate; strongly sexually dimorphic (female with smaller pleotelsonic ornamentation). Head without rostrum. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins. Pleotelson with prominent median process; posterior margin with ventral thickened rim, with simple rectangular or rounded notch; ventrolateral margins forming ridge. Antennular peduncle article 1 robust, longer and more robust than 2 and 3 combined; article 3 longer than article 2; flagellum about as long as peduncle. Epistome acute anteriorly (with indistinct tubercle in middle). Mandibular molar process surface smooth with palisade of spines on proximal margin. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes set apart basally, short (not extending beyond pleopod peduncles), straight. Pleopod 2 appendix masculina inserted distally, about as long as endopod. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod without transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropod attached posteriorly, at sides of pleotelson posterior margin; peduncle without endopod; exopod cylindrical, longer than endopod, with hard distal terminal spike.

Subtidal, shelf. Central Indo-Pacific, Temperate South America, Temperate Southern Africa (Australia, Argentina, South Africa). 3 species (Bruce, 2003).

Cassidina H. Milne Edwards, 1840

Diagnosis. Body vaulted weakly, dorsal surfaces smooth, unable to conglobate; weakly sexually dimorphic. Rostrum truncate, separating antennular bases (with epistome). Eyes more dorsal than lateral, or lateral. Coxal plates truncate. Pleonite 1 fused medially to pleonite 2, narrower than remainder of pleon, not extending to pleon lateral margins; pleon with 1 partial suture visible on fused part; sutures running to lateral margin. Pleotelson flat; posterior margin simple, arcuate, without exit channel; ventrolateral margins simple. Antennular peduncle articles 1 and 2 flat, expanded as anterior and/or anterolateral lobes, with first articles separated by prominent epistome; article 1 produced anteriorly (longer than wide); article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Epistome extended prominently anteriorly and elongate (shorter than head length), wide anteriorly. Mandibular molar process surface smooth with palisade of spines on proximal margin. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 expanded. Pereopod 1 ambulatory, with elongate propodus. Penial processes set apart basally, short (not extending beyond pleopod peduncles), straight. Pleopod 2 appendix masculina basally about as long as endopod. Pleopod 4 exopod without transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod without transverse suture, without thickened transverse ridges, with 3 discrete scale patches; endopod without thickened transverse ridges. Uropodal rami forming part of continuous body outline; uropodal endopod narrowly rounded distally; exopod inserted near midpoint of lateral margin of peduncle-endopod, reduced, mobile, narrowly rounded distally.

Shelf (18–110 m). Temperate Australasia (New Zealand). 1 species (Bruce, 1994c: rediagnosis).

Cassidinella Whitelegge, 1901

Diagnosis. Body dorsal surfaces smooth, without setae or densely setose, unable to conglobate; not or weakly sexually dimorphic. Head with ventral rostrum. Pereonite 7 narrower than pereonite 6, coxa not reaching as ventrally as coxa 6. Coxal plates ventrally acute, 2–7 not overlapping. Pleonite 1 narrower than remainder of pleon, not extending to pleon lateral margins; dorsal surface with medial dorsal boss. Pleotelson with median dorsal boss or with paired submedial bosses; posterior margin trilobate; ventrolateral margins simple. Antennular peduncle articles 1 and 2 robust, article 3 slender, articles not flattened or articles 1 and 2 flattened strongly (compressed dorsoventrally

but not part of anterior margin); article 2 without anterodistal lobe, or with distinct anterodistal lobe; with articles 2 and 3 colinear or article 3 offset posteriorly, article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Epistome wide anteriorly. Mandibular incisor unicuspid; molar process surface smooth, surrounded with basal fine setae. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes set apart basally, short (not extending beyond pleopod peduncles). Pleopod 2 appendix masculina about as long as endopod. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 4 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod acute distally; exopod reduced, mobile, acute distally.

Shelf (27–204 m). Temperate SE Australia. 2 species (Bruce, 1994b: rediagnosis, key to 2 species).

Cassidinidea Hansen, 1905

Diagnosis. Body flat, coxae without visible sutures, directed laterally, dorsal surfaces smooth or with nodular ornamentation, coxal and other margins with fringe of short setae, unable to conglobate; not or weakly sexually dimorphic. Head without rostrum. Eyes more dorsal than lateral. Coxal plates truncate. Pleonite 1 fused medially to pleonite 2, narrower than remainder of pleon, not extending to pleon lateral margins; fused part of pleon with acute lateral margin; sutures absent. Pleotelson flat; posterior margin simple, arcuate, without exit channel; ventrolateral margins simple. Antennular peduncle article 1 robust, longer and more robust than 2 and 3 combined; article 3 longer than article 2; flagellum shorter than peduncle. Epistome extended prominently anteriorly as flat, anteriorly convex lobe, wide anteriorly. Mandibular molar process surface smooth with palisade of spines on proximal margin. Maxillipedal palp articles 2–4 mesial margins not lobate, article 2 not expanded. Pereopod 1 with elongate propodus. Penial processes fused along most or entire length. Pleopod 2 appendix masculina basally with straight margins. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 2 discrete scale patches; endopod without thickened transverse ridges. Uropodal rami forming part of continuous body outline; endopod acute distally; exopod reduced, mobile, narrowly rounded distally.

Estuarine, marine, intertidal, subtidal. Tropical Atlantic, Western and Central Indo-Pacific, Temperate Southern Africa. 13 species (some doubtful) (Bruce, 1994c: rediagnosis; Schotte and Kensley, 2005: rediagnosis; Khalaji-Pirbalouty and Bruce, 2021: redescription of type species, distribution of New World species, species list).

Cassidinopsis Hansen, 1905

Diagnosis. Body dorsal surfaces smooth, able to conglobate; not or weakly sexually dimorphic. Head without rostrum. Coxal plates truncate. Pleonite 1 narrower than remainder of pleon, not extending to pleon lateral margins. Pleotelson posterior margin simple, arcuate, with incomplete ventral groove or channel. Antennular peduncle article 1 robust, longer and more robust than 2 and 3 combined, with first articles meeting medially; article 3 as long as or shorter than article 2; flagellum about as long as peduncle. Epistome acute anteriorly. Mandibular molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins lobate (scarcely on 4), article 2 not expanded. Pereopod 2 more slender and longer than pereopods 1 and 3. Penial processes in contact basally, short (not extending beyond pleopod peduncles). Pleopod 2 appendix masculina about as long as endopod. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod with transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod without transverse suture, with thickened transverse ridges, with 2 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod obliquely truncate distally, forming concavity with end of telson; exopod inserted near midpoint of lateral margin of peduncle-endopod, reduced, mobile or shorter than endopod, acute distally.

Intertidal–shelf. Temperate Australasia, Southern Ocean. (New Zealand, Subantarctic Australia). 3 species (Brandt, 1998: redescription of female of type species).

Ceratocephalus Woodward, 1877

Diagnosis. Body dorsal surfaces coarsely pitted or granular, unable to conglobate; strongly sexually dimorphic. Head with anterior margin with 2 long, slender, anterolateral processes in male. Pereonite 7 narrower than pereonite 6. Pleotelson posterior margin produced. Antennular peduncle article 1 robust, longer and more robust than 2 and 3 combined. Epistome produced in male as upturned spike over half as long as body, twice length of head anterolateral processes. Maxillipedal palp articles 2–4 mesial margins extended, forming finger-like lobes. Penial processes close-set basally, long (extending to pleopod rami). Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, with thickened transverse ridges, scale patches distally continuous; endopod with thickened transverse ridges. Uropodal endopod oblique distally with subdistal tooth; exopod reduced, mobile, acute distally.

Subtidal. Temperate SE Australia. 1 species (Bruce, 1994b: redescription).

Cerceis H. Milne Edwards, 1840

Diagnosis. Body dorsal surfaces smooth or with nodular ornamentation, with sparse setae, coxal and other margins with fringe of short setae, unable to conglobate; not or weakly sexually dimorphic. Head with ventral rostrum; with anterior margin produced, overriding antennules. Coxal plates tapering, rounded or coxal plates truncate. Pleonite 1 posterior margin with single flush median lobe, as wide as remainder of pleon, extending to pleon lateral margins. Pleotelson weakly bi-domed; with posteriorly produced narrow lobe over excision; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, with first articles meeting medially;

article 1 with produced acute distal angles; article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Epistome acute anteriorly. Mandibular molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes close-set basally, short (not extending beyond pleopod peduncles), straight. Pleopods 1, 2 (sometimes 3) exopods lateral margins serrate, especially distally. Pleopod 2 appendix masculina inserted near midpoint of mesial margin, with straight margins or swollen basally ("flask-shaped"), about as long as endopod or longer than and extending beyond endopod. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod acute distally; exopod falcate distally.

Intertidal–shelf. Temperate Northern Atlantic, Temperate Northern Pacific, Western and Central Indo-Pacific, Temperate Australasia. 16 species (Harrison and Holdich, 1982b: rediagnosis).

Cercosphaera Bruce, 1994

Diagnosis. Body dorsal surfaces with nodular ornamentation; not or weakly sexually dimorphic. Head with anterior margin produced, overriding antennules. Pereonite 7 forming part of body outline (almost as wide). Coxal plates truncate. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins; sutures short; dorsal surface with pair of prominent elongate submedian keels; posterior margin with 2 distinct submedian lobes. Pleotelson with posteriorly directed median process over posterior margin; posterior margin with ventral thickened rim, with posteriorly directed solid tuberculate process; ventrolateral margins forming ridge. Antennular peduncle article 1 robust, longer and more robust than 2 and 3 combined; article 1 anterodistal margin produced; article 3 as long as or shorter than article 2; flagellum about as long as peduncle. Epistome narrow anteriorly. Mandibular incisor unicuspid; molar process surface smooth, surrounded with basal fine setae. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes in contact basally, long (extending to pleopod rami) (folding into groove on mesial margin of pleopod 1 endopod). Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, scale patches distally continuous; endopod with thickened transverse ridges. Uropod attached anterolaterally to pleotelson, cylindrical (not especially flattened); peduncle-endopod lamellar (nodulose), broadly rounded distally (variously notched); exopod reduced, mobile, acute distally.

Subtidal, shelf (1–52 m). Temperate S Australia. 3 species (Bruce, 1994a: diagnosis, key to 3 species).

Chitonopsis Whitelegge, 1902

Diagnosis. Body flat, coxae without visible sutures, directed laterally, dorsal surfaces smooth, coxal and other margins with fringe of short setae, unable to conglobate; not or weakly sexually dimorphic. Rostrum truncate, separating antennular bases (with epistome). Eyes more dorsal than lateral. Coxal plates truncate. Pleonite 1 fused medially to pleonite 2, narrower than remainder of pleon, not extending to pleon lateral margins; pleon with 1 partial suture visible on fused part; sutures running to lateral margin. Pleotelson flat, narrower anteriorly than pleon; posterior margin simple, arcuate, without exit channel; ventrolateral margins simple. Antennular peduncle articles 1 and 2 flat, expanded as anterior and/or anterolateral lobes, with first articles separated by prominent epistome; article 1 produced anteriorly (wider than long); article 2 with distinct anterodistal lobe; article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Epistome extended prominently anteriorly and elongate (longer or subequal to head length), wide anteriorly. Mandibular molar process surface smooth with palisade of spines on proximal margin. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 expanded. Pereopod 1 with elongate propodus. Penial processes in contact basally, short (not extending beyond pleopod peduncles), straight. Pleopod 2 appendix masculina spatulate terminally. Pleopod 4 exopod without transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod without transverse suture, without thickened transverse ridges, with 3 discrete scale patches; endopod without thickened transverse ridges. Uropodal rami forming part of continuous body outline; uropodal endopod narrowly rounded distally; exopod inserted near midpoint of lateral margin of peduncle-endopod, reduced, mobile, narrowly rounded distally.

Estuarine, marine, intertidal–shelf. Central Indo-Pacific, Temperate Australasia. 3 species (Holdich and Harrison, 1981b: rediagnosis, key to 3 Australian species; Bruce, 1994c: rediagnosis, key to 3 species).

Chitonosphaera Kussakin and Malyutina, 1993

Diagnosis. Body vaulted weakly, dorsal surfaces smooth, coxal and other margins with fringe of short setae, unable to conglobate. Rostrum acute, not separating antennular bases. Eyes more dorsal than lateral. Coxal plates truncate. Pleon with 2 partial sutures visible on fused part; first suture reaching lateral margin; second suture reaching posterior margin. Pleotelson posterior margin simple, arcuate, with incomplete ventral groove or channel. Antennular peduncle articles 1 and 2 flat, expanded as anterior and/or anterolateral lobes, with first articles meeting medially; article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Epistome acute anteriorly. Maxillipedal palp articles 2–4 mesial margins not lobate. Pleopod 2 appendix masculina spatulate terminally. Pleopod 3 exopod with incomplete transverse suture. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod without transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Uropodal rami forming part of continuous body outline; endopod narrowly rounded distally; exopod subtriangular, narrowly rounded distally.

Intertidal, subtidal. Temperate Northern W Pacific (Japan, China, Vietnam). 2 species (Kussakin and Malyutina, 1993).

Cilicaea Leach, 1818

Diagnosis. Body dorsal surfaces with nodular ornamentation, with sparse setae, able to conglobate; strongly sexually dimorphic. Coxal plates 2–7 not overlapping. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins; posterior margin with process directed posteriorly. Pleotelson with paired submedial bosses; with rectangular or rounded notch bearing median tooth. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum about as long as peduncle. Epistome wide anteriorly. Mandibular incisor unicuspid. Maxillipedal palp articles 2–4 mesial margins extended, forming finger-like lobes, article 2 not expanded. Penial processes close-set basally, short (not extending beyond pleopod peduncles). Pleopod 2 appendix masculina reflexed, folded back on itself, about twice as long as endopod. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 4 discrete scale patches or with 5 discrete scale patches; endopod with thickened transverse ridges. Uropod attached posteriorly, at sides of pleotelson posterior margin; peduncle endopod reduced, stub-like; exopod cylindrical, longer than endopod, distally with hard terminal spike or narrowly rounded.

Subtidal, shelf. Western and Central Indo-Pacific, Temperate Australasia. 15 accepted species (Harrison and Holdich, 1984: rediagnosis, list of species, some doubtful).

Cilicaeopsis Hansen, 1905

Diagnosis. Body dorsal surfaces with nodular ornamentation or granular, with sparse setae, able to conglobate; strongly sexually dimorphic. Coxal plates 2–7 not overlapping. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins; posterior margin with process directed posteriorly. Pleotelson with paired submedial bosses or tuberculate; with simple rectangular or rounded notch; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum about as long as peduncle. Epistome wide anteriorly. Mandibular incisor unicuspid. Maxillipedal palp articles 2–4 mesial margins extended, forming finger-like lobes, article 2 not expanded. Penial processes fused basally or separate, long (extending to pleopod rami). Pleopod 2 appendix masculina tapering to point. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 4 discrete scale patches; endopod with thickened transverse ridges. Uropod attached posteriorly, at sides of pleotelson posterior margin; peduncle-endopod reduced, stub-like; exopod cylindrical, longer than endopod, rounded narrowly distally.

Subtidal, shelf, slope (1–411 m). Central Indo-Pacific, Temperate Australasia. 13 species, plus many undescribed species (Harrison and Holdich, 1984: rediagnosis, list of species).

Cliamenella Kussakin and Malyutina, 1987

Diagnosis. Body dorsal surfaces smooth, able to conglobate. Pleotelson domed; posterior margin narrowed posteriorly, with subapical foramen connected to apex by narrow slit. Antennular peduncle articles 1–3 of similar stoutness (or tapering); article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Maxillipedal palp articles 2–4 mesial margins not lobate. Penial processes fused along basal half to two thirds of length. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod without transverse suture, without thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod narrowly rounded distally; exopod narrowly rounded distally.

Shelf, bathyal. Temperate Northern W Pacific. 1 species (Kussakin, 1979; Kussakin and Malyutina, 1987: redescription).

Cymodetta Bowman and Kühne, 1974

Diagnosis. Body dorsal surfaces smooth, unable to conglobate; not or weakly sexually dimorphic. Pleonite 1 narrower than remainder of pleon, not extending to pleon lateral margins; dorsal surface of male smooth, of female with paired tubercles. Pleotelson of male smooth dorsally, of female with paired tubercles; posterior margin produced, without exit channel. Antennular peduncle articles 1 and 2 robust, article 3 slender, with first articles meeting medially; article 3 longer than article 2; flagellum about as long as peduncle. Epistome narrow anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 expanded. Penial processes close-set basally, long (extending to pleopod rami). Pleopod 2 appendix masculina with distal part reflexed. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 2 discrete scale patches; endopod without thickened transverse ridges. Uropod attached anterolaterally to pleotelson, cylindrical (not especially flattened); peduncle without endopod; exopod cylindrical, exceeding telson apex, acute distally.

Estuarine, freshwater. Temperate and tropical eastern Australia. 2 species (Holdich and Harrison, 1983: rediagnosis).

Cymodoce Leach, 1814

Diagnosis. Body dorsal surfaces with nodular ornamentation, unable to conglobate; strongly sexually dimorphic. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins; posterior margin with 2 distinct submedian lobes. Pleotelson with paired submedial bosses or with paired longitudinal carinae; posterior margin with ventral thickened rim, with 2 longitudinal bilateral grooves; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum shorter than peduncle. Epistome acute anteriorly. Mandibular incisor unicuspid. Maxillipedal palp articles 2–4 mesial margins extended, forming finger-like lobes, article 2 not expanded. Penial processes set apart basally, long (extending to pleopod rami). Pleopod 2 appendix masculina about as long as endopod. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened

transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod truncate or acute distally; exopod lanceolate, similar in length to or shorter than endopod, acute distally.

Estuarine, marine, intertidal–shelf. Temperate Northern Atlantic, Tropical Atlantic, Temperate Northern Pacific, Western and Central Indo-Pacific, Temperate Southern Africa, Temperate Australasia (cosmopolitan, except polar seas). 72 species (Dumay, 1972; Harrison and Holdich, 1984: rediagnosis, list of species; Schotte and Kensley, 2005: rediagnosis, key to 12 Indian Ocean species; Khalaji-Pirbalouty et al., 2013: rediagnosis, list of only 21 species). The genus remains in a confused state with many misplaced species.

Cymodocella Pfeffer, 1887

Diagnosis. Body dorsal surfaces smooth or with nodular ornamentation, coxal and other margins smooth or with fringe of short setae; not or weakly sexually dimorphic. Coxal plates truncate. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins. Pleotelson weakly bi-domed; posterior margin narrowed posteriorly, forming ventrally closed tube directed posteriorly; ventrolateral margins simple. Antennular peduncle article 1 robust, longer and more robust than 2 and 3 combined; article 3 as long as or shorter than article 2; flagellum shorter than peduncle, shorter than peduncular article 3. Epistome narrow anteriorly. Mandibular incisor multicuspid, or unicuspid; molar process surface smooth, surrounded with basal fine setae. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes close-set basally, short (not extending beyond pleopod peduncles), straight. Pleopod 1 rami operculate, mesial margin of endopod and exopod indurate. Pleopod 2 appendix masculina spatulate terminally or narrowed abruptly distally or tapering to point, about as long as endopod or longer than and extending beyond endopod. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with incomplete transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod and exopod broadly rounded distally.

Subtidal. Temperate South America (Brazil), Temperate Southern Africa, Temperate Australasia, Southern Ocean. 15 species (Hurley and Jansen, 1977: key to 3 New Zealand species; Harrison and Holdich, 1982a: rediagnosis, distribution; Brandt and Wägele, 1989: redescription of *Cymodocella tubicauda* Pfeffer, 1887; Bruce, 1995: rediagnosis, key to 3 Australian species). Probably only some of the Australasian species belong to this genus.

Cymodopsis Baker, 1926

Diagnosis. Body dorsal surfaces smooth, able to conglobate; strongly sexually dimorphic. Pereonite 7 as wide as pereonite 6, forming part of body outline or narrower than pereonite 6, coxa not reaching as ventrally as coxa 6. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins; dorsal surface smooth, or slightly elevated. Pleotelson with median dorsal process or with paired submedial bosses; posterior margin rounded broadly or produced, with posteriorly produced lobe over ventrally directed groove. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2. Epistome flush with head anteriorly, not projecting or projecting anteriorly, not conspicuous dorsally, wide anteriorly or narrow anteriorly. Maxillipedal palp articles 2–4 mesial margins extended, forming finger-like lobes. Pleopod 2 appendix masculina tapering, extending beyond endopod, longer than and extending beyond endopod. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod without transverse suture, without thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod truncate distally or with distal notch; exopod lamellar or styliform, reduced, mobile, narrowly rounded distally or acute or bifid.

Subtidal, shelf. Temperate Australia. 5 species (Baker, 1926; Hurley and Jansen, 1977: dubious rediagnosis; Wetzer et al., 2018). The monophyly of this genus is entirely uncertain; all species are in need of redescription. The three New Zealand species are here excluded.

Diclidocella Bruce, 1995

Diagnosis. Body dorsal surfaces smooth or with nodular ornamentation, unable to conglobate; not or weakly sexually dimorphic. Rostrum not separating antennular bases. Pereonite 6 simple, without bosses, processes or marginal extensions, or with bosses. Pereonite 7 narrower than pereonite 6, coxa not reaching as ventrally as coxa 6, without dorsal bosses, processes or marginal extensions or with bosses. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins. Pleotelson without dorsal process or with paired submedial bosses or bi-domed weakly; posterior margin narrowed posteriorly, forming ventrally closed tube, directed posteriorly; ventrolateral margins simple. Antennular peduncle articles 1 and 2 robust; article 3 slender, articulating at right angles; article 2 with distinct anterodistal lobe; flagellum shorter than peduncle. Epistome wide anteriorly. Mandibular molar process surface with transverse ridges or smooth, surrounded with basal fine setae. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 expanded. Pereopod 2 more slender and longer than pereopods 1 and 3. Penial processes close-set basally or in contact basally, short (not extending beyond pleopod peduncles), straight. Pleopod 1 rami operculate, mesial margin of endopod and exopod indurate. Pleopod 2 appendix masculina with straight margins or spatulate terminally. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Uropodal endopod rounded broadly distally; exopod inserted near midpoint of lateral margin of peduncle-endopod, similar in length to endopod, broadly rounded distally.

Subtidal (3–17 m). Temperate Australia. 3 species (Bruce, 1995: key to 3 species).

Discerceis Richardson, 1905

Diagnosis. Body dorsal surfaces granular, able to conglobate; strongly sexually dimorphic. Pleonite 1 narrower than remainder of pleon, not extending to pleon lateral margins. Pleotelson tuberculate; with rectangular or rounded notch bearing prominent median tooth. Antennular peduncle article 1 robust, longer and more robust than 2 and 3 combined; article 3 longer than article 2; flagellum about as long as peduncle. Epistome acute anteriorly. Maxillipedal palp articles 2–4 mesial margins extended, forming finger-like lobes. Penial processes set apart basally, short (not extending beyond pleopod peduncles). Pleopods 1, 2 exopods lateral smooth. Pleopod 2 appendix masculina inserted near midpoint of mesial margin. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with incomplete transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropod with minute endopod; exopod cylindrical, much longer than reduced endopod, extending beyond pleotelson apex, truncate or bifid distally.

Intertidal, subtidal. Tropical Atlantic, Tropical Eastern Pacific (Central America). 3 species (Schotte, 2005: rediagnosis, key to species).

Discidina Bruce, 1994

Diagnosis. Body flat, coxae without visible sutures, directed laterally, dorsal surfaces smooth, densely setose (short scales and plumose setae), coxal and other margins with sheathed plumed setae, unable to conglobate; not or weakly sexually dimorphic. Rostrum not separating antennular bases. Eyes more dorsal than lateral. Coxal plates truncate. Pleonite 1 narrower than remainder of pleon, not extending to pleon lateral margins. Pleotelson flat; posterior margin simple, arcuate, without exit channel; ventrolateral margins simple. Antennular peduncle articles 1 and 2 flat, expanded as anterior and/or anterolateral lobes, with first articles meeting medially; article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Epistome narrow anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 expanded. Penial processes in contact basally, long (extending to pleopod rami), widest near base. Pleopod 1 endopod folded distally, forming a tube. Pleopod 2 appendix masculina enrolled distally, forming a groove, Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod with incomplete transverse suture, without thickened transverse ridges, with 3 discrete scale patches; endopod without thickened transverse ridges. Uropodal rami forming part of continuous body outline; endopod acute distally; exopod embedded and flush with margin of endopod.

Subtidal. Temperate S Australia. 1 species (Bruce, 1994c).

Dynamene Leach, 1818

Diagnosis. Body dorsal surfaces smooth or granular, with sparse setae, coxal and other margins with fringe of short setae, able to conglobate; strongly sexually dimorphic. Pereonite 6 with pair of spine-like projections. Pleotelson tuberculate or smooth; terminating in terminal foramen which may be tube-like. Antennular peduncle article 1 robust, longer and more robust than 2 and 3 combined; article 3 longer than article 2. Epistome narrow anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate. Penial processes set apart basally. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod without transverse suture, with thickened transverse ridges, with 2 discrete scale patches; endopod with thickened transverse ridges. Uropod with minute endopod, acute distally; exopod longer than endopod, acute distally.

Intertidal, subtidal. Temperate NE Atlantic to Black Sea, Central Indo-Pacific (NE Australia). 8 species (Holdich, 1970: habitats; Holdich and Harrison, 1980: rediagnosis; Vieira et al., 2016: rediagnosis; key to males of 8 species from Atlantic and Black Sea).

Dynamenella Hansen, 1905

Diagnosis. Body dorsal surfaces smooth or with nodular ornamentation, with sparse setae, able to conglobate; strongly sexually dimorphic. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins; sutures short. Pleotelson tuberculate or smooth; posterior margin with ventral thickened rim, with subapical circular, Y- or T-shaped foramen connected to posterior by narrow slit; ventrolateral margins flattening posteriorly, or directed medially, or with narrow outcurved ridges meeting in posterior midline. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum shorter than peduncle. Epistome narrow anteriorly. Mandibular molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes fused basally, long (extending to pleopod rami), tapering smoothly from midlength. Pleopod 2 appendix masculina swollen basally ("flask-shaped"), about as long as endopod or longer than and extending beyond endopod. Pleopod 3 exopod with or without transverse suture. Pleopod 4 exopod with or without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod broadly rounded distally; exopod inserted laterally near anterolateral angle of peduncle-endopod, broadly rounded distally.

Intertidal, subtidal. Widespread in all oceans, principally tropical and subtropical habitats; absent from cold and polar waters; no records from the eastern Atlantic. 28 species (Harrison and Holdich, 1982a: rediagnosis, distribution; Schotte and Kensley, 2005: rediagnosis, key to 8 Indian Ocean species).

Dynameniscus Richardson, 1905

Diagnosis. Body dorsal surfaces with nodular ornamentation, able to conglobate; strongly sexually dimorphic. Coxal plates 1, 2 triangular, directed laterally; coxal plates 2–5, pleonite 2 with spike-like ventral process. Pleotelson tuberculate; posterior margin simple, arcuate, with incomplete ventral groove or channel (visible in ventral view); ventrolateral margins simple.

Antennular peduncle articles 1–3 of similar stoutness (or tapering); article 3 as long as or shorter than article 2; flagellum shorter than peduncle, shorter than peduncular article 3. Epistome narrow anteriorly. Mandibular incisor bicuspid. Maxillipedal palp articles 2–4 mesial margins lobate. Penial processes long (extending to pleopod rami). Pleopod 2 appendix masculina about as long as endopod. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod with incomplete transverse suture, without thickened transverse ridges, with 3 discrete scale patches; endopod without thickened transverse ridges. Uropod attached anterolaterally to pleotelson, cylindrical (not especially flattened); peduncle-endopod reduced, stub-like; exopod cylindrical, much longer than endopod, acute distally.

Slope (550–1260 m). Temperate Northern and Tropical Atlantic. 1 species (Richardson, 1905: description of type species; Kensley and Bruce, 2001: redescription).

Dynamenoides Hurley and Jansen, 1977

Diagnosis. Body dorsal surfaces smooth, able to conglobate; not or weakly sexually dimorphic. Pereonite 6 twice as long as pereonite 5 in dorsal midline, with posterior margin bilobed. Pereonite 7 with pair of triangular submedial posterior dorsal projections. Pleotelson tuberculate or smooth; with subapical circular foramen connected to posterior by narrow slit. Antennular peduncle articles 1 and 2 robust, article 3 slender, as long as or shorter than article 2; flagellum shorter than peduncle. Epistome wide anteriorly. Penial processes set apart basally, short (not extending beyond pleopod peduncles). Pleopod 2 appendix masculina inserted near midpoint of mesial margin, shorter than endopod. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with thickened transverse ridges; endopod with thickened transverse ridges. Uropodal endopod broadly rounded distally; exopod longer than endopod, acute distally.

Intertidal. Temperate New Zealand. 2 species (Hurley and Jansen, 1977).

Dynamenopsis Baker, 1908

Diagnosis. Body dorsal surfaces smooth, able to conglobate; not or weakly sexually dimorphic. Pereonite 7 expanded posteriorly (at least longer than pereonite 6) dorsally. Coxal plates truncate. Pleonite 1 narrower than remainder of pleon, not extending to pleon lateral margins; sutures absent. Pleotelson tuberculate or smooth; with subapical foramen connected to apex by narrow slit. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum shorter than peduncle. Epistome narrow anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate. Penial processes fused basally, long (extending to pleopod rami). Pleopod 2 appendix masculina tapering to point, about as long as endopod. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod truncate or broadly rounded distally; exopod broadly rounded distally.

Intertidal, subtidal. Temperate Southern Africa, Temperate Australasia. 3 species (Baker, 1908; Hurley and Jansen, 1977: rediagnosis, New Zealand species; Harrison and Holdich, 1982a: rediagnosis). Species from Angola doubtful.

Dynoides Barnard, 1914

Diagnosis. Body dorsal surfaces smooth or granular, with sparse setae, coxal and other margins with fringe of short setae, able to conglobate; strongly sexually dimorphic. Pleon sutures long; posterior margin with or without median posterior process. Pleotelson tuberculate or smooth; with elongate serrate sinus. Antennular peduncle articles 1–3 of similar stoutness (or tapering); article 3 longer than article 2; flagellum shorter than peduncle. Epistome narrow anteriorly. Mandibular molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins lobate (weakly), article 2 not expanded. Penial processes fused along basal half to two-thirds of length, long (extending to pleopod rami). Pleopod 2 appendix masculina reflexed, folded back on itself, about twice as long as endopod. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with incomplete transverse suture, without thickened transverse ridges, with 2 or 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod broadly rounded distally; exopod broadly rounded distally.

Intertidal–shelf. Tropical Atlantic, Temperate Northern Pacific, Western and Central Indo-Pacific, Tropical Eastern Pacific, Temperate Southern Africa, Temperate Australasia. 19 species (Li, 2000: rediagnosis, key to 16 species; Khalaji-Pirbalouty and Gagnon, 2021: NE Pacific species). *Dynoides* is a genus bedevilled by nomenclatural confusion resulting from the repeated failure of authors to recognise juvenile and immature males as the same species as adults. Some species names are likely junior synonyms of others. *Clianella* Boone, 1923 has been placed in and taken out of synonymy, entirely on the basis of presence or absence of a pleonal process, until sufficient intermediates were shown to occur. *Clianella* is a junior synonym of *Dynoides* (Li, 2000).

Eterocerceis Messana, 1990

Diagnosis. Body dorsal surfaces smooth, able to conglobate; not or weakly sexually dimorphic. Head with anterior margin produced, overriding antennules. Rostrum ventral. Pleonite 1 narrower than remainder of pleon, not extending to pleon lateral margins. Pleotelson with prominent submedian pair of smooth ridges, square in lateral view; posterior margin with shallow median indentation, with incomplete ventral groove or channel. Antennular peduncle articles 1 and 2 robust, article 1 with produced acute distal angles; article 3 slender longer than article 2; flagellum about as long as peduncle. Epistome acute anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate. Penial processes close-set basally, short (not extending beyond pleopod peduncles). Pleopods 1, 2 exopods lateral margins serrate, especially distally. Pleopod 2 appendix masculina inserted near midpoint of mesial margin, about as long as endopod. Pleopod 4 exopod without transverse suture,

with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with incomplete transverse suture, with thickened transverse ridges, with 2 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod broadly rounded distally; exopod with 2 or 3 distal teeth.

Subtidal. Western Indo-Pacific (Somalia). 1 species (Messana, 1990).

Exocerceis Baker, 1926

Diagnosis. Body dorsal surfaces coarsely pitted, able to conglobate; not or weakly sexually dimorphic. Rostrum directed posteroventrally, not separating antennular bases; head with anterior margin produced, overriding antennules. Pleon dorsal surface with 4 or 5 pairs of sublateral granular longitudinal ridges. Pleotelson with 2 large bosses, compressed bilaterally; with apical notch between 2 acute points, third dorsal median point projecting over notch. Antennular peduncle articles 1 and 2 robust, article 3 slender, with first articles meeting medially; article 3 longer than article 2; flagellum shorter than peduncle. Epistome acute anteriorly. Maxillipedal palp articles 2–4 mesial margins extended, forming finger-like lobes. Penial processes set apart basally, short (not extending beyond pleopod peduncles). Pleopods 1, 2 (sometimes 3) exopods lateral margins serrate, especially distally (obsolete except on 2). Pleopod 2 appendix masculina inserted near midpoint of mesial margin. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod without transverse suture, with thickened transverse ridges, with 2 discrete scale patches. Uropodal endopod serrate distally; exopod deeply serrate distally.

Shelf (20–204 m). Temperate E Australia. 1 species (Bruce, 1994b: rediagnosis, redescription of type species).

Exosphaeroides Holdich and Harrison, 1983

Diagnosis. Body dorsal surfaces smooth, able to conglobate; not or weakly sexually dimorphic. Pereonite 7 narrower than pereonite 6, coxa not reaching as ventrally as coxa 6. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins. Pleotelson posterior margin rounded broadly, without exit channel; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum about as long as peduncle. Epistome narrow anteriorly. Mandibular molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes close-set basally, short (not extending beyond pleopod peduncles), straight. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 2 discrete scale patches; endopod without thickened transverse ridges. Uropodal endopod broadly rounded distally; exopod broadly rounded distally.

Freshwater, estuarine. Central Indo-Pacific (coastal and karstic streams). 3 species (species from Easter I. doubtful) (Holdich and Harrison, 1983; Kensley, 2003; Jaume and Queinnec, 2007: species from karstic stream and cave sink 390 m above sea level in Vanuatu).

Exosphaeroma Stebbing, 1900

Diagnosis. Body vaulted, dorsal surfaces smooth or coarsely pitted, occasionally rugose; able to conglobate; not or weakly sexually dimorphic. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins; posterior margin with 2 submedian directed posteriorly flat lobes. Pleotelson posterior margin simple, arcuate, with incomplete ventral groove or channel; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum about as long as peduncle. Epistome widest about midlength. Mandibular molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Pereopods 1–3 ischium upper margin without long stiff slender setae or ischium upper margin with few long stiff slender setae. Penial processes close-set basally, short (not extending beyond pleopod peduncles), straight. Pleopod 4 exopod with incomplete transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod without transverse suture, without thickened transverse ridges, with 3 discrete scale patches or with 4 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod broadly rounded distally; exopod broadly rounded distally.

Estuarine, marine, intertidal, subtidal (0–100 m). Western Indo-Pacific, Tropical Eastern Pacific, Temperate South America, Temperate Southern Africa, Temperate Australasia, Southern Ocean. 39 species (Brandt and Wägele, 1989: redescription of type species *E. gigas* (Leach, 1818)). Northern and Southern Hemisphere species likely to belong to different genera.

Geocerceis Menzies and Glynn, 1968

Diagnosis. Body dorsal surfaces smooth, able to conglobate; strongly sexually dimorphic. Pleon dorsal surface with median and pair of sublateral tubercles. Pleotelson with pair of sublateral longitudinal rounded triangular ridges; posterior margin with deep notch, with incomplete ventral groove or channel; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender. Epistome wide anteriorly. Maxillipedal palp articles 2–4 mesial margins extended, forming finger-like lobes. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod without transverse suture, with thickened transverse ridges, with 2 discrete scale patches; endopod with thickened transverse ridges. Uropod attached posteriorly, at sides of pleotelson posterior margin; peduncle without endopod; exopod cylindrical, longer than endopod, acute distally.

Intertidal, subtidal. Tropical Atlantic (W Atlantic, Caribbean). 1 species (Menzies and Glynn, 1968; Kensley and Schotte, 1989: rediagnosis, figure of male; Monroy-Velázquez and Alvarez, 2016: photo of male, mention of male characters).

Gnorimosphaeroma Menzies, 1954

Diagnosis. Body dorsal surfaces smooth or polished in appearance, coxal and other margins smooth, able to conglobate; not or weakly sexually dimorphic. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins; sutures (except first) running to ventrolateral margin. Pleotelson posterior margin simple, arcuate, without exit channel; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum about as long as peduncle. Epistome narrow anteriorly. Mandibular molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins lobate. Penial processes close-set basally, short (not extending beyond pleopod peduncles). Pleopod 3 exopod without transverse suture or with incomplete transverse suture. Pleopod 4 exopod without transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod without thickened transverse ridges, with 2 discrete scale patches; endopod without thickened transverse ridges. Uropodal endopod broadly or narrowly rounded distally; exopod inserted laterally near anterolateral angle of peduncle-endopod, exopod shorter than endopod, narrowly rounded distally.

Freshwater, estuarine, subtidal. Temperate Northern Pacific, Western Indo-Pacific. 27 species (14 marine) (Menzies, 1954; Nunomura, 1998: key to 10 species from Japan; Wetzer et al., 2021: redescription of type species, phylogeny, key to 5 species; Tomikawa et al., 2023: review, phylogeny, species list, distribution). In our view the number of described species is excessive.

Haswellia Haswell, 1881

Diagnosis. Body dorsal surfaces smooth, able to conglobate; strongly sexually dimorphic. Head with ventral rostrum. Pereonite 7 with single dorsal process directed posteriorly (usually overreaching and sometimes as wide as pleotelson). Coxal plates truncate. Pleotelson with paired submedial bosses or tuberculate; posterior margin trilobate. Antennular peduncle articles 1 and 2 robust, article 3 slender, as long as or shorter than article 2; flagellum shorter than peduncle. Epistome acute anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate. Pleopods 1, 2 (sometimes 3) exopods lateral margins serrate, especially distally. Pleopod 2 appendix masculina inserted near midpoint of mesial margin, about as long as endopod. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, with thickened transverse ridges, with 3 discrete scale patches. Uropod endopod lamellar or minute; exopod similar in length to endopod or much longer than reduced endopod.

Intertidal, subtidal. Temperate Australasia. 7 species (Baker, 1926: 4 species; 1928: 2 species (Harrison and Holdich, 1982b: rediagnosis, redescription of type species).

Hemisphaeroma Hansen, 1905

Diagnosis. Pleotelson posterior margin simple, arcuate, without exit channel; ventrolateral margins laterally expanded, directed more ventrally than coxae. Mandibular incisor elongate, deeply bicuspid. Maxillipedal palp articles 2–4 mesial margins not lobate. Pereopods 1–3 ischium, merus and propodus upper margins each with rows of long stiff slender setae. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges.

Probably estuarine or tidal riverine. Central Indo-Pacific (Surabaya, Indonesia). 1 species (Hansen, 1905: poorly known, not figured). Hansen (1905) provided few details of this species; specimens exist in museums; the species needs redescription.

Heterodina Schotte and Kensley, 2005

Diagnosis. Body vaulted weakly, dorsal surfaces smooth, coxal and other margins with fringe of short setae or with membrana cingula (membranous setose fringe), unable to conglobate; not or weakly sexually dimorphic. Eyes more dorsal than lateral. Coxal plates truncate. Pleonite 1 wholly fused to pleonite 2; pleon comprising a single unit; sutures (except first) running to posterior or posterolateral margin or sutures absent. Pleotelson flat; posterior margin simple, arcuate, without exit channel; ventrolateral margins simple. Antennular peduncle article 1 robust, longer and more robust than 2 and 3 combined; article 3 longer than article 2; flagellum shorter than peduncle. Epistome extended prominently anteriorly as flat, anteriorly convex lobe, wide anteriorly. Maxillipedal palp articles 2–4 mesial margins not lobate, article 2 not expanded. Penial processes fused basally, long (extending to pleopod rami), tapering smoothly from midlength. Pleopod 1 endopod c. 0.5 as long and 0.5 as wide as exopod. Pleopod 2 appendix masculina sub-basal, stout or flask-shaped, about as long as endopod or longer than and extending beyond endopod. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, with thickened transverse ridges (very weak); endopod without thickened transverse ridges. Pleopod 5 exopod with incomplete transverse suture, with thickened transverse ridges (very weak), with 2 discrete scale patches; endopod without thickened transverse ridges. Uropodal rami forming part of continuous body outline; endopod narrowly rounded distally; exopod inserted near midpoint of lateral margin of peduncle-endopod, reduced, mobile, narrowly rounded distally.

Subtidal. Tropical Atlantic, Western Indo-Pacific (Belize, Persian Gulf). 3 species (Schotte and Kensley, 2005: diagnosis; Khalaji-Pirbalouty and Bruce, 2014: rediagnosis, key to species).

Heteruropus Verhoeff, 1942

Diagnosis. Body dorsal surfaces smooth; not or weakly sexually dimorphic. Pleon dorsal surface with pair of low submedian ridges. Pleotelson with pair of low submedian ridges; with 2 small sublateral notches. Antennular peduncle article 1 robust, longer and more robust than 2 and 3 combined. Epistome wide anteriorly. Maxillipedal palp articles 2–4 mesial margins extended, forming finger-like lobes. Penial processes fused basally, long (extending to pleopod rami).

Pleopod 2 appendix masculina curved, barely reaching beyond apex of ramus, distally acuminate. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with 2 discrete scale patches. Uropodal endopod truncate distally; exopod longer than endopod (shorter in female), acute distally.

Intertidal, subtidal. Tropical Atlantic (USA, Florida, Texas, Gulf of Mexico). 1 species (Menzies and Miller, 1955: description of type species; Kensley, 1987: diagnosis as junior synonym *Harrieta* Kensley, 1987).

Holotelson Richardson, 1909

Diagnosis. Body dorsal surfaces smooth, able to conglobate; not or weakly sexually dimorphic. Pereonite 7 with pair of posterior submedial dorsal lobes. Pleotelson tuberculate or with 1 or 2 rows of 3 tubercles; apex with prominent median projection and short tubercle each side. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum about as long as peduncle. Epistome wide anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate. Penial processes set apart basally, short (not extending beyond pleopod peduncles). Pleopod 2 appendix masculina inserted near midpoint of mesial margin. Pleopod 3 exopod with or without transverse suture. Pleopods 4, 5 exopods and endopods with thickened transverse ridges. Uropodal endopod rounded broadly distally; exopod rounded broadly distally.

Intertidal, subtidal. Temperate Northern W Pacific (Japan). 4 species (Nunomura, 2004, 2013; Richardson, 1909).

Ischyromene Racovitza, 1908

Diagnosis. Body dorsal surfaces smooth or with nodular ornamentation or granular, with sparse setae, coxal and other margins with fringe of short setae, able to conglobate; not or weakly sexually dimorphic. Rostrum not separating antennular bases. Pereonite 7 without dorsal bosses, processes or marginal extensions or posterior margin with posteriorly directed rim. Coxal plates truncate. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins; pleon sutures long, extending to pleon posterior margin. Pleotelson posterior margin with ventral thickened rim, forming ventrally open tube directed posteriorly or with short tube directed dorsally, enclosed ventrally and posteriorly or with subapical Y-shaped foramen connected to posterior by narrow slit; ventrolateral margins simple. Antennular peduncle articles 1–3 of similar stoutness (or tapering); article 2 usually shorter than articles 1 or 3; flagellum shorter than peduncle. Epistome narrow anteriorly. Mandibular molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes in contact basally, short (not extending beyond pleopod peduncles), straight. Pleopod 1 rami operculate, mesial margin of endopod and exopod indurate. Pleopod 2 appendix masculina with straight margins or spatulate terminally, about as long as endopod. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod broadly rounded distally; exopod similar in length to endopod, broadly rounded distally.

Intertidal, subtidal. Temperate Northern Atlantic, Tropical Atlantic, Temperate South America, Temperate Southern Africa, Temperate Australasia. 25 species (Harrison and Holdich, 1982a: rediagnosis, distribution; Schüller and Wägele, 2005a, b: redescription of type species). *Ischyromene* appears twice in the key.

Isocladus Miers, 1876

Diagnosis. Body dorsal surfaces smooth, able to conglobate; strongly sexually dimorphic. Pereonite 7 with prominent horizontal long dorsal spine. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins. Pleotelson posterior margin with distinct median point, with incomplete ventral groove or channel; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum about as long as peduncle. Epistome wide anteriorly. Mandibular molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes close-set basally, short (not extending beyond pleopod peduncles), straight. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, with obsolete thickened transverse ridges, with 2 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod truncate distally or with shallow concavity; exopod truncate or acute distally.

Intertidal, subtidal. Central Indo-Pacific, Temperate South America, Temperate Southern Africa, Temperate Australasia (New Zealand, S Australia, Chile, Indonesia, Magellan Straits, South Africa, Subantarctica). 17 species (Hurley and Jansen, 1977: rediagnosis, key to 6 New Zealand species; Carvacho, 1997: rediagnosis, list of species). Females are very similar to *Exosphaeroma*.

Juletta Bruce, 1993

Diagnosis. Body vaulted weakly, dorsal surfaces smooth, unable to conglobate; not or weakly sexually dimorphic. Pereonite 7 narrower than pereonite 6, coxa not reaching as ventrally as coxa 6. Coxal plates truncate. Pleonite 1 narrower than remainder of pleon, not extending to pleon lateral margins; pleon with all pleonites fused to pleotelson with 1 lateral suture visible. Posterior margin fused medially to pleotelson. Pleotelson flat; posterior margin narrowed posteriorly, without exit channel or with incomplete ventral groove or channel; ventrolateral margins forming ridge. Antennular peduncle articles 1–3 of similar stoutness (or tapering); with article 3 posteriorly offset, article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Epistome wide anteriorly. Mandibular incisor unicuspid; molar process surface smooth, surrounded with basal fine setae. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Pereopods 2, 3 propodal palm with

proximal lobe. Penial processes close-set basally, short (not extending beyond pleopod peduncles), straight. Pleopod 1 rami operculate, mesial margin of endopod and exopod indurate. Pleopod 2 appendix masculina about as long as endopod. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with incomplete transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod rounded broadly distally; exopod inserted laterally near anterolateral angle or midpoint of peduncle-endopod, reduced, mobile, rounded broadly distally.

Subtidal. Temperate Australia. 2 species (Bruce, 1993).

Koremasphaera Bruce, 2003

Diagnosis. Body dorsal surfaces granular, with dense beds of setae across pereonites 2–7 and pleon; not or weakly sexually dimorphic. Rostrum not separating antennular bases. Coxal plates acute posterolaterally. Pleotelson with paired longitudinal carinae; posterior margin simple, arcuate, without exit channel; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum shorter than peduncle. Epistome narrow anteriorly. Mandibular molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins extended, forming finger-like lobes, article 2 not expanded. Penial processes in contact basally, short (not extending beyond pleopod peduncles), tapering smoothly from midlength. Pleopod 2 appendix masculina spatulate terminally. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 2 discrete scale patches; endopod without thickened transverse ridges. Uropodal endopod styliform, acute distally; exopod styliform, with hard distal terminal spike.

Shelf (13 m). Temperate SE Australia. 1 species (Bruce, 2003).

Kranosphaera Bruce, 1992

Diagnosis. Body dorsal surfaces with nodular ornamentation and coarse pits, unable to conglobate; not or weakly sexually dimorphic. Head without rostrum. Pereonite 7 narrower than pereonite 6, coxa not reaching as ventrally as coxa 6. Coxal plate 5 overlapping coxal plates 4 and 6 when folded. Pleonite 1 narrower than remainder of pleon, not extending to pleon lateral margins. Pleotelson with paired submedial bosses; posterior margin with ventral thickened rim, with incomplete ventral groove or channel; ventrolateral margins simple. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum shorter than peduncle. Epistome extended prominently anteriorly and elongate, produced as cone beyond antennulae. Mandibular incisor unicuspid; molar process surface smooth, surrounded with basal fine setae. Maxillipedal palp articles 2–4 mesial margins extended, forming finger-like lobes, article 2 not expanded. Pereopod 5 of male greatly enlarged, smooth, with swollen carpus and propodus, 1.5 times as long as other pereopods. Penial processes in contact basally, long (extending to pleopod rami), sinuate. Pleopod 2 appendix masculina tapering evenly to apex, about as long as endopod. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropod attached anterolaterally to pleotelson, cylindrical (not especially flattened); endopod narrowly rounded distally; exopod absent.

Shelf (39–52 m). Central Indo-Pacific (NW Australia). 1 species (Bruce, 1992).

Lekanesphaera Verhoeff, 1943

Diagnosis. Body dorsal surfaces with ridges or tubercles, able to conglobate; not or weakly sexually dimorphic. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins. Pleotelson posterior margin simple, arcuate, without exit channel; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum about as long as peduncle. Epistome narrow anteriorly. Mandibular molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 expanded. Pereopods 1–3 ischium and merus upper margins each with rows of long stiff slender setae. Penial processes close-set basally, short (not extending beyond pleopod peduncles). Pleopod 3 exopod without transverse suture. Pleopod 4, 5 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Uropodal endopod narrowly rounded distally; exopod lateral margin serrate or smooth, acute distally.

Estuarine, marine intertidal. Temperate Northern Atlantic (E Atlantic, Mediterranean, Baltic). 14 species (Jacobs, 1987: rediagnosis, key to 13 species).

Leptosphaeroma Hilgendorf, 1885

Diagnosis. Body flat, coxae without visible sutures, directed laterally, dorsal surfaces smooth, coxal and other margins with membrana cingula (membranous setose fringe), unable to conglobate; not or weakly sexually dimorphic. Rostrum acute, not separating antennular bases. Eyes more dorsal than lateral. Coxal plates truncate. Pleon with 2 partial sutures visible on fused part; sutures running to lateral margin. Pleotelson flat, narrower than pleon anteriorly; posterior margin with shallow median indentation, with incomplete ventral groove or channel. Antennular peduncle articles 1 and 2 flat, expanded as anterior and/or anterolateral lobes, with first articles meeting medially; article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Epistome acute anteriorly. Maxillipedal palp articles 2–4 mesial margins not lobate. Pereopod 3 more slender than others. Penial processes set apart basally, short (not extending beyond pleopod peduncles). Pleopod 2 appendix masculina spatulate terminally. Pleopod 4 exopod with incomplete transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod without transverse suture, without thickened transverse

ridges, with 3 discrete scale patches; endopod without thickened transverse ridges. Uropodal rami forming part of continuous body outline; uropodal endopod truncate distally, endopods in contact posteriorly; exopod subtriangular, acute distally.

Intertidal. Temperate Northern W Pacific (Japan). 1 species (Nishimura, 1976: redescription).

Margueritta Bruce, 1993

Diagnosis. Body vaulted, dorsal surfaces smooth, with sparse setae, coxal and other margins with fringe of short setae, unable to conglobate; not or weakly sexually dimorphic. Pereonite 7 narrower than pereonite 6 or narrower than pereonite 6, coxa not reaching as ventrally as coxa 6. Coxal plates truncate, coxal plates 2–7 not overlapping. Pleonite 1 narrower than remainder of pleon, not extending to pleon lateral margins; pleon fused to pleotelson with 1 lateral suture visible. Pleon posterior margin fused medially to pleotelson. Pleotelson posterior margin with shallow median indentation, forming ventrally open tube or closed tube, directed posteriorly; ventrolateral margins forming ridge. Antennular peduncle articles 1–3 of similar stoutness (or tapering); with article 3 offset posteriorly, article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Epistome wide anteriorly. Mandibular incisor unicuspid; molar process surface smooth, surrounded with basal fine setae. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes close-set basally, short (not extending beyond pleopod peduncles), straight. Pleopod 1 rami operculate, mesial margin of endopod and exopod indurate. Pleopod 2 appendix masculina spatulate terminally, about as long as endopod. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod without transverse suture, with thickened transverse ridges, with 2 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod broadly rounded or acute distally; exopod inserted laterally near anterolateral angle of peduncle-endopod, reduced, mobile (slightly), broadly rounded distally.

Subtidal. Temperate southern Western Australia. 2 species (Bruce, 1993).

Maricoccus Poore, 1994

Diagnosis. Body flat, scale-like, coxae without visible sutures, directed laterally, dorsal surfaces smooth, unable to conglobate; not or weakly sexually dimorphic. Head with anterior margin produced, overriding antennules, such that antennules are directed posteroventrally. Eyes more dorsal than lateral (also visible ventrally). Coxal plates truncate. Pleonite 1 wholly fused to pleonite 2; pleon comprising a single unit; sutures absent. Pleon posterior margin fused medially to pleotelson. Pleotelson flat; posterior margin with shallow median indentation, without exit channel; ventrolateral margins simple. Antennular peduncle articles 1 and 2 robust, article 3 slender; article 2 about as long as article 1, extended distally so that article 3 articulates on posterior margin; with article 3 offset posteriorly, article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Epistome wide anteriorly. Mandibular incisor unicuspid; molar process surface smooth, surrounded with basal fine setae. Maxillipedal palp articles 2–4 mesial margins lobate (2 barely), article 2 not expanded. Penial processes in contact basally, short (not extending beyond pleopod peduncles). Pleopod 1 rami operculate, mesial margin of endopod and exopod indurate. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod without transverse suture, with thickened transverse ridges, with 2 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopods broadly rounded distally, in contact posteriorly; exopod inserted near midpoint of lateral margin of peduncle-endopod, shorter than endopod, broadly rounded distally.

Shelf. Temperate Australia. 1 species (Poore, 1994).

Moruloidea Baker, 1908

Diagnosis. Body dorsal surfaces with nodular ornamentation, able to conglobate or unable to conglobate; not or weakly sexually dimorphic. Head with rostrum visible dorsally or without rostrum; not produced or forming broad semicircular plate. Eyes lateral, or absent. Coxal plate 5 overlapping coxal plates 4 and 6 when folded. Pleon dorsal surface smooth, or with dorsal bosses. Pleotelson without dorsal process or with median dorsal process or with median dorsal boss; posterior margin with ventral thickened rim, with incomplete ventral groove or channel or with small triangular (widest posteriorly) notch; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum shorter than peduncle. Antennal peduncle article 5 strongly reflexed (male only), peduncular articles 4 and 5 enlarged. Epistome narrow anteriorly. Mandibular incisor unicuspid; molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Pereopod 1 ambulatory (more compact in male). Penial processes in contact basally, short (not extending beyond pleopod peduncles). Pleopod 4 exopod with transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod truncate distally, slightly excavate; exopod reduced, mobile, acute distally or falcate.

Shelf, slope. Temperate Australasia, Southern Ocean. 11 species (Kussakin, 1967: diagnosis of *Caecocassidias*; Harrison, 1984b; Brandt, 1998: redescription of *C. patagonicus*; Bruce, 2003: rediagnosis; Calderón López and Doti, 2025: rediagnosis). *Caecocassidias* Kussakin, 1967 is a considered here as a subjective junior synonym of *Moruloidea* (new synonym).

Naesicopea Stebbing, 1893

Diagnosis. Body vaulted weakly, dorsal surfaces granular; strongly sexually dimorphic. Head without rostrum, antennular bases not separated; with anterior margin produced, overriding antennules. Eyes absent. Pereonite 7 narrower than pereonite 6, coxa not reaching as ventrally as coxa 6. Coxal plate 5 overlapping coxal plates 4 and 6 when folded. Pleonite 1 posterior margin with single flush median lobe, narrower than remainder of pleon, not extending to pleon lateral margins.

Pleon posterior margin entire. Pleotelson with median dorsal process; posterior margin simple, arcuate; ventrolateral margins simple. Antennular peduncle articles 1 and 2 robust, article 3 slender; article 2 with distinct anterodistal lobe; article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Epistome wide anteriorly. Uropod attached posteriorly, at sides of pleotelson posterior margin; peduncle-endopod reduced, stub-like; exopod cylindrical, much longer than peduncle-endopod, cylindrical, curving medially and meeting posteriorly, acute distally, meeting posteriorly.

Slope (1958 m). Central Indo-Pacific (Papua New Guinea). 1 species in need of redescription (Beddard, 1886).

Neonaesa Harrison and Holdich, 1982

Diagnosis. Body dorsal surfaces granular, with sparse setae, able to conglobate; strongly sexually dimorphic. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins; pleon sutures short. Pleotelson with median dorsal boss and with paired submedial bosses; with median notch and 2 small sublateral notches; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum shorter than peduncle. Epistome wide anteriorly. Mandibular incisor multicuspid; molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes set apart basally, short (not extending beyond pleopod peduncles), straight. Pleopod 2 appendix masculina inserted near midpoint of mesial margin, shorter than endopod. Pleopod 4 exopod with transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with incomplete transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropod attached posteriorly, at sides of pleotelson posterior margin; peduncle without endopod; exopod cylindrical, longer than endopod, with hard distal terminal spike.

Subtidal. Indo West-Pacific (coral reefs). 1 species (Harrison and Holdich, 1982b; Müller, 1991: redescription, distribution). More species have been collected in East Africa.

Neosphaeroma Baker, 1926

Diagnosis. Body dorsal surfaces smooth. Pleotelson posterior margin rounded broadly, without exit channel; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum about as long as peduncle. Epistome wide anteriorly. Maxillipedal palp articles 2–4 mesial margins extended, forming finger-like lobes. Pleopod 2 appendix masculina sinuate, extending well beyond endopod. Pleopod 3 endopod with transverse ridges. Pleopod 4 exopod with transverse suture; endopod with thickened transverse ridges. Uropodal endopod acute distally or with distal notch; exopod lateral margin with distal notch, truncate distally.

Subtidal, shelf. Temperate SE Australia. 2 species (Whitelegge, 1901: figs of limbs; Baker, 1926: diagnosis, descriptions of 2 species, third possibly belongs to another genus; Harrison and Holdich, 1984: rediagnosis, species discussion).

Oxinasphaera Bruce, 1997

Diagnosis. Body dorsal surfaces with hard cuticular spines, densely setose, able to conglobate; strongly sexually dimorphic. Rostrum ornate. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins; pleon posterior margin without process or with 2 distinct submedian lobes or with process directed posteriorly. Pleotelson posterior margin with ventral thickened rim, with posteriorly produced narrow lobe over excision or with 2 longitudinal bilateral grooves; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender; inferior margin with hard cuticular teeth; article 3 longer than article 2; flagellum shorter than peduncle. Epistome narrow anteriorly. Mandibular molar process surface smooth, surrounded with basal fine setae. Maxillipedal palp articles 2–4 mesial margins extended, forming finger-like lobes, article 2 not expanded. Penial processes in contact basally, short (not extending beyond pleopod peduncles). Pleopod 2 appendix masculina about as long as endopod. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 4 discrete scale patches; endopod with thickened transverse ridges. Uropod attached anterolaterally to pleotelson, cylindrical (not especially flattened); peduncle-endopod round in section, with hard distal terminal spike; exopod inserted near midpoint of lateral margin of peduncle-endopod, cylindrical, reduced, mobile, distally with distal terminal spike.

Subtidal, shelf. Western and Central Indo-Pacific, Temperate Australasia (East Africa to Philippines and New Caledonia in the east). 27 species (Bruce, 1997: diagnosis, descriptions and key to 23 species; Schotte and Kensley, 2005: rediagnosis, key to 5 Indian Ocean species).

Paracassidina Baker, 1911

Diagnosis. Body flat, coxae without visible sutures, directed laterally or vaulted weakly, dorsal surfaces smooth or with nodular ornamentation, without setae or with sparse setae, coxal and other margins with fringe of short setae, unable to conglobate; not or weakly sexually dimorphic (sometimes dimorphic in antennules and ornamentation). Rostrum truncate, separating antennular bases (with epistome). Eyes more dorsal than lateral. Coxal plates truncate. Pleonite 1 fused medially to pleonite 2, narrower than remainder of pleon, not extending to pleon lateral margins; pleon with 1 partial suture visible on fused part. Pleotelson flat, narrower than pleon anteriorly; posterior margin simple, arcuate, without exit channel; ventrolateral margins simple. Antennular peduncle articles 1 and 2 flat, more or less expanded as anterior and/or anterolateral lobes, with first articles separated by prominent epistome; article 1 produced anteriorly (sometimes bilobed as antlers); article 2 with or without anterodistal lobe; article 3 as long as or shorter than article 2; flagellum shorter than peduncle, shorter than peduncular article 3. Epistome extended prominently anteriorly and elongate, wide anteriorly. Mandibular molar process surface smooth with palisade of spines on proximal margin. Maxillipedal palp articles 2–4

mesial margins lobate or extended, forming finger-like lobes, article 2 expanded. Pereopod 1 with elongate propodus; propodus club-shaped (dilated distally with dactylus subterminal); merus with long setose lobe on upper margin. Pereopods 1–3 ischium upper margin with few long stiff slender setae. Penial processes in contact basally, short (not extending beyond pleopod peduncles), straight. Pleopod 2 appendix masculina spatulate terminally. Pleopod 4 exopod without transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod without transverse suture, without thickened transverse ridges, with 3 discrete scale patches; endopod without thickened transverse ridges. Uropodal rami forming part of continuous body outline; uropodal endopod acute distally; exopod inserted near midpoint of lateral margin of peduncle-endopod, reduced, mobile, narrowly rounded distally.

Intertidal, subtidal, shelf, slope (rare). Central Indo-Pacific, Temperate Australasia. 14 species (Bruce, 1994c: rediagnosis, key to species).

Paracassidinopsis Nobili, 1906

Diagnosis. Body dorsal surfaces smooth, able to conglobate. Pleon dorsal surface tuberculate, or with 2 pairs of tubercles. Pleotelson with 2 pairs of ridges; posterior margin rounded broadly, with incomplete ventral groove or channel. Antennular peduncle articles 1 and 2 robust, article 3 slender or articles 1–3 of similar stoutness (or tapering); article 3 longer than article 2; flagellum shorter than peduncle. Epistome wide anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate. Penial processes fused basally, long (extending to pleopod rami). Pleopod 1 endopod comprising small basal part and long filamentous thread. Pleopod 2 appendix masculina tapering to point. Pleopod 4 exopod with transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with thickened transverse ridges; endopod with thickened transverse ridges. Uropodal endopod broadly rounded distally; exopod reduced, mobile, broadly rounded distally.

Intertidal, subtidal. Western and Eastern Indo-Pacific (French Polynesia, Madagascar, Kenya). 2 species (Roman, 1974; Müller, 1991: second species, redescription of type species, synonymy).

Paracerceis Hansen, 1905

Diagnosis. Body dorsal surfaces smooth, able to conglobate; strongly sexually dimorphic. Pleonite 1 narrower than remainder of pleon, not extending to pleon lateral margins; pleon posterior dorsal surface with pair of low submedian ridges; posterior margin with 2 distinct submedian lobes. Pleotelson with proximal median and submedian tubercles; posterior margin produced, with wide notch bearing median tooth and sometimes pair of teeth. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum longer than peduncle. Epistome narrow anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate. Penial processes set apart basally, short (not extending beyond pleopod peduncles). Pleopods 1, 2 (sometimes 3) exopods lateral margins serrate, especially distally. Pleopod 2 appendix masculina inserted near midpoint of mesial margin, about as long as endopod. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod without transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropod with minute acute endopod; exopod cylindrical, exopod much longer than reduced endopod, extending beyond pleotelson apex, acute distally.

Subtidal. Temperate Northern Atlantic, Tropical Atlantic, Temperate Northern Pacific, Western and Central Indo-Pacific, Tropical Eastern Pacific, Temperate South America, Temperate Australasia. 13 species (Harrison and Holdich, 1982b: rediagnosis; Kensley, 1984: review of 4 species from Western Atlantic; Espinosa-Perez and Hendrickx, 2002: eastern Pacific species). *Paracerceis sculpta* (Holmes, 1904) has been introduced to tropical and temperate Australia, Brazil, Hawaii, Atlantic coast of Europe, Mediterranean and Hong Kong (Hewitt and Campbell, 2001) and to Japan (Ariyama and Otani, 2004).

Paracilicaea Stebbing, 1910

Diagnosis. Body dorsal surfaces with nodular ornamentation, with sparse setae, able to conglobate; strongly sexually dimorphic. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins. Pleotelson without dorsal process or with paired submedial bosses; with 2 small sublateral notches or with rectangular or rounded notch bearing median tooth; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum about as long as peduncle. Epistome wide anteriorly. Mandibular incisor unicuspid. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes close-set basally, long (extending to pleopod rami). Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 4 discrete scale patches; endopod with thickened transverse ridges. Uropod attached posteriorly, at sides of pleotelson posterior margin; peduncle-endopod reduced, stub-like; exopod cylindrical, longer than endopod, rounded narrowly distally.

Intertidal, subtidal, shelf, slope (0–454 m). Temperate Southern Africa, Temperate Australasia, Indo-West Pacific (greatest diversity in the Western Indian Ocean). 22 species (several doubtful) (Baker, 1926: figure; Harrison and Holdich, 1984: rediagnosis, history, species list; Benvenuti and Messana, 2000: rediagnosis, key to 20 species; Schotte and Kensley, 2005: rediagnosis, key to 13 Indian Ocean species).

Paradella Harrison and Holdich, 1982

Diagnosis. Body dorsal surfaces smooth or with nodular ornamentation, without setae or with sparse setae, able to conglobate; strongly sexually dimorphic. Pereonite 7 without dorsal bosses, processes or marginal extensions or with bifid process directed posteriorly. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins; merging, pleon

sutures short. Pleotelson tuberculate or smooth; posterior margin with ventral thickened rim, with subapical Y-shaped foramen connected to posterior by narrow slit; ventrolateral margins with broad, low, straight, outfolded ridges not meeting in posterior midline. Antennular peduncle articles 1 and 2 robust, article 3 slender; with articles 2 and 3 colinear, article 3 longer than article 2; flagellum shorter than peduncle. Epistome narrow anteriorly. Mandibular molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes fused basally, long (extending to pleopod rami), tapering smoothly from midlength. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with incomplete transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod broadly rounded distally; exopod broadly or narrowly rounded, or acute, distally.

Estuarine, marine, subtidal (widespread in shallow water habitats, temperate and tropical regions; probably worldwide). 15 species (Harrison and Holdich, 1982a; Bruce and Wetzer, 2004: remarks on difference from *Dynamenella*).

Paraimene Javed and Ahmed, 1988

Diagnosis. Body dorsal surfaces smooth or with ridges or tubercles, able to conglobate; strongly sexually dimorphic. Pleon dorsal surface smooth, or tuberculate; posterior margin with pair of sublateral lobes. Pleotelson with 1 or 2 pairs of longitudinal tubercles; with vertical slit visible posteriorly. Antennular peduncle articles 1–3 of similar stoutness (or tapering); article 3 longer than article 2; flagellum shorter than peduncle. Epistome wide anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate. Penial processes close-set basally, short (not extending beyond pleopod peduncles). Pleopod 4 exopod with transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod and exopod broadly rounded distally.

Intertidal. Tropical Atlantic, Western Indo-Pacific (Pakistan, Iran, Caribbean). 5 species (Javed and Ahmed, 1988: diagnosis; Ortiz et al., 2012: key to species; Arian and Khalaji-Pirbalouty, 2021: rediagnosis, redescription of type species).

Paraleptosphaeroma Buss and Iverson, 1981

Diagnosis. Body flat, coxae without visible sutures, directed laterally, dorsal surfaces smooth, coxal and other margins with membrana cingula (membranous setose fringe), unable to conglobate; not or weakly sexually dimorphic. Rostrum not separating antennular bases. Eyes more dorsal than lateral. Coxal plates truncate. Pleon comprising a single unit; sutures absent. Pleotelson flat, narrower than pleon anteriorly; posterior margin with shallow median indentation, with incomplete ventral groove or channel. Antennular peduncle articles 1 and 2 flat, expanded as anterior and/or anterolateral lobes, with first articles meeting medially; article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Maxillipedal palp articles 2–4 mesial margins not lobate. Penial processes in contact basally. Pleopod 2 appendix masculina inserted distally, ovoid, short. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod without transverse suture, without thickened transverse ridges, with 2 discrete scale patches; endopod without thickened transverse ridges. Uropodal rami forming part of continuous body outline; endopods in contact posteriorly; exopod embedded and flush with margin of endopod, rounded narrowly distally.

Intertidal. Temperate Northern Pacific, Western Indo-Pacific, Tropical Eastern Pacific. 4 species (Buss and Iverson, 1981).

Parasphaeroma Stebbing, 1902

Diagnosis. Body dorsal surfaces smooth. Coxal plates truncate. Pleonite 1 narrower than remainder of pleon, not extending to pleon lateral margins; sutures (except first) running to ventrolateral margin; pleon dorsal surface with posterior medial triangular dorsal projection. Pleotelson with small median triangular dorsal projection; posterior margin simple, arcuate, without exit channel. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum about as long as peduncle. Epistome extended prominently anteriorly and elongate, wide anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate. Pereopod 2 more robust than pereopods 1 and 3. Penial processes short (not extending beyond pleopod peduncles). Pleopod 2 appendix masculina spatulate terminally. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod without transverse suture, with obsolete thickened transverse ridges, with 3 discrete scale patches. Uropodal endopod truncate distally; exopod longer than endopod, acute distally.

Subtidal. Temperate Southern Africa. 1 species (Stebbing, 1902; Bruce, 2001: rediagnosis, redescription).

Parisocladus Barnard, 1914

Diagnosis. Body dorsal surfaces smooth, able to conglobate; strongly sexually dimorphic. Pereonite 7 with prominent horizontal dorsal spine. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins. Pleotelson posterior margin with distinct median point, with subapical foramen connected to apex by narrow slit; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum about as long as peduncle. Epistome wide anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges. Uropodal endopod broadly rounded distally; exopod narrowly rounded or rounded with acute mesiodistal point.

Intertidal. Temperate Southern Africa. 2 species (Kensley, 1978: rediagnosis, key and figures of species).

Pedinura Bruce, 2003

Diagnosis. Body dorsal surfaces smooth, unable to conglobate; not or weakly sexually dimorphic. Head without rostrum. Coxal plates tapering, rounded or coxal plates truncate. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins. Pleotelson posterior margin simple, arcuate, without exit channel; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 flattened strongly (compressed dorsoventrally but not part of anterior margin), with first articles meeting medially; article 1 produced anteriorly (but deflected posteroventrally in one species); article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Epistome wide anteriorly or acute anteriorly. Mandibular molar process surface smooth, surrounded with basal fine setae. Maxillipedal palp articles 2–4 mesial margins not lobate, article 2 not expanded. Pereopods 2 and 3 more slender than others. Penial processes in contact basally or narrowly separated, short (not extending beyond pleopod peduncles), straight. Pleopod 2 appendix masculina inserted near midpoint of mesial margin. Pleopod 4 exopod with transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod without transverse suture, with thickened transverse ridges, with 2 discrete scale patches or with 3 discrete scale patches; endopod with thickened transverse ridges. Uropod attached anteriorly, directed ventrally, not visible in dorsal view; endopod rounded broadly distally; exopod inserted near midpoint of lateral margin of peduncle-endopod, minute, immobile, broadly rounded distally.

Intertidal, subtidal, shelf (0–21 m). Temperate Australia. 2 species (Bruce, 2003).

Pistorius Harrison and Holdich, 1982

Diagnosis. Body dorsal surfaces with nodular ornamentation, coxal and other margins with fringe of short setae, able to conglobate; strongly sexually dimorphic. Rostrum not separating antennular bases. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins; pleon sutures short. Pleotelson vaulted; with short tube directed dorsally, enclosed ventrally and posteriorly; ventrolateral margins simple. Antennular peduncle article 1 robust, longer and more robust than 2 and 3 combined, with first articles meeting medially; article 3 longer than article 2; flagellum about as long as peduncle. Epistome narrow anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes close-set basally, long (extending to pleopod rami). Pleopod 2 appendix masculina basally swollen ("flask-shaped"). Pleopod 3 exopod without transverse suture. Pleopod 4 exopod with incomplete transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropod attached anterolaterally to pleotelson, cylindrical (not especially flattened); without endopod; exopod cylindrical, longer than endopod, falcate distally.

Intertidal. Western and Central Indo-Pacific (southern Great Barrier Reef, Thailand, Japan). 2 species (Harrison and Holdich, 1982b; Nunomura, 1990).

Platycerceis Baker, 1926

Diagnosis. Body flat, coxae without visible sutures, directed laterally, dorsal surfaces smooth, unable to conglobate; not or weakly sexually dimorphic. Head with ventral rostrum. Coxal plates posterolaterally acute, coxal plate 7 shorter than coxal plate 6. Pleonite 1 narrower than remainder of pleon, not extending to pleon lateral margins. Pleotelson flat; posterior margin with deep notch, with incomplete ventral groove or channel. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum longer than peduncle. Epistome acute anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate. Penial processes close-set basally, short (not extending beyond pleopod peduncles). Pleopods 1, 2 exopods lateral margins serrate, especially distally. Pleopod 2 appendix masculina inserted near midpoint of mesial margin, about twice as long as endopod. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, with thickened transverse ridges, with 2 discrete scale patches; endopod with thickened transverse ridges. Uropodal rami extending well beyond pleotelson; peduncle-endopod styliform, acute distally; exopod styliform, acute distally.

Shelf. Temperate Australia. 1 species (Baker, 1926; Harrison, 1984b: rediagnosis, redescription of only species).

Platynympha Harrison, 1984

Diagnosis. Body flat, coxae without visible sutures, directed laterally, dorsal surfaces smooth; not or weakly sexually dimorphic. Rostrum not separating antennular bases. Coxal plates truncate. Pleotelson flat; posterior margin posteriorly narrowed, with posteriorly produced sharp lobe over excision; ventrolateral margins forming ridge. Antennular peduncle article 1 robust, longer and more robust than 2 and 3 combined; article 1 with lower distal angle produced; article 3 as long as or shorter than article 2; flagellum longer than peduncle. Epistome narrow anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes in contact basally, long (extending to pleopod rami). Pleopod 2 appendix masculina tapering evenly to apex. Pleopod 4, 5 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Uropodal rami extending well beyond pleotelson; peduncle-endopod styliform, acute distally; exopod styliform.

Subtidal. Temperate Australia. 1 species (Harrison, 1984b).

Platysphaera Holdich and Harrison, 1981

Diagnosis. Body flat, coxae without visible sutures, directed laterally, dorsal surfaces smooth, coxal and other margins with membrana cingula (membranous setose fringe), unable to conglobate; not or weakly sexually dimorphic. Rostrum acute, not separating antennular bases. Eyes more dorsal than lateral. Coxal plates truncate. Pleon comprising a single unit; sutures absent. Pleotelson flat, narrower than pleon anteriorly; posterior margin simple, arcuate, without exit channel; ventrolateral margins simple. Antennular peduncle articles 1 and 2 flat,

expanded as anterior and/or anterolateral lobes, with first articles meeting medially; article 3 as long as or shorter than article 2; flagellum shorter than peduncle, shorter than peduncular article 3. Epistome wide anteriorly. Mandibular molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins not lobate, article 2 not expanded. Pereopods 2 and 3 more slender than others. Pereopods 1–3 ischium upper margin with few long stiff slender setae. Penial processes in contact basally, short (not extending beyond pleopod peduncles), straight. Pleopod 1 endopod much shorter than exopod. Pleopod 2 appendix masculina twice as long as endopod, rounded bluntly distally. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod without transverse suture, without thickened transverse ridges, with 2 discrete scale patches; endopod without thickened transverse ridges. Uropodal rami forming part of continuous body outline; uropodal endopod rounded broadly distally; exopod inserted anterior to lateral margin of peduncle-endopod, subtriangular.

Subtidal. Central Indo-Pacific (N Australia, Papua New Guinea). 1 species (Holdich and Harrison, 1981b; Bruce, 1994c: rediagnosis, redescription).

Pooredoce Bruce, 2009

Diagnosis. Body dorsal surfaces granular, densely setose, unable to conglobate; strongly sexually dimorphic. Pereonite 7 narrower than pereonite 6. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins; pleon posterior margin with broad plate-like extension. Pleotelson posterior margin with ventral thickened rim, with 2 small submedian foramens and with hardened boss anterior to median notch; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum about as long as peduncle. Epistome narrow anteriorly. Mandibular molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins extended, forming finger-like lobes, article 2 not expanded. Penial processes in contact basally, short (not extending beyond pleopod peduncles). Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 3 discrete scale patches; endopod without thickened transverse ridges. Uropod attached anterolaterally to pleotelson, cylindrical (not especially flattened); endopod round in section, with hard distal terminal spike; exopod inserted near midpoint of lateral margin of peduncle-endopod, cylindrical, reduced, mobile, with hard distal terminal spike.

Subtidal (0–7 m). Central Indo-Pacific (Northern Great Barrier Reef, Australia). 1 species (Bruce, 2009).

Pseudocerceis Harrison and Holdich, 1982

Diagnosis. Body dorsal surfaces smooth or with nodular ornamentation, unable to conglobate; not or weakly sexually dimorphic. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins. Pleotelson with 3 weak longitudinal carinae; with medially indented process directed posteriorly; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, with first articles meeting medially; article 1 with produced acute distal angles; article 3 longer than article 2; flagellum about as long as peduncle or flagellum shorter than peduncle. Epistome acute anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes set apart basally, short (not extending beyond pleopod peduncles), straight. Pleopods 1, 2 (sometimes 3) exopods lateral margins serrate, especially distally (obsolete serrations). Pleopod 2 appendix masculina inserted near midpoint of mesial margin, about as long as endopod. Pleopod 3 exopod with or without transverse suture. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod broadly rounded distally; exopod lateral margin finely serrate or smooth or serrate, broadly rounded distally.

Intertidal, subtidal. Western and Central Indo-Pacific, Temperate Australia (Great Barrier Reef, southern Australia, Somalia and Caribbean, Fiji). 4 species (Harrison and Holdich, 1982b). The Caribbean species *P. latistylis* Kensley and Schotte, 1994 is incorrectly placed in this genus.

Pseudosphaeroma Chilton, 1909

Diagnosis. Body dorsal surfaces with nodular ornamentation, able to conglobate; not or weakly sexually dimorphic. Rostrum not separating antennular bases. Pleon dorsal surface with 2 or more pairs of tubercles. Pleotelson with 2 pairs of sublateral tubercles; posterior margin with upturned dorsal rim, with incomplete ventral groove or channel; ventrolateral margins forming ridge. Antennular peduncle article 1 robust, longer and more robust than 2 and 3 combined; article 3 longer than article 2; flagellum longer than peduncle. Epistome narrow anteriorly. Maxillipedal palp articles 2–4 mesial margins not lobate, article 2 not expanded. Pereopods 1–3 ischium upper margin with few long stiff slender setae. Penial processes close-set basally, short (not extending beyond pleopod peduncles). Pleopod 2 appendix masculina spatulate terminally. Pleopod 4 exopod with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with incomplete transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod broadly rounded distally; exopod inserted laterally near anterolateral angle or near midpoint of lateral margin of peduncle-endopod, broadly rounded distally.

Intertidal, subtidal. Eastern Indo-Pacific, Temperate South America, Temperate Australasia. 7 species (Harrison, 1984b: rediagnosis, 3 species excluded). An undescribed species, previously misidentified as *P. campbellense* Chilton, 1909 has been introduced to the Pacific coast of North America (Bruce and Wetzer, 2008).

Ptyosphaera Holdich and Harrison, 1983

Diagnosis. Body dorsal surfaces smooth; strongly sexually dimorphic. Pleonite 1 as wide as remainder of pleon, extending to

pleon lateral margins. Pleotelson posterior margin with posteriorly directed, flat, acute triangular extension longer than main dome. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum about as long as peduncle. Epistome narrow anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate. Penial processes set apart basally, short (not extending beyond pleopod peduncles), straight. Pleopod 3 exopod with incomplete transverse suture. Pleopod 4 exopod with incomplete transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with incomplete transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal rami flat, grossly enlarged, broad, as long as head and pereon; uropodal endopod broadly rounded distally; exopod broadly rounded distally.

Estuarine. Central Indo-Pacific, Temperate Australia. 1 species (Holdich and Harrison, 1983).

Scutuloidea Chilton, 1883

Diagnosis. Body vaulted weakly, dorsal surfaces smooth, unable to conglobate; not or weakly sexually dimorphic. Pleotelson posterior margin with shallow median indentation or broadly rounded, with incomplete ventral groove or channel. Antennular peduncle articles 1–3 of similar stoutness (or tapering). Maxillipedal palp articles 2–4 mesial margins not lobate. Penial processes close-set basally, long (extending to pleopod rami). Pleopod 2 appendix masculina inserted near midpoint of mesial margin. Pleopod 4 exopod with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal peduncle-endopod a single broad plate alongside pleotelson, narrowly rounded distally; exopod absent.

Intertidal, subtidal. Temperate New Zealand. 2 species (Stephenson and Riley, 1996: rediagnosis, second species).

Sphaeramene Barnard, 1914

Diagnosis. Body dorsal surfaces covered with large separate tubercles, in transverse rows on pereonites, able to conglobate. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins. Pleotelson tuberculate; posterior margin produced, with (or without) narrow slit widening anteriorly to oval foramen. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum shorter than peduncle. Maxillipedal palp articles 2–4 mesial margins lobate. Penial processes set apart basally, short (not extending beyond pleopod peduncles), straight. Pleopod 4 exopod with transverse suture; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod distally with shallow concavity; exopod longer than endopod, acute distally.

Intertidal, subtidal (0–22 m). Temperate Southern Africa. 3 species (Barnard, 1914; Loyola e Silva, 1966: key to species).

Sphaeroma Bosc, 1801

Diagnosis. Body dorsal surfaces with nodular ornamentation, with sparse setae, able to conglobate; not or weakly sexually dimorphic. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins. Pleotelson posterior margin simple, arcuate, without exit channel; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum about as long as peduncle. Epistome narrow or acute anteriorly. Mandibular molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins not lobate, article 2 not expanded. Pereopods 1–3 ischium, merus and propodus upper margins each with rows of long stiff slender setae. Penial processes close-set basally, short (not extending beyond pleopod peduncles). Pleopod 3 exopod without transverse suture. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 5 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod narrowly rounded or acute distally; exopod lateral margin serrate, narrowly rounded or acute distally.

Estuarine, marine, intertidal, subtidal (0–46 m). Temperate Northern Atlantic, Tropical Atlantic, Temperate Northern Pacific, Indo West-Pacific, Temperate South America, Temperate Southern Africa, Temperate Australasia. 38 species (Harrison and Holdich, 1984; Jacobs, 1987: diagnosis, key to 3 species, review) There are several fossil species.

Sphaeromopsis Holdich and Jones, 1973

Diagnosis. Body dorsal surfaces smooth or polished in appearance, coxal and other margins with fringe of short setae (weakly developed), able to conglobate; not or weakly sexually dimorphic. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins; pleon sutures short. Pleotelson posterior margin simple, arcuate, arched in posterior view; ventrolateral margins simple. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum about as long as peduncle. Epistome narrow anteriorly. Mandibular molar process surface with transverse ridges. Maxillipedal palp articles 2–4 mesial margins not lobate, article 2 not expanded. Pereopods 1–3 ischium upper margin with few long stiff slender setae. Penial processes fused basally, long (extending to pleopod rami). Pleopod 2 appendix masculina about as long as endopod. Pleopod 3 exopod with or without transverse suture. Pleopod 4 exopod without transverse suture, with thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, with thickened transverse ridges, with 3 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod broadly rounded distally; exopod broadly rounded or acute distally.

Subtidal, intertidal, sandy beaches. Tropical Atlantic, Western and Central Indo-Pacific. 14 species (Holdich and Harrison, 1981a: rediagnosis; Anil and Jayaraj, 2021: rediagnosis).

Stathmos Barnard, 1940

Diagnosis. Body flat, coxae 2–7 with visible sutures, directed laterally, dorsal surfaces smooth, unable to conglobate. Pleotelson flat; posterior margin produced, without exit channel. Antennular peduncle articles 1 and 2 flat, separately expanded anteriorly; article 3 longer than article 2; flagellum shorter than peduncle. Epistome extended prominently anteriorly and elongate, narrow anteriorly. Maxillipedal palp articles 2–4 mesial margins extended, forming finger-like lobes. Pleopod 2 appendix masculina distal quarter reflexed. Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 3 discrete scale patches; endopod without thickened transverse ridges. Uropodal endopod distally with shallow concavity; exopod truncate distally.

Intertidal–shelf (0–17 m). Temperate Southern Africa. 1 species (Bruce, 2001: rediagnosis, redescription of only species).

Striella Glynn, 1968

Diagnosis. Body flat, coxae without visible sutures, directed laterally, dorsal surfaces smooth, coxal and other margins with fringe of short setae, unable to conglobate. Head without rostrum. Eyes more dorsal than lateral. Coxal plates truncate. Pleon sutures short, converging to single point on posterior margin. Pleotelson flat; posterior margin rounded broadly, with minute median notch, without exit channel. Antennular peduncle articles 1–3 of similar stoutness (or tapering); article 3 as long as or shorter than article 2; flagellum about as long as peduncle. Maxillipedal palp articles 2–4 mesial margins not lobate. Penial processes fused basally, long (extending to pleopod rami). Pleopod 2 appendix masculina tapering from thick base. Pleopod 4 exopod without transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod without transverse suture, without thickened transverse ridges, with 1 discrete scale patch; endopod without thickened transverse ridges. Uropodal endopod broadly rounded distally; exopod shorter than endopod, broadly rounded distally.

Intertidal. Tropical Eastern Pacific (Panama, in barnacle shells). 1 species (Glynn, 1968).

Syncassidina Baker, 1928

Diagnosis. Body flat, coxae without visible sutures, directed laterally, dorsal surfaces smooth, with sparse setae, coxal and other margins with fringe of short setae, unable to conglobate; not or weakly sexually dimorphic. Eyes more dorsal than lateral. Coxal plates truncate. Pleon comprising a single unit (with acute lateral margins); pleon sutures absent. Pleotelson flat; posterior margin with ventral thickened rim (flat and broad), without exit channel; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 flat, expanded as anterior and/or anterolateral lobes, with first articles separated by prominent epistome; article 1 produced anteriorly; article 2 with distinct anterodistal lobe; article 3 as long as or shorter than article 2; flagellum shorter than peduncle. Epistome extended prominently anteriorly and elongate, acute anteriorly. Mandibular molar process surface smooth with palisade of spines on proximal margin. Maxillipedal palp articles 2–4 mesial margins not lobate, article 2 not expanded. Pereopod 1 with elongate propodus. Pereopods 1–3 ischium upper margin with few long stiff slender setae. Penial processes fused basally. Pleopod 2 appendix masculina spatulate terminally (with minute teeth over tapering distal half). Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 3 discrete scale patches (distal end entirely scaled); endopod without thickened transverse ridges. Uropodal rami forming part of continuous body outline; exopod minute, immobile.

Estuarine, marine, subtidal. Temperate Australia. 1 species (Holdich and Harrison, 1981b: rediagnosis, redescription of type species; Bruce, 1994c: rediagnosis, redescription of type species).

Tholozodium Eleftheriou, Holdich and Harrison, 1980

Diagnosis. Body strongly vaulted, dorsal surfaces smooth, able to conglobate; not or weakly sexually dimorphic. Eyes minute. Pleon sutures short. Pleotelson posterior margin simple, arcuate, without exit channel. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum shorter than peduncle. Epistome projecting anteriorly, not conspicuous dorsally. Mandibular palp absent or represented by 1 seta. Maxillipedal palp articles 2–4 mesial margins not lobate. Pereopods 3–6 especially setose. Penial processes in contact basally, long (extending to pleopod rami). Pleopod 2 appendix masculina inserted near midpoint of mesial margin, spatulate. Pleopod 3 exopod without transverse suture. Pleopod 4 exopod without transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges. Pleopod 5 exopod without transverse suture, without thickened transverse ridges, with 2 discrete scale patches; endopod without thickened transverse ridges. Uropodal endopod narrowly rounded distally; exopod acute distally.

Estuarine, marine, intertidal. Western Indo-Pacific, Temperate South America (India, eastern South America). 2 species (Eleftheriou et al., 1980; Pires, 1982).

Waiteolana Baker, 1926

Diagnosis. Body dorsal surfaces with nodular ornamentation, able to conglobate; not or weakly sexually dimorphic. Head without rostrum. Pleonite 1 narrower than remainder of pleon, not extending to pleon lateral margins; pleon dorsal surface tuberculate. Pleotelson posterior margin simple, arcuate, with incomplete ventral groove or channel; ventrolateral margins forming ridge. Antennular peduncle articles 1–3 of similar stoutness (or tapering); article 2 without anterodistal lobe, or with distinct anterodistal lobe; article 3 as long as or shorter than article 2 or longer than article 2; flagellum shorter than peduncle. Epistome narrow anteriorly. Mandibular incisor multicuspid, or unicuspid; molar process surface reduced to thin acute cutting blade. Maxillipedal palp articles 2–4 mesial margins lobate, article 2 not expanded. Penial processes in

contact basally, long (extending to pleopod rami). Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod without thickened transverse ridges, or with obsolete transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 5 discrete scale patches; endopod without thickened transverse ridges, or with obsolete transverse ridges. Uropodal endopod with distal notch; exopod reduced, mobile, lateral margin with subdistal notch, acute distally.

Subtidal, shelf. Temperate Australia, Temperate South America. 3 species (Holdich and Harrison, 1981b; Harrison, 1984b: rediagnoses; Kussakin, 1967).

Xynosphaera Bruce, 1994

Diagnosis. Body globular, highly vaulted, dorsal surfaces smooth, unable to conglobate; not or weakly sexually dimorphic. Head without rostrum. Coxal plates truncate. Pleonite 1 as wide as remainder of pleon, extending to pleon lateral margins; pleon sutures running to ventral margin; pleonal epimeron 2 ventrally well beyond epimera 3 and 4. Pleotelson posterior margin narrowed posteriorly; ventrolateral margins simple. Antennular peduncle articles 1 and 2 robust, article 3 slender, as long as or shorter than article 2; flagellum about as long as peduncle. Epistome wide anteriorly. Mandibular incisor unicuspid. Maxillipedal palp articles 2–4 mesial margins not lobate, article 2 not expanded. Pereopods 1–6 largely without setae; carpus partly fused with propodus on pereopods 2–6. Penial processes set apart basally, short (not extending beyond pleopod peduncles). Pleopod 4 exopod with transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, without thickened transverse ridges, with 4 discrete scale patches; endopod with thickened transverse ridges. Uropodal endopod narrowly rounded distally; exopod longer than endopod, narrowly rounded distally.

Subtidal (coral reefs; commensal burrowing into alcyonaceans). Western and Central Indo-Pacific (Philippines, northeastern Australia, Madagascar). 1 species (Bruce, 1994a).

Zuzara Leach, 1818

Diagnosis. Body dorsal surfaces smooth, able to conglobate; strongly sexually dimorphic. Pereonite 7 with prominent horizontal long dorsal spine. Pleotelson tuberculate; posterior margin trilobate, with median, posterior extension overhanging pleotelson; ventrolateral margins forming ridge. Antennular peduncle articles 1 and 2 robust, article 3 slender, longer than article 2; flagellum about as long as peduncle. Epistome wide anteriorly. Maxillipedal palp articles 2–4 mesial margins lobate. Penial processes close-set basally, short (not extending beyond pleopod peduncles), straight. Pleopod 2 appendix masculina spatulate terminally. Pleopod 4 exopod without transverse suture, without thickened transverse ridges; endopod with thickened transverse ridges. Pleopod 5 exopod with transverse suture, with thickened transverse ridges, with 3 discrete scale patches. Uropodal endopod broadly rounded distally; exopod broadly rounded distally.

Intertidal, subtidal. Central Indo-Pacific, Temperate Southern Africa, Temperate Australia. 5 species (Harrison and Holdich, 1984: rediagnosis).

Freshwater genera excluded from key

Five of the six exclusively freshwater genera are restricted to the inland ground waters of the Dinaric karst and neighbouring territories in Europe (Jaume and Queinnec, 2007; Sket, 1986). One occurs in hot freshwater springs in southwestern United States and Mexico. Other genera that have representative species in estuaries or brackish ponds may extend their ranges upriver into fresh water, or are found on beaches subject to freshwater flow at low tide (e.g. Holdich and Harrison, 1983) are included in the key and list above.

Bilistra Sket and Bruce, 2004. Three species from karst areas in the northwest of South Island, New Zealand (Sket and Bruce, 2004: diagnosis, key to species). *Pseudosphaeroma barnardi* Monod, 1931 belongs to this genus.

Caecosphaeroma Dollfus, 1896. Two species in two subgenera in underground streams in Europe (Sket, 1986).

Makarasphaera Bruce, 2005. One species from maritime freshwater streams and seeps in New Zealand (Bruce, 2005).

Merozoon Sket, 2012. One species from Croatia (Sket, 2012).

Monolistra Gerstaecker, 1856. Nineteen species in five subgenera (Prevorčnik and Sket, 2007; Sket, 1986; Prevorčnik et al., 2010: phylogeny and key to species of subgenus *Microlistra* Racovitza, 1929).

Thermosphaeroma Cole and Bane, 1978. Eight species from hot freshwater springs in the southwestern United States and central Mexico (Bowman, 1981: rediagnosis; Schotte, 2000: key to species).

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Tecticipitidae Iverson, 1982

Figure 9.22

The small family with a single genus is confined to the North Pacific. Iverson (1982) provided an extensive diagnosis but treated the group as a subfamily of Sphaeromatidae. Bruce (1993) rediagnosed it as a family. At least one species is locally very abundant on sandy beaches in Japan (Udagawa et al., 2004).

Diagnosis. Body oval, flat; head free from pereonite 1; pereonites 1–7 visible dorsally, separated by sutures. Coxal dorsal plates 2–7 delimited from tergite by suture; dorsal coxal plate 7 similar to plate 6. Pleon with pleonite 1 almost hidden dorsally, pleonites 2–5 fused, indicated laterally by 2 sutures. Pleotelson broad, triangular. Antennular and antennal peduncles cylindrical, not part of margin of body. Mandibular incisor cultrate, with or without cusps; molar process absent. Maxillula mesial endite with 3 long pectinale spines; lateral endite with about 13 spines. Maxilla with prominent mesial endite with plumose setae; second and lateral endites with long serrate setae. Maxillipedal palp of 5 free articles. Pereopod 1 subchelate, propodus swollen, palm with row of close-set robust setae. Pereopod 2 subchelate in males only. Pleopods 1–3 peduncles subquadrate, with terminal rami. Uropods attached anterolaterally to pleotelson; endopod fused to peduncle (laminar), exopod laminar.

Tecticeps Richardson, 1897

Intertidal sand beaches to bathyal. Temperate Northern Pacific. 12 species (Birstein, 1963; Kussakin, 1979: rediagnosis, key to 11 species).

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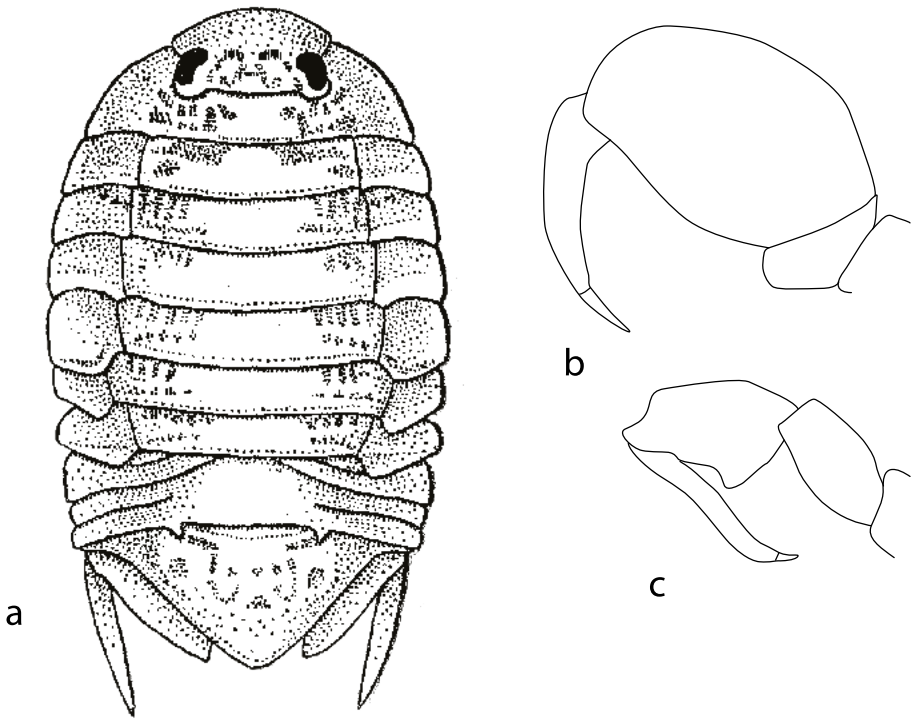


Figure. 9.22. Tecticipitidae. *Tecticeps alascaensis* Richardson, 1897. a, habitus; b, c, carpus–dactylus of pereopods 1, 2 (male).

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Chapter 10. Suborder Valvifera

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Diagnoses and illustrated keys are provided for 12 families and 90 genera of marine isopods of the suborder Valvifera. The ecology and distribution of each taxon are discussed with citation of literature critical for further investigation.

Keywords Antarcturidae, Arcturidae, Arcturididae, Austrarcturellidae, Holidoteidae, Pseudidotheidae, Rectarcturidae, Thermoarcturidae, Xenarcturidae, Chaetiliidae, Hologнathidae, Idoteidae, dichotomous keys

Introduction

Isopods of the suborder Valvifera G.O. Sars, 1883 are distinguished from all other suborders by the manner in which the uropods attach laterally on the pleotelson and are modified to form opercular plates covering the pleopods ventrally. With the exception of one species, all valviferans lack a mandibular palp. Valviferans range in size from a few millimetres long to some of the largest isopods known. In Antarctica, *Glyptonotus antarcticus* Eights, 1852 grows up to 90 mm long (Held and Wägele, 2005).

Valviferans fall naturally into two groups, differentiated on the basis of general body shape, fusion of the head and pereonite 1, arrangement of pereopods, and sexual modification of the male pleopod 1 (see key and diagnoses). Although not recognised formally previously, they are treated as superfamilies here: Arcturoidea Dana, 1849 and Idoteoidea Samouelle, 1819.

Arcturoidea generally have cylindrical bodies with fused head and pereonite 1 and long modified pleopods 1. Some arcturoids use their long setose pereopods 2–4 as filter-feeding baskets (Wägele, 1987) while others have these pereopods modified in other ways. Some arcturoids reach the deepest parts of the ocean. The Idoteoidea are flat with free heads and unmodified first pleopods; they include some of the few herbivorous isopods (Poore et al., 2017).

An early comprehensive review of the systematics and phylogeny of the Valvifera (Brusca, 1984) recognised six families (one, Idoteidae, with five subfamilies). More recent revisions recognise 12 families (Poore, 2001, 2015).

Diagnosis. Head-pereonite 1 free, or fused. Dorsal pereopodal coxal plates present (reduced secondarily in some species); coxal plate of pereopod 1 fused to tergite; coxal plate 7 present; ventral coxal plates 1–7 (medial extension of coxa replacing sternite) extending to midpoint (well defined and separated by suture). Pleonites 4–6 fused into pleotelson, pleonites 1–3 free or fused variously. Pleotelson underside vaulted, branchial chamber defined by ridges along mesial margin of lateral edge; ventrolateral margins of pleon and pleotelson narrow. Penial processes medial, on anterior margin or directly on pleonite 1. Mandibular lacinia mobilis present on both sides; molar usually a cylindrical process with triturative flat end; palp absent (present in *Hologнathus stewarti* (Filhol, 1885)). Maxilla trilobed. Maxillipedal endite reaching at least distal margin of palp article 2, usually truncate distally and setose. Pereopods 1–3 more or less prehensile, directed anteriorly; pereopods 4–7 directed posteriorly. Pleopodal exopods uniarticulate. Pleopod 1 biramous. Pleopod 2 biramous. Pleopod 3 biramous; endopod roughly triangular (or at least with inner angle sharper than outer). Telsonic region of pleotelson elongate, anus situated anteriorly on pleotelson. Uropod situated anterolaterally on pleotelson; peduncle and short rami enclosing pleopods in branchial chamber; rami lateral to margin of pleotelson, articulating in longitudinal axis and folding down alongside branchial chamber.

Key to families of Valvifera

1. Head free from pereonite 1 (rarely fused). Pereopod 1 subchelate and similar to or larger than pereopod 2. Pleopod 1 peduncle as long or shorter than rami; exopod of male laminar, about twice as long as wide, with distal setae shorter than rami (fig. 10.18v) ..... Idoteoidea ... 2

– Head fused with pereonite 1. Pereopod 1 smaller than pereopod 2, sometimes gnathopod-like, very different in structure from pereopod 2. Pleopod 1 peduncle elongate, distinctly longer than rami; exopod of male more than twice as long as wide, laminar with lateral notch or thickened with groove on posterior face, with distal setae longer than rami (fig. 10.4q, t) ..... Arcturoidea ... 4

2. Pereopods 1, 1–3, 1–5 or 1–6 subchelate or prehensile and different from remaining limbs. Head with flat lateral lobes, sometimes notched. Uropod with 2 rami (figs 10.13, 10.14) ..... Chaetiliidae ... p. 459

– Only pereopod 1 subchelate, others ambulatory. Head without flat lateral lobes, never deeply notched. Uropod with 1 or rarely 2 rami 3

3. Pereopod 4 similar to other pereopods. Body oval or elongate; pleotelson acute posteriorly, rarely rounded (figs 10.16–10.18) ..... Idoteidae ... p. 466

– Pereopod 4 shorter than others and with spinose distal articles. Body more or less parallel-sided. Pleotelson rounded posteriorly (fig. 10.15) ..... Hognathidae ... p. 464

4. Pereopod 1 coxal plate and head expanded ventrally and enclosing gnathopod-like pereopod 1. Male pleopod 1 exopod laminar, with lateral notch, a tuft of fine setae, 2 or 3 long plumose setae, or a combination of these (figs 10.3, 10.4) ..... Arcturidae ... p. 442

– Pereopod 1 coxal plate not expanded to enclose pereopod 1. Pereopod 1 a grasping limb (fig. 10.2c). Male pleopod 1 exopod thickened, with groove or with lateral secondary ramus 5

5. Uropodal rami each with apical strong robust seta, exopod minute, shorter than wide. Penial plate bifid apically and splayed. Exopod of male pleopod 1 with overlapping rows of simple and plumose setae along lateral margin, terminating at subdistal excavation into which groove opens. Body cylindrical or often flattened (fig. 10.8) ..... Holidoteidae ... p. 451

– Uropodal rami, if present, without apical strong robust seta, exopod longer than wide, usually with 2 or 3 long apical setae. Penial plate apically simple or weakly bifid. Exopod of male pleopod 1 with simple row of setae along lateral margin; groove opens distolaterally or laterally. Body cylindrical or rarely flattened 6

6. Body strongly geniculate between pereonites 4 and 5 7

– Body straight, not flexed between pereonites 4 and 5 9

7. Pleotelson variously sculptured, often with paired posterior pleotelsonic spines, but without single medial posterior spine dorsal to apex. Pereopods 2–4 with dactylus strong, unguis short (rarely setiform). Pereopods 2–4 similar. Pleonite 1 not articulating with pleotelson; groove on exopod of male pleopod 1 opening distolaterally or laterally 8

– Pleotelson with dorsolateral ridges usually ending in middorsal posterior spine dorsal to apex (or transverse ridge of spines). Pereopods 2–4 with dactylus shortened, unguis setiform, longer than dactylus. Pereopod 4 usually smaller and less setose than pereopods 2 and 3. Pleonite 1 weakly or not articulating with pleotelson. Groove on exopod of male pleopod 1 opening distolaterally or exopod with prominent basally derived lateral lobe (figs 10.6, 10.7) ..... Austrarcturellidae ... p. 448

8. Pereopods 2–4 with closely space pairs of long flexible "filter-setae" and associated shorter finer setae. Uropodal exopod rectangular with distal setae, shorter than endopod. Cuticle smooth (figs 10.1, 10.2) ..... Antarcturidae … p. 435

– Pereopods 2–4 with widely spaced, more or less alternating lateral and mesial stiff setae, without associated groups of shorter finer setae. Uropodal rami triangular, exopod slightly smaller than endopod, both rami with terminal robust setae. Cuticle covered in fur of fine setae (fig. 10.11) ..... Thermoarcturidae ... p. 458

9. Body dorsoventrally flattened, dorsally setose, without spines. Pereopods 2 and 3 with even rows of long setae, pereopods 4–7 ambulatory (fig. 10.12) ..... Xenarcturidae ... p. 458

– Body cylindrical, ornamented. Pereopods 2–4 differentiated from ambulatory pereopods 5–7 or 2–7 10

10. Pereonites cylindrical, longer than wide, each with paired simple dorsal spines. Pereopods 2–7 similar, ambulatory (fig. 10.5) ..... Arcturididae ... p. 448

– Pereonites wider than long, with complex dorsal plate-like spination. Pereopods 2–4 differentiated from ambulatory pereopods 5–7 11

11. Pereopods 1–4 with strong robust setae on broad articles, dactyli with short unguis. Exopod of male pleopod 1 with groove ending on distolateral apical extension (fig. 10.9) ..... Pseudidotheidae ... p. 453

– Pereopods 2–4 with weak rows of long setae, dactyli with long, setiform unguis. Exopod of male pleopod 1 with groove ending distolaterally (fig. 10.10) ..... Rectarcturidae ... p. 454

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Credits

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Fig. 10.1a, Kussakin and Vasina (1995); b, d, g, Schultz (1981); c, e, Beddard (1886); f, Poore (1998); h, Brandt (1990); i, Baltzer et al. (2000); j, Kussakin and Vasina (1998); k, Kussakin and Vasina (1994). Fig. 10.2a, Hale (1946); b, e, Beddard (1886); c, Poore (2012); d, Kussakin (1967); f, Vanhöffen (1914); g, Pereira et al. (2019). Fig. 10.3a, h, Kensley et al. (2007); d, e, Menoui and Poore (2008); f, King and Poore (2001); g, Sars (1897); k, King (2003b); l, Stransky et al. (2020). Fig. 10.5a, Hale (1946). Fig. 10.6a, b, d, Poore and Bardsley (1992); c, Poore (1998). Fig. 10.8a–f, Kensley (1978). Fig. 10.9, Poore and Bardsley (2004). Fig. 10.10a–d, g, h, Poore (2013); e, f, Park and Wägele (1995). Fig. 10.11a, Schultz (1966); b, Kensley (1978). Fig. 10.12a, b, Park (1995). Fig. 10.13a, Poore (1978); b, k, l, Poore (1985); c, King and Cawood (2007); d, m, Poore (1984); e, Wägele (1991); f, Poore et al. (2009); g, Jones and Fenwick (1978); h, Roman (1991); j, Holthuis (1964). Fig. 10.15a, b, Poore and Lew Ton (1990). Fig. 10.16b, e, g, h, j, m, s, Poore and Lew Ton (1993); c, Miers (1881); f, Brandt (1990); n, King and Poore (2001); o, Moreira (1974). Fig. 10.17a, Park and Wägele (1995); b, Santos and Xavier (2011); c–e, Poore and Lew Ton (1993); f, Poore and Hurley (2015).

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Superfamily Arcturoidea Dana, 1849

Arcturoids differ from idoteids in the fusion of pereonite 1 to the head, gnathopod-like first pereopod and the modified pleopod 1, that of the male interacting with the appendix masculina on pleopod 2 as a spermatophore-transfer device.

Diagnosis. Body more or less cylindrical, without coxal dorsal plates or pleonal epimera (*Xenarcturus* excepted). Head and pereonite 1 fused. Pereopod 1 smaller than pereopod 2, sometimes gnathopod-like, very different in structure from pereopod 2. Pleopod 1 peduncle more elongate than rami, longer than on other pleopods; exopod of male thickened and with groove on posterior face, or laminar, with proximolateral notch.

Antarcturidae Poore, 2001

Figures 10.1, 10.2

Antarcturids lack the elongate pereonite 4 that characterises Arcturidae (Poore, 2001). The anterior body is held erect to allow filter feeding using long setae on pereopods 2–4 (Wägele, 1987). The mouthparts are visible in lateral view. The family is diverse, especially in deep water of the Southern Ocean (Wägele, 1991). The major revision of Brandt (1990) established many of the current genera. Keys to identify some species can be found in Wägele (1991) and Kussakin (1982), the latter in Russian and now somewhat outdated. A cladistic analysis using morphological features of representatives of eight genera found that not all are monophyletic (Pereira et al., 2019).

Diagnosis. Body more or less cylindrical, without coxal dorsal plates or pleonal epimera, flexed between pereonites 4 and 5, anterior segments held slightly erect. Pereopod 1 gnathopod-like; pereopods 2–4 elongated, with even rows of long filter-setae, differentiated from ambulatory pereopods 5–7; with prominent dactyli, unguis short. Uropodal exopod (smaller ramus) tapering (with terminal seta or setae only). Pleopod 1 peduncle more elongate than rami, longer than on other pleopods; exopod of male thickened and with groove on posterior face, ending distolaterally or laterally on simple margin.

Implicit generic attributes. Head with pair of submedian spines between eyes; pereonites without supracoxal spines (tubercles at most); without paired sublateral spines; without paired submedian spines; without middorsal spines. Pleonites without middorsal spines; without marginal lateral spines. Eyes pigmented. Pereopods 2–4 with regular rows of long setae along flexor margins of merus–propodus; dactylus linear, with few short setae along flexor margin; unguis short, curved.

Key to genera of Antarcturidae

1. Pereopods 2–4 with regular rows of long setae along flexor margins of merus–dactylus (figs 10.1f, g, 10.2m) 2
– Pereopods 2–4 with regular rows of long setae along flexor margins of merus–propodus; dactylus with few short setae (fig. 10.2b) 5
2. Pleonite 1 free from remaining pleotelson; pleonites 2 and 3 with middorsal spine; pleotelson with marginal lateral spines (fig. 10.2d) ..... *Mixarcturus*
– Pleonite 1 fused to remaining pleotelson; pleonites 2 and 3 without middorsal spine; pleotelson without lateral spines 3
3. Pereonites 1 and 3 only with prominent supracoxal spines (fig. 10.1c). Pereopods 2–4 unguis setiform (figs 10.1d, 10.2m) ..... *Caecarcturus*
– Pereonites 1–7 variously spinose. Pereopods 2–4 unguis short or absent 4
4. Pereonites 1, 2 with supracoxal spines directed anteriorly; 4–7 with triangular spines; pereon otherwise smooth (fig. 10.1j) ..... *Glaberarcturus*
– Pereonites 1–7 with supracoxal, sublateral, submedian and middorsal spines (fig. 10.1d, e) ..... *Chaetarcturus*
5. Pleotelson with pair of prominent posterolateral spines longer than lateral spines (figs 10.1c, h, i, 10.2b, c, e) 6
– Pleotelson without pair of prominent posterolateral spines 11
6. Pleotelson with prominent medial posterior spine dorsal to margin (fig. 10.2c, e) 7
– Pleotelson without medial posterior spine dorsal to margin (fig. 10.1c, h, i, 10.2b) 8
7. Pereonites 1–5 with middorsal spines on posterior margins. Pleonites 5 and 6 with middorsal spines (fig. 10.2c) ..... *Marmachius*
– Pereonites 1–5 without middorsal spines. Pleonites 5 and 6 without middorsal spines (fig. 10.2e) ..... *Oxyarcturus*
8. Head without pair of submedian spines between eyes 9
– Head with pair of submedian spines between eyes 10
9. Pleonite 1 articulating with pleotelson. Posterolateral spines on pleotelson about half as long as pleotelson (fig. 10.1i) ..... *Furcarcturus*
– Pleonite 1 fused with pleotelson. Posterolateral spines on pleotelson about one-fifth as long as pleotelson (fig. 10.2b) ..... *Litarcturus*
10. Antennal flagellum of 9 or more short articles (fig. 10.2i). Pereopods 2–4 unguis short, curved (fig. 10.2l) ..... *Antarcturus*
– Antennal flagellum of 3 or more articles plus claw (fig. 10.2j). Pereopods 2–4 unguis setiform (fig. 10.2n) ..... *Fissarcturus*

11. Pereonites with sublateral and supracoxal mushroom-like tubercles; pereonites 1–4 with middorsal tubercles on posterior margins (fig. 10.2f). Antennal flagellum of 9 or more short articles ..... *Tuberarcturus*

– Pereonites ornamented with spines or tubercles, without mushroom-like tubercles. Antennal flagellum of 4 or fewer articles 12

12. Pleotelson prominently produced posteriorly (figs 10.1b, g, 10.2g) 13

– Pleotelson not prominently produced posteriorly 15

13. Pereon and pleotelson without spines or tubercles (fig. 10.1g). Pereopods 2–4 unguis setiform ..... *Cylindrarcturus*

– Pereon and pleotelson spinose or tuberculate. Pereopods 2–4 unguis short, curved 14

14. Body spinose (fig. 10.1b). Antennal flagellum of 4 similar articles (fig. 10.2h). Uropod with 1 short ramus, tenth length of peduncle (fig. 10.2o) ..... *Acantharcturus*

– Body tuberculate at most (fig. 10.2g). Antennal flagellum of 2 articles and claw (fig. 10.2k). Uropod with 1 long ramus, half length of peduncle (fig. 10.2p) ..... *Xiphoarcturus*

15. Head without submedian spines. Pereon without supracoxal, sublateral and submedian spines. Pleotelson dorsal surface bulbous, as long as wide (fig. 10.1k) ..... *Globarcturus*

– Head with submedian spines. Pereon with supracoxal, sublateral and submedian spines or tubercles. Pleotelson dorsal surface convex, longer than wide 16

16. Eyes present. Pereon with prominent tubercles. Pleotelson with prominent middorsal blade-like tubercles, with marginal lateral projections (fig. 10.2a) ..... *Halearcturus*

– Eyes absent. Pereon with small tubercles and paired sublateral spines. Pleotelson with lateral and sublateral tubercles (fig. 10.1a) ..... *Abyssarcturus*

Abyssarcturus Kussakin and Vasina, 1995

Diagnosis. Pereonites with supracoxal spines on all pereonites; with paired sublateral tubercles; with paired submedian tubercles (spines on pereonites 1 and 2). Pleonite 1 free from remaining segments of pleotelson. Pleotelson without paired submedian spines; with pairs of sublateral tubercles. Eyes absent. Antennal flagellum of 3 articles. Pereopods 2–4 unguis half as long as dactylus. Pleopod 1 of male exopod groove opening distolaterally on margin, scarcely produced at opening. Pleopod 2 of male, appendix masculina acute, about as long as endopod. Uropod with triangular endopod and smaller exopod.

Abyssal. Southern Ocean. 1 species (Kussakin and Vasina, 1995).

Acantharcturus Schultz, 1981

Diagnosis. Pereonites with supracoxal spines on all pereonites; with paired sublateral spines; with paired submedian spines; with middorsal spines on posterior margins of pereonites 1–5. Pleonite 1 free from remaining segments of pleotelson. Pleotelson with paired submedian spines or tubercles; with few pairs of sublateral spines, none more prominent than others; with marginal lateral spines; produced prominently posteriorly. Antennal flagellum of 4 articles. Pleopod 1 of male exopod groove opening distolaterally on lobe-like apex beset with numerous fine setae. Pleopod 2 of male, appendix masculina elongate, acute, considerably longer than endopod. Uropod with short endopod only.

Abyssal. Southern Ocean. 3 species (Schultz, 1981; Wägele, 1991: rediagnosis, key to 2 species).

Antarcturus zur Strassen, 1902

Diagnosis. Pereonites with supracoxal spines on all pereonites; with paired sublateral spines; without paired submedian spines (sometimes with tubercles). Pleonite 1 fused to remaining pleotelson. Pleotelson with paired submedian spines or tubercles; with pairs of sublateral tubercles, or with few pairs of sublateral spines, none more prominent than others, or with prominent pair of sublateral spines on pleonite 3; with marginal lateral spines; with pair of prominent posterolateral spines longer than other sublateral spines. Antennal flagellum of 9 or more short articles. Pleopod 1 of male exopod groove opening distolaterally on margin, scarcely produced at opening. Pleopod 2 of male, appendix masculina acute, about as long as endopod. Uropod with triangular endopod and smaller exopod.

Shelf–abyssal. Temperate Northern W Pacific, Southern Ocean. 26 species (Brandt, 1990: rediagnosis, species descriptions; Wägele, 1991: rediagnosis, key to 15 Antarctic species).

Caecarcturus Schultz, 1981

Diagnosis. Head without pair of submedian spines between eyes; pereonites with prominent supracoxal spines on pereonites 1 and 3 only. Pleonite 1 fused to remaining pleotelson. Pleotelson without paired submedian spines; with prominent pair of sublateral spines on pleonite 3. Eyes absent. Antennal flagellum of 4 articles. Pereopods 2–4 with regular rows of long setae along flexor margins of merus-dactylus; unguis setiform. Pleopod 1 of male exopod groove opening

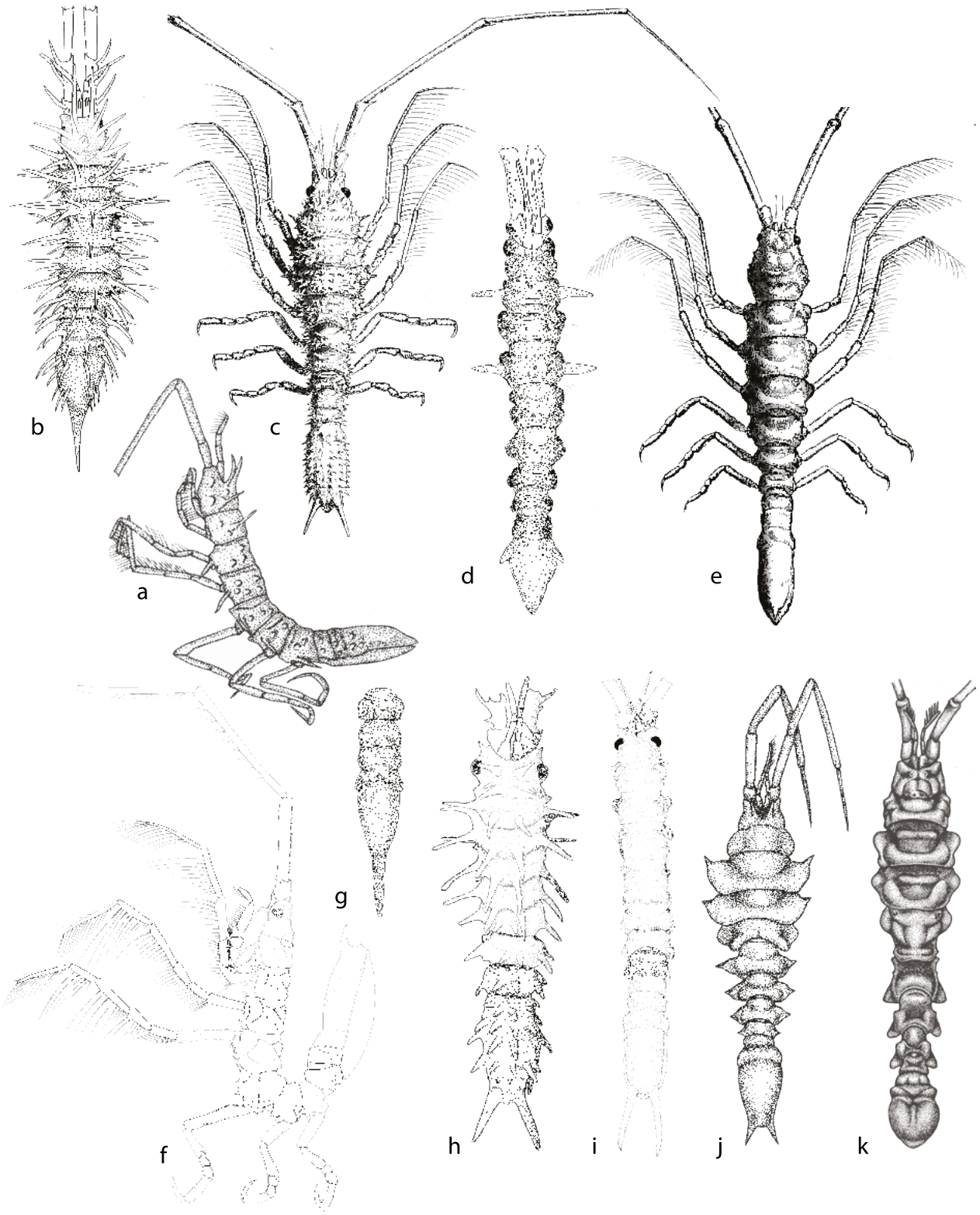


Figure 10.1. Antarcturidae. a, *Abyssarcturus averincevi* Kussakin and Vasina, 1995; b, *Acantharcturus acutipleon* Schultz, 1981; c, *Antarcturus glacialis* (Beddard, 1886); d, *Caecarcturus quadraspinosus* Schultz, 1981; e, *Chaetarcturus abyssicolus* (Beddard, 1886); f, *Chaetarcturus crosnieri* Poore, 1998; g, *Cylindrarcturus elongatus* Schultz 1981 (pereonite 7, pleotelson); h, *Fissarcturus emarginatus* Brandt, 1990; i, *Furcarcturus polarsterni* Baltzer, Held and Wägele, 2000; j, *Glaberarcturus stellae* Kussakin andVasina, 1998; k, *Globarcturus angelikae* Kussakin and Vasina, 1994.

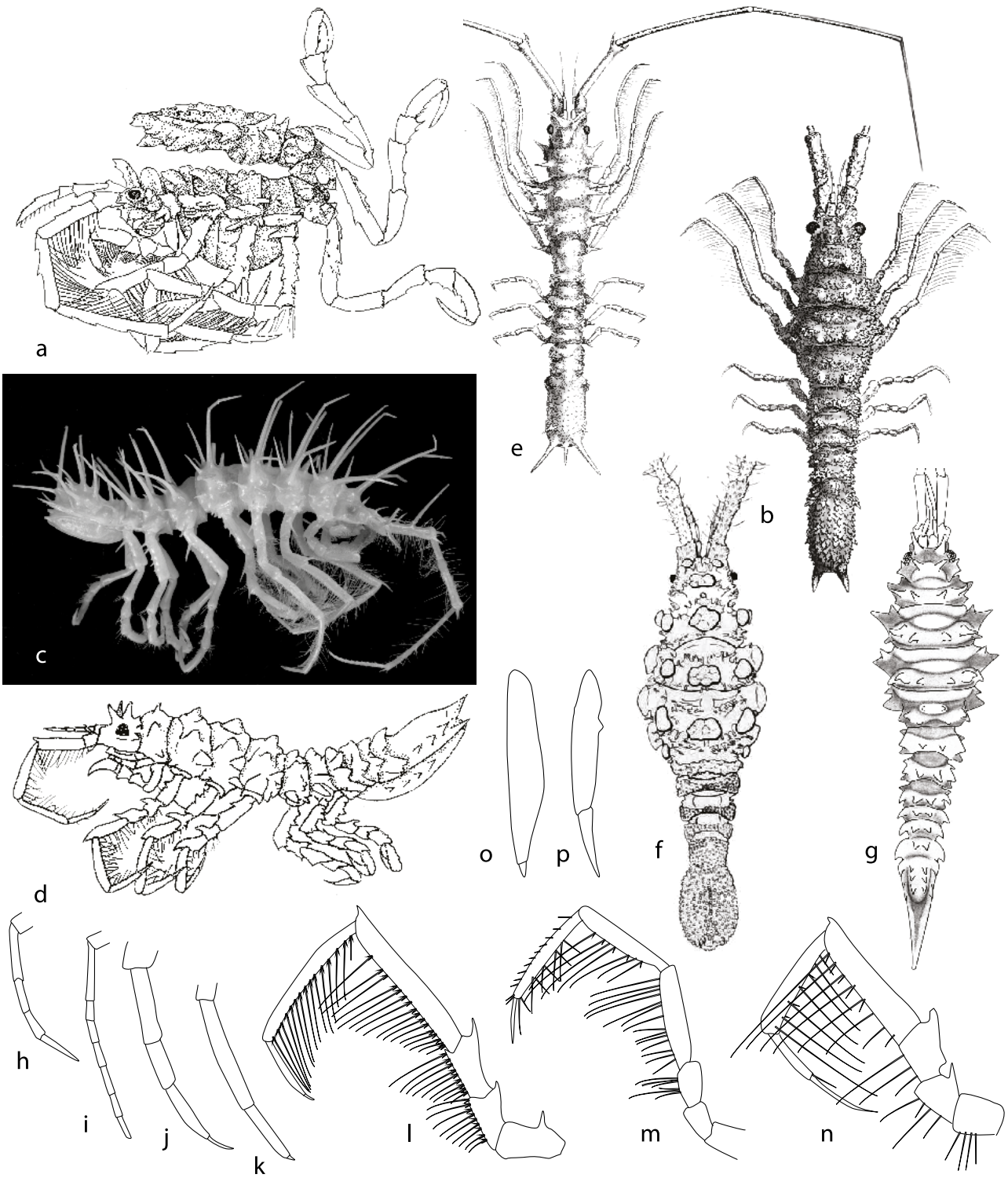


Figure 10.2. Antarcturidae. a, *Halearcturus serrulatus* (Whitelegge, 1904); b, *Litarcturus americanus* (Beddard, 1886); c, *Marmachius fortunae* Poore, 2012; d, *Mixarcturus abnormis* (Kussakin, 1967); e, *Oxyarcturus spinosus* (Beddard, 1886); f, *Tuberarcturus drygalskii* (Vanhöffen, 1914); g, *Xiphoarcturus kussakini* Pereira, Roccatagliata and Doti, 2019. Antennal flagellum: h, *Acantharcturus*; i, *Antarcturus*; j, *Fissarcturus*; k, *Xiphoarcturus*. Pereopod 2: l, *Antarcturus*; m, *Caecarcturus*; n, *Fissarcturus*. Uropod: o, *Acantharcturus*; p, *Xiphoarcturus*.

distolaterally on margin, scarcely produced at opening. Pleopod 2 of male, appendix masculina acute, about as long as endopod. Uropod with short endopod only (uncertain).

Shelf–bathyal. Southern Ocean (subantarctic New Zealand). 1 species (Schultz, 1981).

Chaetarcturus Brandt, 1990

Diagnosis. Pereonites with supracoxal spines on all pereonites; with paired sublateral spines; with paired submedian spines; with middorsal spines on posterior margins of pereonites 1–5. Pleonite 1 fused to remaining pleotelson. Pleotelson with paired submedian spines or tubercles; with few pairs of sublateral spines, none more prominent than others; with pair of prominent posterolateral spines longer than other sublateral spines; with prominent medial posterior spine dorsal to margin. Antennal flagellum of 3–7 articles. Pereopods 2–4 with regular rows of long setae along flexor margins of merus-dactylus. Pleopod 1 of male exopod groove opening distolaterally on subterminal triangular projection. Uropod with triangular endopod and smaller exopod.

Shelf–bathyal. Temperate Northern W Pacific, Central Indo-Pacific, Temperate South America, Temperate Australasia, Southern Ocean. 25 species (Brandt, 1990; Wägele, 1991: rediagnosis, key to 6 Antarctic species; Poore, 1998: list of species).

Cylindrarcturus Schultz, 1981

Diagnosis. Head without pair of submedian spines between eyes. Pleonite 1 fused to remaining pleotelson. Pleotelson without paired submedian spines; prominently posteriorly produced. Antennal flagellum of 4 articles. Pereopods 2–4 unguis setiform. Uropod with short endopod only.

Shelf–abyssal. Southern Ocean. 3 species (Schultz, 1981; Wägele, 1991: rediagnosis; Brandt, 2002).

Fissarcturus Brandt, 1990

Diagnosis. Pereonites with supracoxal spines on all pereonites; with paired sublateral spines, or with paired sublateral tubercles; without paired submedian spines, or with paired submedian spines. Pleonite 1 fused to remaining pleotelson. Pleotelson with paired submedian spines or tubercles; with few pairs of sublateral spines, none more prominent than others; with marginal lateral spines; with pair of prominent posterolateral spines longer than other sublateral spines. Antennal flagellum of 4 or more articles plus claw. Pereopods 2–4 unguis setiform. Pleopod 1 of male exopod groove opening laterally on margin, covered with small lobe. Pleopod 2 of male, appendix masculina elongate, acute, considerably longer than endopod. Uropod with triangular endopod and smaller exopod.

Shelf–bathyal. Southern Ocean. 22 species (Brandt, 1990; Wägele, 1991: keys to species as *Fissarcturus* and *Neoarcturus*; Poore, 2003: corrections to Wägele's use of *Neoarcturus*; Brandt, 2007).

Furcarcturus Baltzer, Held and Wägele, 2000

Diagnosis. Head without pair of submedian spines between eyes. Pleonite 1 free from remaining segments of pleotelson. Pleotelson without paired submedian spines; with pair of prominent posterolateral spines half as long as pleotelson. Antennal flagellum of 9 or more short articles. Pleopod 1 of male exopod groove opening laterally on margin, covered with small lobe. Pleopod 2 of male, appendix masculina acute, about as long as endopod. Uropod with triangular endopod and smaller exopod.

Bathyal. Southern Ocean. 1 species (Baltzer et al., 2000).

Glaberarcturus Kussakin and Vasina 1998

Diagnosis. Pereonites with supracoxal spines directed anteriorly on pereonites 2, 3, triangular spines on 5–7. Pleonite 1 fused to remaining pleotelson. Pleotelson without paired submedian spines; with pair of prominent posterolateral spines one fifth as long as pleotelson. Eyes absent. Antennal flagellum of 2 articles plus short claw. Pereopods 2–4 with regular rows of long setae along flexor margins of merus–dactylus. Uropod with triangular endopod and smaller exopod.

Bathyal. Southern Ocean. 1 species (Kussakin and Vasina, 1998).

Globarcturus Kussakin and Vasina 1994

Diagnosis. Head without pair of submedian spines between eyes. Pleonite 1 free from remaining segments of pleotelson. Pleotelson dorsal surface bulbous, as wide as long; pleotelson without paired submedian spines. Eyes absent. Antennal flagellum of 4 articles plus claw. Pleopod 1 of male exopod groove opening distolaterally on margin, scarcely produced at opening. Pleopod 2 of male, appendix masculina elongate, acute, considerably longer than endopod. Uropod with triangular endopod and smaller exopod.

Hadal. Southern Ocean. 1 species (Kussakin and Vasina, 1994).

Halearcturus Poore, 2015

Diagnosis. Pereonites with supracoxal spines on all pereonites; with paired sublateral tubercles. Pleonite 1 fused to remaining pleotelson. Pleotelson with 2 middorsal tubercles near apex; pleotelson without paired submedian spines; with pairs of sublateral tubercles; with marginal lateral projections. Antennal flagellum of 1 long and 1 minute articles. Pleopod 1 of male exopod groove opening distolaterally on margin, scarcely produced at opening. Pleopod 2 of male, appendix masculina elongate, acute, considerably longer than endopod. Uropod with short endopod only.

Shelf. Temperate SE Australia. 1 species (Poore, 2015).

Litarcturus Brandt, 1990

Diagnosis. Head without pair of submedian spines between eyes. Pleonite 1 fused to remaining pleotelson. Pleotelson without paired submedian spines; with pair of prominent posterolateral spines one fifth as long as pleotelson. Antennal flagellum of 9 or more short articles. Pereopods 2–4 unguis half as long as dactylus. Pleopod 1 of male exopod groove opening distolaterally on margin, scarcely produced at opening. Uropod with triangular endopod and smaller exopod.

Shelf–bathyal. Southern Ocean. 7 species (Brandt, 1990; Wägele, 1991: rediagnosis, key to 6 Antarctic species).

Marmachius Poore, 2012

Diagnosis. Pereonites with supracoxal spines on all pereonites; with paired sublateral spines (exceptionally long); with paired submedian spines (exceptionally long); with middorsal spines on posterior margins of pereonites 1–5. Pleonite 1 free from remaining segments of pleotelson. Pleotelson dorsal surface bulbous, differentiated from lateral margin by longitudinal groove; pleonites 5 and 6 with middorsal spines; pleotelson with paired submedian spines or tubercles; with few pairs of sublateral spines, none more prominent than others; with marginal lateral spines; with pair of prominent posterolateral spines longer than other sublateral spines; with prominent medial posterior spine dorsal to margin. Antennal flagellum of 9 or more short articles. Pleopod 1 of male exopod groove opening distolaterally on lobe-like apex with numerous fine setae. Pleopod 2 of male, appendix masculina elongate, acute, considerably longer than endopod. Uropod with triangular endopod and smaller exopod.

Slope, abyssal. Temperate SE Australia, Southern Ocean. 2 species (Poore, 2012).

Mixarcturus Brandt, 1990

Diagnosis. Pereonites with supracoxal spines on all pereonites (tubercles only); with paired sublateral tubercles; with paired submedian tubercles. Pleonite 1 free from remaining segments of pleotelson. Pleonites 2 and 3 with middorsal spine; pleotelson without paired submedian spines; with marginal lateral spines; with pair of prominent posterolateral spines longer than other sublateral spines. Antennal flagellum of 3 articles plus claw. Pereopods 2–4 with regular rows of long setae along flexor margins of merus–dactylus. Pleopod 1 of male exopod groove opening distolaterally on margin, scarcely produced at opening. Pleopod 2 of male, appendix masculina elongate, acute, considerably longer than endopod. Uropod with triangular endopod and smaller exopod.

Shelf–bathyal. Southern Ocean. 3 species (Brandt, 1990; Wägele, 1991: rediagnosis, key to 2 Antarctic species).

Oxyarcturus Brandt, 1990

Diagnosis. Pereonites with supracoxal spines on all pereonites; with paired sublateral spines; with paired submedian spines. Pleonite 1 fused to remaining pleotelson. Pleotelson with paired submedian spines or tubercles (pleonites 1–3 only); with few pairs of sublateral spines, none more prominent than others; with pair of prominent posterolateral spines longer than other sublateral spines; with prominent medial posterior spine dorsal to margin. Antennal flagellum of 9 or more short articles. Uropod with triangular endopod and smaller exopod.

Shelf–bathyal. Southern Ocean. 2 species (Brandt, 1990; Wägele, 1991: rediagnosis, key to 3 Antarctic species; Pereira et al., 2023).

Tuberarcturus Brandt, 1990

Diagnosis. Head with pair of submedian spines between eyes (blunt); pereonites with supracoxal mushroom-like tubercles; with paired sublateral tubercles (mushroom-shaped); with middorsal tubercles on posterior margins of pereonites 1–4. Pleonite 1 fused to remaining pleotelson. Pleotelson without paired submedian spines. Antennal flagellum of 9 or more short articles. Uropod with triangular endopod and smaller exopod.

Shelf–bathyal. Southern Ocean. 5 species (Brandt, 1990; Wägele, 1991: rediagnosis, key to 3 Antarctic species).

Xiphoarcturus Pereira, Roccatagliata and Doti, 2019

Diagnosis. With paired sublateral spines, or with transverse ridge. Pleonite 1 fused to remaining pleotelson. Pleotelson with paired submedian spines or tubercles; with few pairs of sublateral spines, none more prominent than others; produced prominently posteriorly. Antennal flagellum of 2 articles plus short claw. Pleopod 1 of male exopod groove opening distolaterally on margin, scarcely produced at opening. Pleopod 2 of male, appendix masculina elongate, acute, considerably longer than endopod. Uropod with endopod only, about half as long as peduncle.

Slope. Temperate South America (Mar del Plata submarine canyon). 2 species (Pereira et al., 2019).

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Arcturidae Bate and Westwood, 1868

Figures 10.3, 10.4

Most arcturids are strongly geniculate between pereonites 4 and 5, the anterior segments held prominently erect, but this is not always the case. Pleonite 4 is usually longer than more anterior pleonites, especially in males, where it can be very thin. Pereopods 2–4 are usually cylindrical and held close under the mouthparts at rest, but are expanded as a filter-basket of long setae for feeding. These limbs can be absent or not so modified.

Poore (2001) restricted Arcturidae to valviferans with mouthparts hidden laterally by plates of the head and pereonite 1, and the exopod of the male pleopod 1 having a lateral notch, usually supporting two or more long plumose setae. He placed other hitherto "arcturids" in Antarcturidae. Amesopodidae Stebbing, 1905 and the subfamily Edwinjoyceinae Müller, 1993 [pro Edwinjoycinae misspelling] are not recognised. Kim and Yoon (2021) were the first to write a key to 14 genera; the one here uses other characters.

Diagnosis. Body more or less cylindrical, without coxal dorsal plates or pleonal epimera, weakly or strongly geniculate between pereonites 4 and 5, anterior segments usually held prominently erect. Pereonite 4 at least 1.5 times as long as pereonite 3 (in males often much longer). Mouthparts and pereopod 1 enclosed in lateral view by lateral plates of head and pereonite 1. Pereopod 1 dactylus with unguis, or without unguis. Pereopod 1 gnathopod-like; pereopods 2–4 usually cylindrical, usually with even rows of long filter-setae, differentiated from ambulatory pereopods 5–7; pereopods 3 and 4 rarely absent; with prominent dactyli, unguis short (or dactylus lost in some pereopods). Uropodal exopod (smaller ramus) tapering (with terminal seta or setae only) (rarely absent). Pleopod 1 peduncle more elongate than rami, longer than on pleopods 2 and 3; exopod of male laminar, with proximolateral notch with 3 or 3 long setae. Basally as wide or wider than endopod.

Implicit generic attributes. Antenna slender, peduncle without tubercles. Maxillipedal palp with 5 free articles. Male ventral appendage absent. Uropod exopod present.

Key to genera of Arcturidae

1. Pereopod 2 ambulatory or vestigial, pereopods 3 and 4 absent, or pereopod 4 vestigial (figs 10.3a, 10.4n) 2
– Pereopods 1–7 present and fully formed (fig. 10.3f, g, k, l) 5
2. Pereopod 2 present as a small plate (fig. 10.3i). Antenna 2 flagellum terminal article with comb of strong setae (fig. 10.4b). Maxillipedal palp articles 2, 3 fused (fig. 10.4e) ..... *Edwinjoycea*
– Pereopod 2 ambulatory or setose. Antenna 2 flagellum of 3 articles, with or without unguis (fig. 10.4a, c). Maxillipedal palp articles free (fig. 10.4d) 3
3. Pereopod 2 ambulatory (figs 10.3a, 10.4i) ..... *Amesopous*

– Pereopod 2 held against mouthparts, setose (fig. 10.3e) 4

4. Pereopod 4 absent. Pereonites 3 and 4 much wider than head, rounded (fig. 10.3d, e) ..... *Arcturinoides*

– Pereopod 4 vestigial (fig. 10.4n). Pereonites 2, 3 short, pereonite 4 much longer, with broad triangular wings in female (fig. 10.3c) ..... *Arcturinella*

5. Pereopods 2–4 with flexion between carpus and propodus, without dactylus (fig. 10.4l) 6

– Pereopods 2–4 without flexion between carpus and propodus, usually with dactylus (fig. 10.4j, k, m) 8

6. Pleotelson with dorsolateral triangular wings (fig. 10.3h). Male without prominent ventral pereonal projection ..... *Astacilla*

– Pleotelson without dorsolateral triangular wings. Male with prominent ventral projection on pereonite 3 (fig. 10.3f) or 5 (fig. 10.3m). 7

7. Male with prominent spoon-shaped or trifid ventral projection on pereonite 3 (fig. 10.3f) ..... *Arcturopsis*

– Male with prominent bifurcate ventral projection on pereonite 5 (fig. 10.3m) ..... *Arctopsis*

8. Pereopod 1 dactylus with unguis (fig. 10.4f, g) 9

– Pereopod 1 dactylus without unguis (fig. 10.4h) 10

9. Pereonites 2–4 similar, cylindrical, often sculptured (fig. 10.3g). Pereopods 2–4 cylindrical, with rows of setae (fig. 10.4k) ..... *Arcturus*

– Pereonites 2–4 in female together forming rhomboid shape (fig. 10.3b), in male cylindrical with dorsal ridge, pereonite 4 longer than pereonites 2, 3. Pereopods 2–4 flattened, with few setae (fig. 10.4j) ..... *Arcturina*

10. Pereopods 2–4 flattened, with few short setae (fig. 10.4m) ..... *Parastacilla*

– Pereopods 2–4 cylindrical, with dense setae (fig. 10.4k) 11

11. Antenna peduncle articles 2, 3 with spines on upper margin. Pereonite 4 about twice as long as pereonites 2, 3 together, more so in male (fig. 10.3l). North Pacific and North Atlantic only ..... *Spectrarcturus*

– Antenna peduncle articles 2, 3 smooth. Pereonite 4 at least 3 times as long as pereonites 2, 3 together, more so in male 12

12. Body strongly geniculate between pereonites 4 and 5, sometimes sculptured with lobes or spines (fig. 10.3k). Pereopods 5–7 dactylus longer than wide, with 2 ungues (fig. 10.4p) ..... *Neastacilla*

– Body weakly geniculate between pereonites 4 and 5, slightly dorsoventrally flattened (fig. 10.3j). Pereopods 5–7 dactylus reduced, with swollen pad on lower margin, unguis hook-like (fig. 10.4o) ..... *Idarcturus*

Amesopous Stebbing, 1905

Diagnosis. Body weakly geniculate between pereonites 4 and 5, cylindrical, smooth; pereonites 2, 3 of similar width, narrow; pereonite 4 of similar proportions to pereonites 2, 3 in both sexes; pleotelson without dorsolateral posterior wings. Antenna flagellum with 3 articles. Pereopod 1 dactylus without unguis; pereopod 2 ambulatory; pereopods 3, 4 absent; without flexion between carpus and propodus. Pereopods 5–7 dactylus with 2 ungues, secondary unguis robust.

Subtidal, associated with hydroids. Western and Central Indo-Pacific. 2 species (Kensley et al., 2007: redescription of type species; Nunomura, 2011: second species possibly synymous with *Amesopous richardsonae* Stebbing, 1905).

Arctopsis Barnard, 1920

Diagnosis. Body strongly geniculate between pereonites 4 and 5, cylindrical, more or less granular; pereonites 2–4 progressively wider; pereonite 4 more elongate than pereonites 2, 3, male more than twice as long as female; pleotelson without dorsolateral posterior wings. Antenna flagellum with 2 articles and unguis. Pereopod 1 dactylus with unguis; pereopods 2–4 cylindrical, held close to mouthparts; with flexion between carpus and propodus; with rows of setae as long as articles; dactylus absent. Pereopods 5–7 dactylus with 2 ungues, secondary unguis small. Male ventral appendage prominent on pereonite 5.

Shelf; 80 m. Tropical Atlantic. 1 species (Koehler, 1911: description; Barnard, 1920).

Arcturina Koehler, 1911

Diagnosis. Body strongly geniculate between pereonites 4 and 5, with double dorsal ridge; pereonites 2–4 in female together forming rhomboid shape, in male cylindrical; pereonite 4 longer than pereonites 2, 3; pleotelson without dorsolateral posterior wings. Antenna flagellum with 3 articles and unguis. Pereopod 1 dactylus with unguis; pereopods 2–4 flattened;

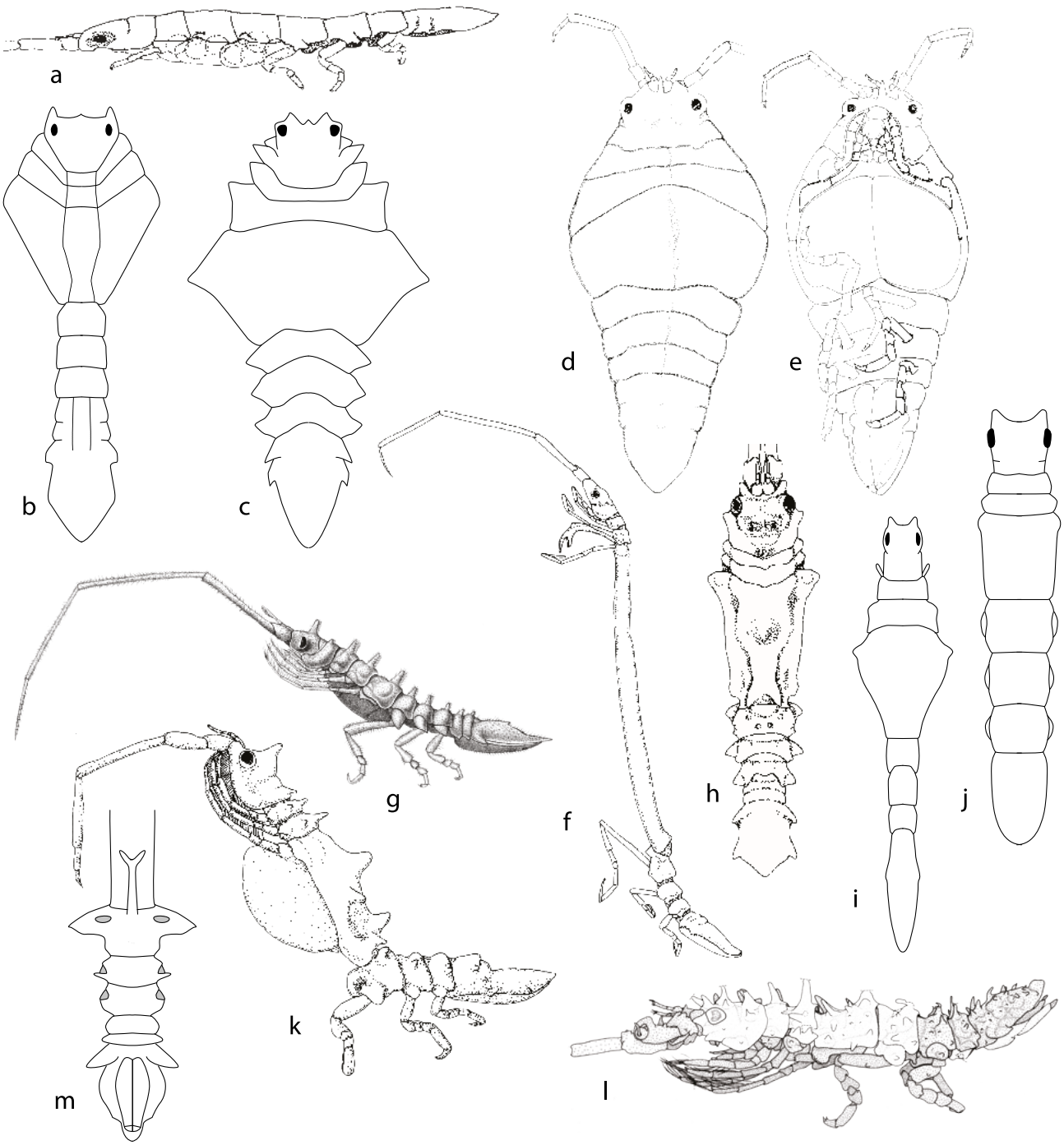


Figure 10.3. Arcturidae. a, *Amesopous richardsonae* Stebbing, 1905 (female); b, *Arcturina* (female); c, *Arcturinella* (female); d, e, *Arcturinoides dakhla* Menioui and Poore, 2008 (female); f, *Arcturopsis giardi* (Bonnier, 1896) (male); g, *Arcturus baffini* G.O. Sars, 1885 (female); h, *Astacilla mccaini* Kensley, Schotte and Poore, 2007 (female); i, *Edwinjoycea*; j, *Idarcturus platysoma* Barnard, 1914; k, *Neastacilla tarni* King 2003 (female); l, *Spectrarcturus toporoki* (Kussakin, 1972); m, pereonites 5–7, pleotelson, *Arctopsis* (male, ventral view).

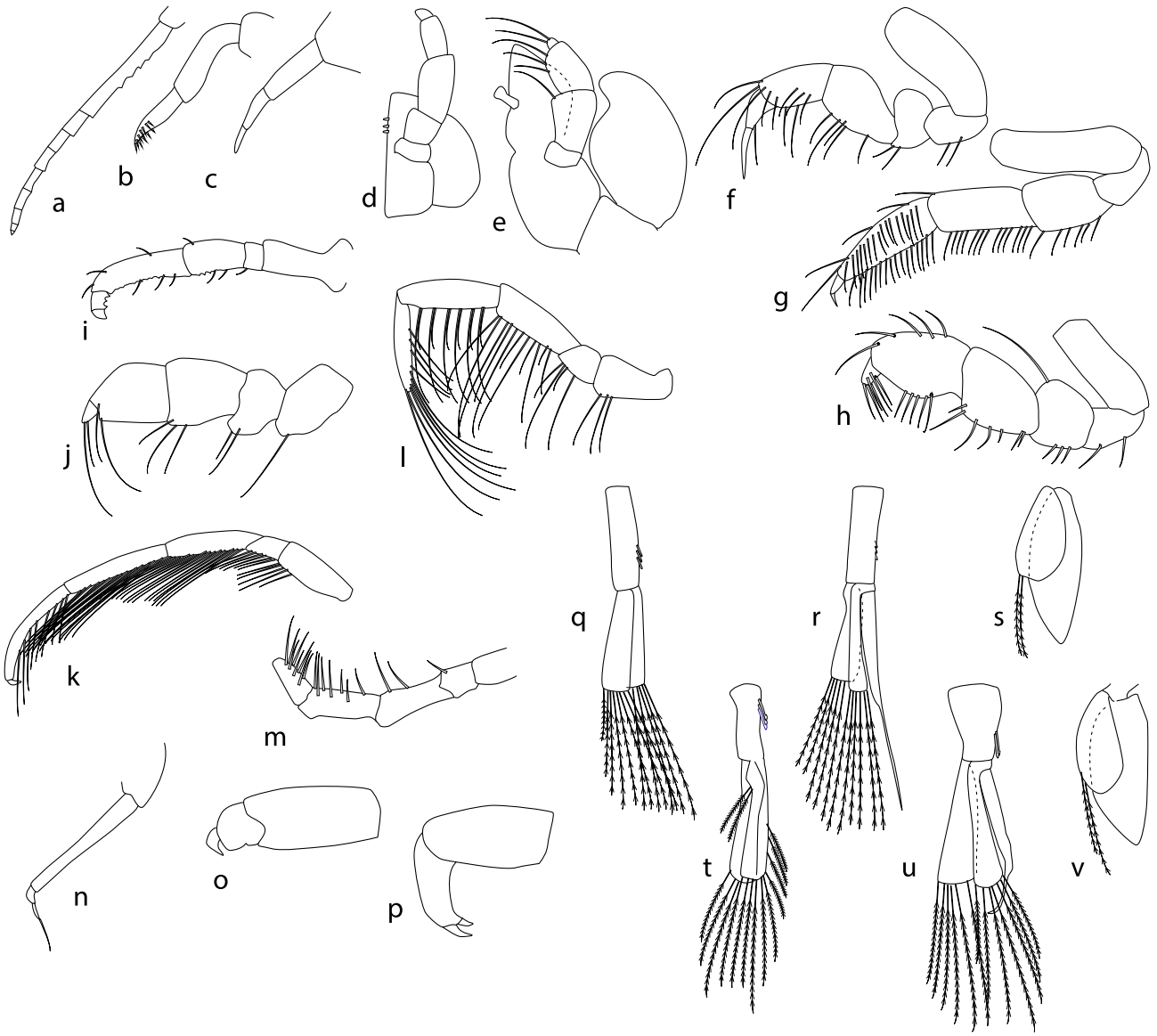


Figure 10.4. Arcturidae. Antennal flagellum: a, *Arcturus*; b, *Edwinjoycea*; c, *Neastacilla*. Maxilliped: d, *Arcturus*; e, *Edwinjoycea*. Pereopod 1: f, *Arcturina*; g, *Arcturus*; h, *Parastacilla*. Pereopod 2: i, *Amesopous*; j, *Arcturina*; k, *Arcturus*; l, *Astacilla*; m, *Parastacilla*. Pereopod 4, propodus, dactylus: n, *Arcturinella*. Pereopod 5, propodus, dactylus: o, *Idarcturus*; p, *Neastacilla*. Male pleopods 1–3: q–s, *Astacilla*; t–v, *Neastacilla*.

without flexion between carpus and propodus; with few setae; propodus less than half length of carpus; dactylus absent. Pereopods 5–7 dactylus without secondary unguis.

Subtidal. Tropical Atlantic, Western and Central Indo-Pacific, Temperate Southern Africa. 7 species (Reboreda et al., 1994: redescription of type species; additional species: Bamber, 2008; Nunomura, 2008).

Arcturinella Poisson and Maury, 1931

Diagnosis. Body weakly geniculate between pereonites 4 and 5, extremely dorsoventrally flattened, with dorsal ridge; pereonites 2, 3 short; pereonite 4 much longer than pereonites 2, 3, with broad triangular wings in female; pleotelson with dorsolateral posterior wings. Antenna flagellum with 3 articles and unguis. Pereopod 1 dactylus without unguis; pereopod 4 vestigial; pereopods 2, 3 cylindrical, similar; without flexion between carpus and propodus; with rows of setae as long as articles; dactylus absent; pereopod 4 reduced. Pereopods 5–7 dactylus without secondary unguis.

Subtidal. Temperate Northern Atlantic (Mediterranean only). 2 species (Poisson and Maury, 1931; Castelló et al., 2018: rediagnosis, possible second species).

Arcturinoides Kensley, 1977

Diagnosis. Body weakly geniculate between pereonites 4 and 5, extremely flattened dorsoventrally, with dorsal ridge; pereonites 2–4 forming rounded or rectangular shape in female; pereonite 4 more elongate than pereonites 2, 3, male and female of similar length; pleotelson with or without dorsolateral posterior wings. Antenna flagellum with 3 articles and unguis. Pereopod 1 dactylus with unguis; pereopod 4 absent; pereopods 2–3 cylindrical, held close to mouthparts; without flexion between carpus and propodus; with few setae; dactylus with unguis. Pereopods 5–7 dactylus with 2 ungues, secondary unguis small.

Subtidal, shelf. Temperate Northern Atlantic, Western Indo-Pacific (African coasts). 4 species (Kensley et al., 2007: rediagnosis, key to species; Menioui and Poore, 2008: key to 3 species).

Arcturopsis Koehler, 1911

Diagnosis. Body strongly geniculate between pereonites 4 and 5, cylindrical, more or less granular; pereonites 2–4 progressively wider; pereonite 4 more elongate than pereonites 2, 3, male more than twice as long as female; pleotelson without dorsolateral posterior wings. Antenna flagellum with 2 articles and unguis. Pereopod 1 dactylus with unguis; pereopods 2–4 cylindrical, held close to mouthparts; with flexion between carpus and propodus; with rows of setae as long as articles; dactylus absent. Pereopods 5–7 dactylus with 2 ungues, secondary unguis small. Male ventral appendage prominent on pereonite 3.

Subtidal–slope; 5–923 m. Temperate Northern and Tropical W Atlantic. 3 species (Koehler, 1911; King and Poore, 2001: rediagnosis, redescription).

Arcturus Latreille, 1829

Diagnosis. Body strongly geniculate between pereonites 4 and 5, cylindrical, more or less granular; pereonites 2, 3 of similar width, narrow; pereonite 4 of similar proportions to pereonites 2, 3 in both sexes; pleotelson without dorsolateral posterior wings. Antenna flagellum with 3–10 articles and unguis. Pereopod 1 dactylus with unguis; pereopods 2–4 cylindrical, held close to mouthparts; without flexion between carpus and propodus; with rows of setae as long as articles; dactylus with unguis. Pereopods 5–7 dactylus with 2 ungues, secondary unguis robust.

Subtidal–bathyal; 5–2670 m. Arctic, Temperate Northern Atlantic, Temperate Northern Pacific. 25 species (Sars, 1896–1899: figures; Kussakin, 1982: key to species from NW Pacific [in Russian]).

Astacilla Cordiner, 1793

Diagnosis. Body strongly geniculate between pereonites 4 and 5, cylindrical, more or less granular; pereonites 2, 3 of similar width, narrow; pereonite 4 about twice as long as pereonites 2, 3, more so in male; pleotelson with dorsolateral posterior wings. Antenna flagellum with 2 or 3 articles and unguis. Pereopod 1 dactylus without unguis, or with unguis (rare); pereopods 2–4 cylindrical, held close to mouthparts; with flexion between carpus and propodus; with rows of setae as long as articles; dactylus absent. Pereopods 5–7 dactylus with 2 ungues, secondary unguis robust. Male ventral appendage on pereonite 3, bud-like.

Subtidal, shelf. Arctic, Temperate Northern Atlantic, Temperate Northern Pacific, Tropical Atlantic, Western and Central Indo-Pacific, Temperate Southern Africa. 50 species (Kussakin, 1982: key to 6 NW Pacific species and 2 species of *Arcturella* [in Russian]; King, 2003a: list of species). *Agularcturus* Kensley, 1984 and *Arcturella* G.O. Sars, 1897 are treated as synonyms.

Edwinjoycea Menzies and Kruczynski, 1983

Diagnosis. Body strongly geniculate between pereonites 4 and 5, smooth; pereonites 2–4 progressively wider; pereonite 4 longer than pereonites 2, 3; pleotelson without dorsolateral posterior wings. Antenna flagellum of 2 articles, second with comb of strong setae. Maxillipedal palp articles 2, 3 fused. Pereopod 1 dactylus without unguis; pereopod 2 present as small plate; pereopods 3, 4 absent. Pereopods 5–7 dactylus without secondary unguis. Uropod exopod absent.

Shelf; 21–73 m, associated with hydroids. Tropical W Atlantic. 1 species (Menzies and Kruczynski, 1983; Müller, 1993: redescription).

Idarcturus Barnard, 1914

Diagnosis. Body weakly geniculate between pereonites 4 and 5, slightly flattened dorsoventrally, without dorsal ridge; pereonites 2–4 progressively wider; pereonite 4 about twice as long as pereonites 2, 3, more so in male; pleotelson without dorsolateral posterior wings, or with or without dorsolateral posterior wings. Antenna flagellum with 3 articles and unguis. Pereopod 1 dactylus without unguis; pereopods 2–4 cylindrical, held close to mouthparts; without flexion between carpus and propodus; with rows of setae as long as articles. Pereopods 5–7 dactylus reduced, with swollen pad on lower margin, unguis hook-like.

Intertidal. Temperate Southern Africa. 1 species (Barnard, 1914). Kim and Yoon (2021) provided a key to four species but these probably belong in *Neastacilla*.

Neastacilla Tattersall, 1921

Diagnosis. Body strongly geniculate between pereonites 4 and 5, sometimes sculptured with lobes or spines; pereonites 2, 3 of similar width, narrow; pereonite 4 at least 3 times as long as pereonites 2, 3, more so in male; pleotelson with or without dorsolateral posterior wings. Antenna flagellum with 2 or 3 articles and unguis. Pereopod 1 dactylus without unguis; pereopods 2–4 cylindrical, held close to mouthparts; without flexion between carpus and propodus; with rows of setae as long as articles; dactylus with unguis, or dactylus absent (rare). Pereopods 5–7 dactylus with 2 ungues, secondary unguis robust. Male ventral appendage on pereonite 3, bud-like.

Intertidal–slope; 0–1050 m. Temperate Northern Pacific, Temperate South America, Temperate Southern Africa, Temperate Australasia, Southern Ocean. 50 species (King, 2003b: rediagnosis, key to 22 Australian and New Zealand species; Kim and Yoon, 2021: key to 17 NW Pacific species).

Parastacilla Hale, 1924

Diagnosis. Body strongly geniculate between pereonites 4 and 5, cylindrical, more or less granular; pereonites 2, 3 of similar width, narrow; pereonite 4 about twice as long as pereonites 2, 3, more so in male; pleotelson with dorsolateral posterior wings. Antenna robust, distal peduncle articles about 5 times as long as wide; flagellum with 2 articles, second reduced, and unguis. Pereopod 1 dactylus without unguis; pereopods 2–4 flattened, held close to mouthparts; without flexion between carpus and propodus; with few short setae; dactylus with unguis present on pereopod 2, absent on 3, 4. Pereopods 5–7 dactylus with 2 ungues, secondary unguis robust. Male ventral appendage on pereonite 3, bud-like.

Subtidal, shelf. Temperate Australia. 4 species (King, 2000: rediagnosis, key to species).

Spectrarcturus Schultz, 1981

Diagnosis. Body weakly geniculate between pereonites 4 and 5, cylindrical, with spines or tubercles; pereonites 2, 3 of similar width, narrow; pereonite 4 about twice as long as pereonites 2, 3, more so in male; pleotelson with dorsolateral posterior wings. Antenna robust, articles 2, 3 with spines on upper margin; flagellum with 3 articles and unguis. Pereopod 1 dactylus without unguis; pereopods 2–4 cylindrical, held close to mouthparts; without flexion between carpus and propodus; with rows of setae as long as articles; dactylus with unguis. Pereopods 5–7 dactylus with 2 ungues, secondary unguis robust.

Subtidal–slope; 5–1150 m. Arctic, Temperate Northern Atlantic, Temperate Northern Pacific. 8 species (Stransky et al., 2020: rediagnosis, key to species).

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Arcturididae Poore, 2001

Figure 10.5

The cylindrical body, paired horns on the head, and essentially similar ambulatory pereopods characterise the family and its only species, *Arcturides cornutus* Studer, 1882. The species is often associated with erect hydroids (Hale, 1946; Poore, 2001) and can be abundant.

Diagnosis. Body more or less cylindrical, without coxal dorsal plates or pleonal epimera, straight, without flexion (fig. 10.5a). Pereopod 1 gnathopod-like; pereopods 2–4 stout, with 2 rows of 5–6 well-spaced setae, scarcely differentiated from ambulatory pereopods 5–7; with prominent dactyli, unguis short. Uropodal exopod (smaller ramus) tapering (with terminal seta or setae only) (fig. 10.5b). Pleopod 1 peduncle more elongate than rami, longer than on other pleopods; exopod of male thickened and with groove on posterior face, ending on tapering distolateral apical extension (fig. 10.5c).

Arcturides Studer, 1882

Shelf, slope. Southern Ocean (Subantarctic islands). 1 species. The three described species are treated as synonyms (descriptions: Hale, 1946; Kensley, 1980).

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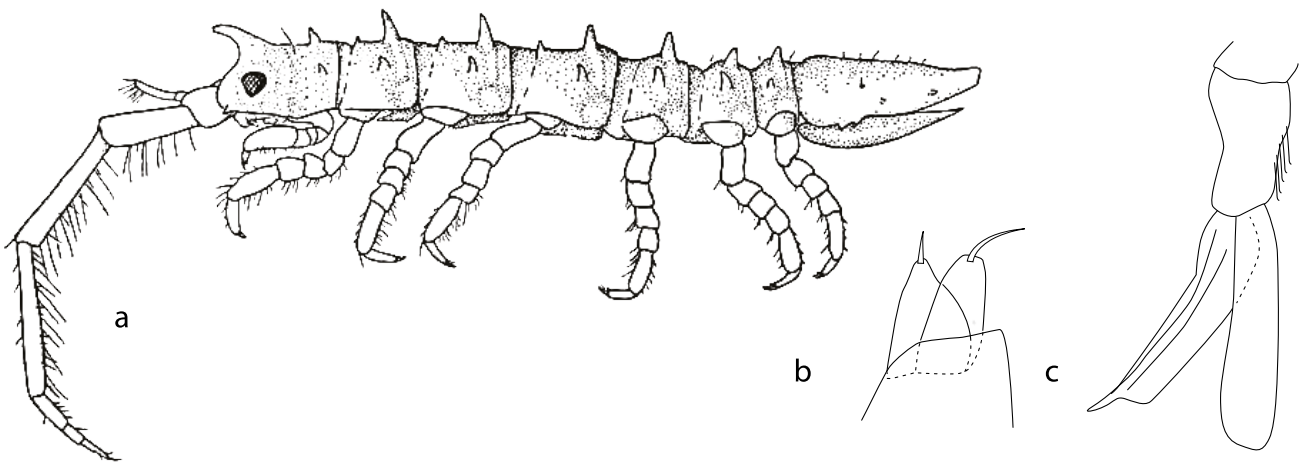


Figure 10.5. Arcturididae, *Arcturides cornutus* Studer, 1882: a, habitus; b, uropodal rami; c, male pleopod 1.

Austrarcturellidae Poore and Bardsley, 1992

Figures 10.6, 10.7

Poore and Bardsley's (1992) review of the family included only four genera; *Dolichiscus* is now recognised as a member (Poore, 2001). The inverted boat-shaped pleotelson and pereopod 4 shorter than pereopods 2 and 3 enable most species to be distinguished from similar genera of Antarcturidae. All are shelf or deep-sea species, concentrated in the Southern Hemisphere.

Diagnosis. Body more or less cylindrical, without coxal dorsal plates or pleonal epimera, flexed between pereonites 4 and 5, anterior segments held slightly erect. Pleotelson with dorsolateral ridges usually ending in mediodorsal posterior spine. Pereopod 1 gnathopod-like; pereopods 2–4 elongated, with even rows of long filter-setae, differentiated from ambulatory pereopods 5–7, pereopod 4 shorter and less setose than pereopods 2 and 3; with minute dactyli, unguis setiform. Uropodal exopod (smaller ramus) tapering (with terminal seta or setae only). Pleopod 1 peduncle more elongate than rami, longer than on pleopods 2 and 3; exopod of male thickened and with groove on posterior face, ending distolaterally or laterally on simple margin (*Dolichiscus*) or ending on basally derived branch of exopod.

Implicit generic attributes. Eyes pigmented; on eyestalks.

Antennal flagellum of 2–4 elongate articles plus claw. Pereopod 1 dactylus with anterior lobe on extensor margin, constricted and tapering distally. Pereopods 2–4 dactylus longer than wide, with unguis as long as propodal setae. Pereopods 5–7 dactylus moderately longer than propodus. Pleopod 1 of male exopod groove ending on basally derived branch of exopod.

Key to genera of Austrarcturellidae

1. Antennal flagellum with 8 or more articles (fig. 10.6c). Male pleopod 1 exopod with groove opening distolaterally on triangular lobe (fig. 10.7j) ..... *Dolichiscus*

– Antennal flagellum with 2 articles (fig. 10.7a, b). Male pleopod 1 exopod with groove ending on basally-derived branch of exopod (fig. 10.7k) 2

2. Eyes absent. Pereopods 2–4 with minute dactylus (shorter than long) and short setiform unguis (shorter than propodal setae) (fig. 10.7g). Pereopods 5–7 with dactylus extremely elongated, about twice as long as propodus (fig. 10.6d). Uropod with 2 rami (fig. 10.7l) ..... *Scyllarcturella*

– Eyes present. Pereopods 2–4 dactylus longer than wide, with setiform unguis as long as propodal setae. Pereopods 5–7 with dactylus moderately long. Uropod without or with rami 3

3. Eyes not on eyestalks (fig. 10.6a). Pereopod 4 with strong setal group distally on basis, with setal row on propodus flexor margin (fig. 10.7h) ..... *Abyssarcturella*

– Eyestalks present. Pereopod 4 with few setae distally on basis, without setal row on propodus flexor margin (fig. 10.7i) (rare exception) 4

4. Antennal flagellum with distal article stout, no longer than preceding flagellar articles (fig. 10.7b). Pereopod 1 dactylus with proximal part narrow and linear (fig. 10.7d). Pereopods 2–4 dactyli with proximal part small, conical, with elongate unguis (fig. 10.7f). Uropod with 1 or 2 rami ..... *Pseudarcturella*

– Antennal flagellum with distal article elongate, usually longest flagellar articles (figs 10.6b, 10.7a). Pereopod 1 dactylus with proximal part anteriorly convex (fig. 10.7c). Pereopods 2–4 dactyli with proximal part minute, with setiform unguis at least as long as propodus (fig. 10.7e). Uropod without rami ..... *Austrarcturella*

Abyssarcturella Poore and Bardsley, 1992

Diagnosis. Eyes not elevated on eyestalks. Antennal flagellum, distal article elongate, usually the longest flagellar article. Pereopod 4 basis with strong setal group distally, with setal row on flexor marigin of propodus. Uropod with 1 or 2 rami.

Slope (1609–1840 m). Central Indo-Pacific (NE Australia). 2 species (Poore and Bardsley, 1992).

Austrarcturella Poore and Bardsley, 1992

Diagnosis. Antennal flagellum, distal article elongate, usually the longest flagellar article. Pereopod 4 basis with few setae distally, without setal row on flexor margin of propodus. Uropod without rami.

Shelf, slope (28–1000 m). Central Indo-Pacific, Temperate Australasia (Australia, New Zealand). 14 species (Poore and Bardsley, 1992: diagnosis, key to 14 species).

Dolichiscus Richardson, 1913

Diagnosis. Antennal flagellum of 9 or more short articles. Pereopod 4 basis with strong setal group distally, with setal row on flexor marigin of propodus. Pleopod 1 of male exopod groove opening distolaterally on triangular lobe. Uropod with triangular endopod and smaller exopod.

Shelf–abyssal (24–4209 m). Central Indo-Pacific, Temperate South America, Southern Ocean. 26 species (Wägele, 1991: rediagnosis, key to 10 Antarctic species and 3 of *Paradolichiscus* Schultz, 1981 treated here as junior synonym; Poore, 1998: 3 species; Kussakin and Vasina, 2001: vertical and horizontal distribution of 21 species).

Pseudarcturella Tattersall, 1921

Diagnosis. Antennal flagellum, distal article no longer than preceding flagellar articles. Pereopod 1 dactylus curved evenly along extensor margin, tapering. Pereopod 4 basis with few setae distally, without setal row on flexor margin of propodus. Uropod with 1 or 2 rami.

Subtidal. Temperate Australasia (New Zealand). 2 species (Poore and Bardsley, 1992: rediagnosis, key to 2 species).

Scyllarcturella Poore and Bardsley, 1992

Diagnosis. Eyes absent. Antennal flagellum, distal article no longer than preceding flagellar articles. Pereopods 2–4 dactylus minute, shorter than long, with unguis shorter than propodal setae. Pereopod 4 basis with few setae distally, without setal row on flexor margin of propodus. Pereopods 5–7 dactylus extremely elongated, about twice as long as propodus. Uropod with triangular endopod and smaller exopod.

Slope (738 m). Central Indo-Pacific (NE Australia). 1 species (Poore and Bardsley, 1992).

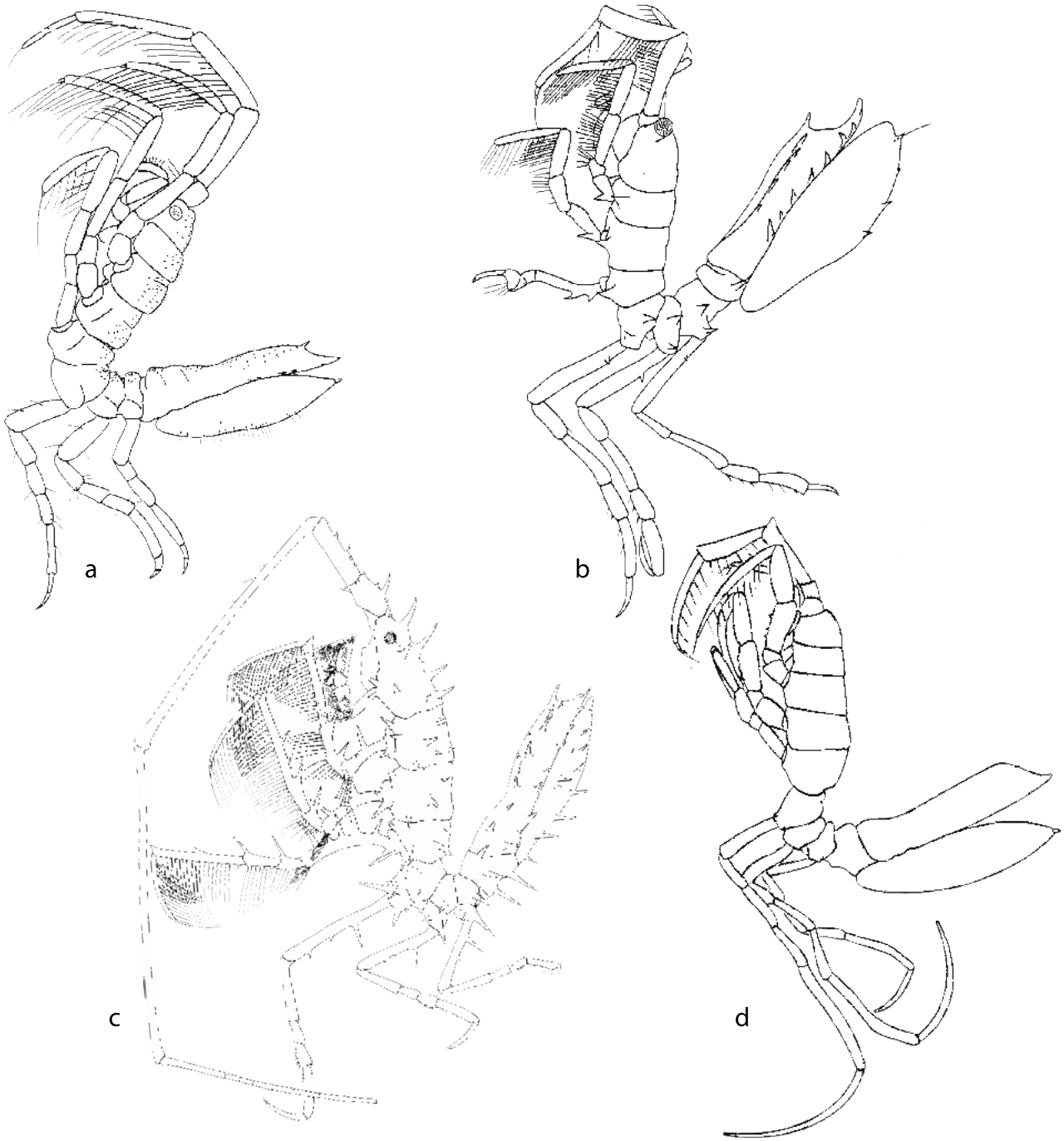


Figure 10.6. Austrarcturellidae. a, *Abyssarcturella panope* Poore and Bardsley, 1992; b, *Austrarcturella oculata* (Beddard, 1886); c, *Dolichiscus tanimbar* Poore, 1998; d, *Scyllarcturella falcata* Poore and Bardsley, 1992.

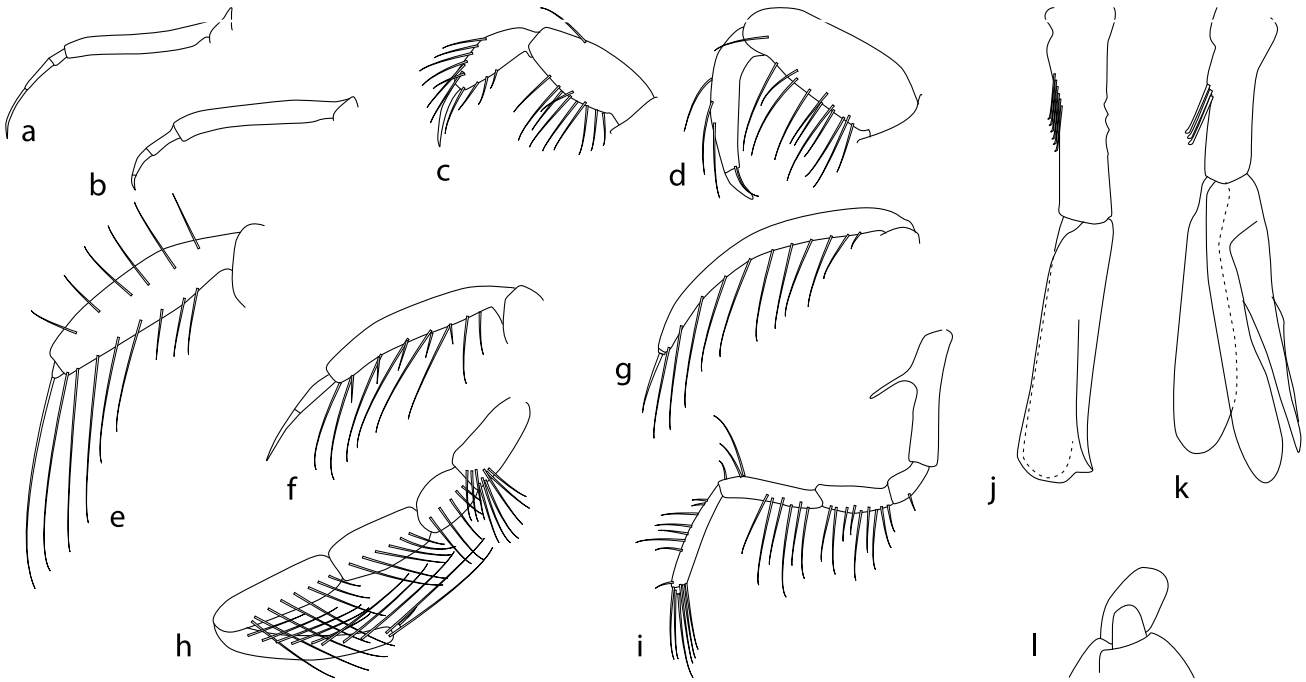


Figure 10.7. Austrarcturellidae. Antennal flagellum: a, *Austrarcturella*; b, *Pseudarcturella*. Pereopod 1, propodus, dactylus: c, *Austrarcturella*; d, *Pseudarcturella*. Pereopod 2, propodus, dactylus: e, *Austrarcturella*; f, *Pseudarcturella*; g, *Scyllarcturella*. Pereopod 4: h, *Abyssarcturella*; i, *Austrarcturella*. Male pleopod 1: j, *Dolichiscus*; k, *Pseudarcturella*. l, uropodal rami, *Scyllarcturella*.

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Holidoteidae Wägele, 1989

Figure 10.8

Holidoteids are confined to southern Africa. Their bodies are flattened or cylindrical, not or scarcely flexed, and possess a uropod with two rami, each with a single strong terminal seta (Poore, 2003).

Diagnosis. Body more or less flattened or semicylindrical, coxae with expanded coxal dorsal plates, pleonites with expanded epimera, straight, or scarcely flexed between pereonites 4 and 5. Mouthparts and pereopod 1 hidden by expanded tergites. Pereopod 1 gnathopod-like; pereopods 2–4 elongated, with even rows of long filter-setae, differentiated from ambulatory pereopods 5–7; with short dactyli, unguis longer, setiform. Uropodal exopod (smaller ramus) tapering (with terminal seta or setae only). Pleopod 1 peduncle more elongate than rami, longer than on pleopods 2 and 3; exopod of male thickened and with groove on posterior face, ending on distolateral lobed tip, separated from most of lateral margin by notch.

Key to genera of Holidoteidae

1. Pleonite 1 articulating with pleotelson (fig. 10.8a, g) 2
– Pleonite 1 fused to pleotelson (fig. 10.8b–f) 3
2. Pereon and pleotelson smooth or tuberculate (fig. 10.8a) ..... *Austroarcturus*
– Pereonites with pair of dorsal spines; pleonites 2, 3 each with median spine (fig. 10.8g) ..... *Pleuroprion*
3. Body cylindrical, tuberculate (fig. 10.8e, f). Pereopods 2–4 with bases held in parallel and in contact along midline of anterior body, enclosing mouthparts; carpus longer than ischium and merus together (fig. 10.8i) ..... *Neoarcturus*
– Body flat, smooth (fig. 10.8d). Pereopods 2–4 with bases held more or less transversely against ridge on ventral coxal plate, bases of pairs barely in contact; carpus almost as long as ischium and merus together (fig. 10.8h) ..... *Holidotea*

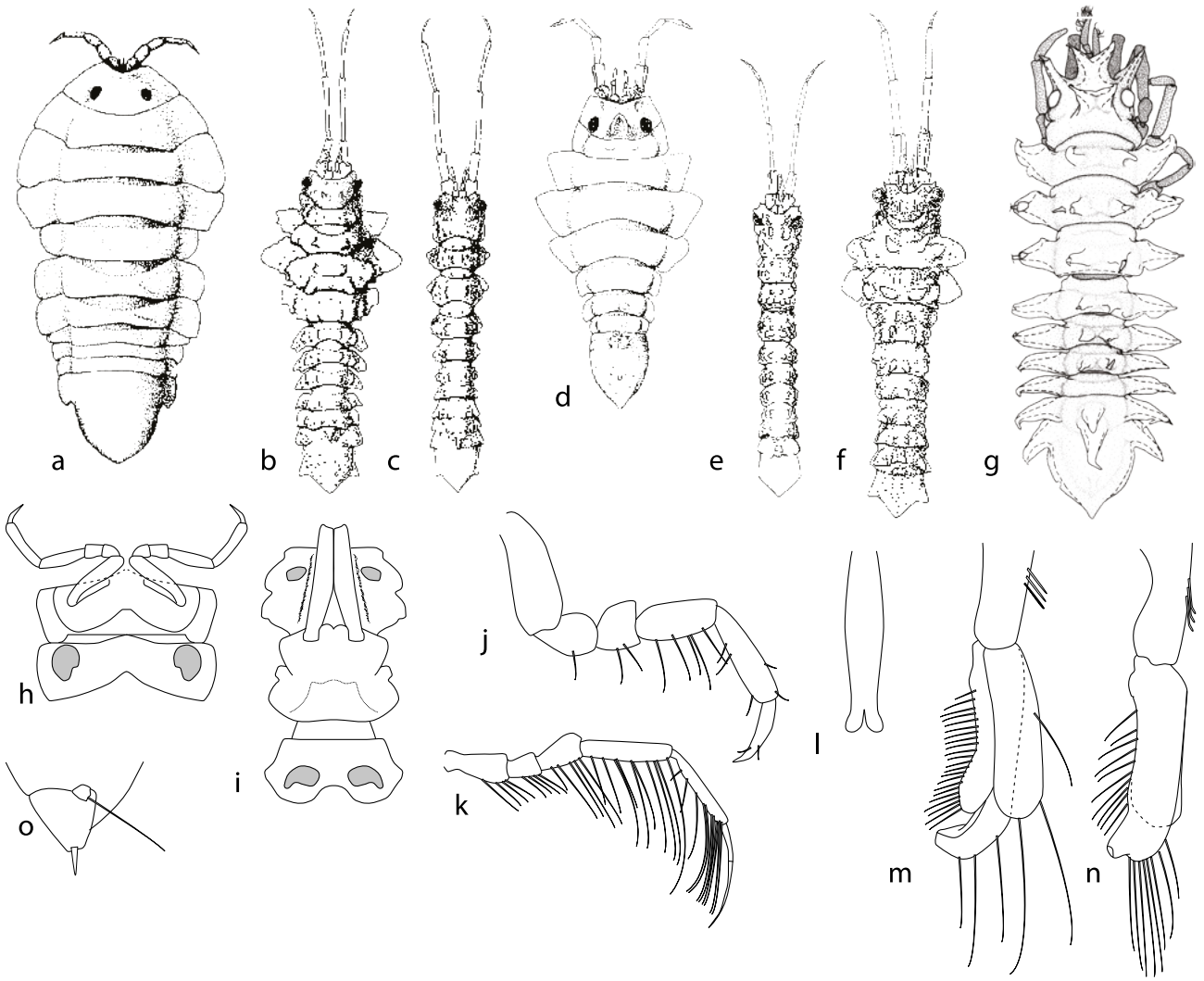


Figure 10.8. Holidoteidae. a, *Austroarcturus africanus* Kensley, 1975; b, c, *Austroarcturus dayi* (Kensley, 1977), female, male; d, *Holidotea unicornis* Barnard, 1920; e, f, *Neoarcturus ornatus* (Kensley, 1975), male, female; g, *Pleuroprion chuni* (zur Strassen, 1902). h, pereonites 4, 5, ventral, pereopods 4, *Austroarcturus*; i, pereonites 3–5, ventral, pereopods 4, *Neoarcturus*. Pereopod 2: j, *Holidotea*; k, *Neoarcturus*. l, penial plate, *Austroarcturus*. Male pleopod 1: m, *Austroarcturus*; n, *Pleuroprion*. o, uropodal rami, *Austroarcturus*.

Austroarcturus Kensley, 1975

Diagnosis. Body straight, flattened, coxal plates splayed; smooth, or tuberculate. Pleonite 1 articulating with fused pleotelson. Pereopods 2–4 held more or less transversely against ridge on ventral coxal plate, bases of pairs barely in contact; carpus longer than ischium and merus together; dactylus fine, unguis about one half length of body of dactylus, total shorter than propodus. Pleopod 1 exopod of male with groove on posterior face ending on distolateral lobed tip, separated from most of lateral margin by notch; with mesial setae ending subdistally on definite lobe.

Shelf. Temperate Southern Africa. 6 species (Kensley, 1978: figures; Poore, 2003: rediagnosis, key to species).

Holidotea Barnard, 1920

Diagnosis. Body straight, flattened, coxal plates splayed; smooth. All pleonites fused into pleotelson. Pereopods 2–4 held more or less transversely against ridge on ventral coxal plate, bases of pairs barely in contact; carpus almost as long as ischium and merus together; dactylus stout, unguis about one third length of body of dactylus, total shorter than propodus. Pleopod 1 exopod of male with groove on posterior face ending in deep subdistal excavation; with mesial setae ending subdistally on slight concave margin.

Shelf. Temperate Southern Africa. 1 species (Kensley, 1978: figure; Poore, 2003: rediagnosis).

Neoarcturus Barnard, 1914

Diagnosis. Body weakly flexed between pereonites 4 and 5, cylindrical; tuberculate. All pleonites fused into pleotelson. Pereopods 2–4 held in parallel and in contact along midline of anterior body, enclosing mouthparts; carpus longer than ischium and merus together; dactylus fine, unguis longer than body of dactylus, total about as long as propodus. Pleopod 1 exopod of male with groove on posterior face ending in deep subdistal excavation; with mesial setae ending subdistally on ridge at base of groove.

Shelf, slope. Temperate Southern Africa. 9 species (Kensley, 1978: figures; Poore, 2003: rediagnosis, key to species).

Pleuroprion zur Strassen, 1903

Diagnosis. Body straight, flattened, coxal plates splayed; with paired dorsal spines on pereonites, median spines on pleonites 2, 3. Pleonite 1 articulating with fused pleotelson. Pereopods 2–4 carpus longer than ischium and merus together; dactylus fine, unguis about one half length of body of dactylus, total shorter than propodus. Pleopod 1 exopod of male with groove on posterior face opening on short distolateral lobe; with mesial setae ending subdistally on slight concave margin.

Shelf. Temperate Southern Africa. 1 species (Stransky et al., 2020: rediagnosis, figures).

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Stransky, B., Poore, G.C.B., and Svavarsson, J. 2020. Revision of *Pleuroprion* zur Strassen, 1903 (Holidoteidae) and re-evaluation of *Spectrarcturus* Schultz, 1981 (Arcturidae) (Crustacea, Isopoda, Valvifera). *Zootaxa* 4894: 1–52. https://doi.org/10.11646/zootaxa.4894.1.1

Pseudidotheidae Ohlin, 1901

Figure 10.9

Five species in one genus confined to southern latitudes comprise Pseudidotheidae. The body is straight and pereopods 2–4 are short, stubby and armed with strong robust setae (Poore and Bardsley, 2004; Noli et al., 2022).

Diagnosis. Body more or less cylindrical, without coxal dorsal plates or pleonal epimera, straight, without flexion. Pereopod 1 gnathopod-like; pereopods 2–4 raptorial, articles broad, with robust setae on flexor margins, differentiated from ambulatory pereopods 5–7; with prominent dactyli, unguis short. Uropodal exopod (smaller ramus) tapering (with terminal seta or setae only). Pleopod 1 peduncle more elongate than rami, longer than on pleopods 2 and 3; exopod of male thickened and with groove on posterior face, ending on tapering distolateral apical extension.

Pseudidothea Ohlin, 1901

Subtidal–slope (7–500 m). Temperate Australasia, Southern Ocean. 5 species (Poore and Bardsley, 2004; Noli et al., 2022: rediagnosis, key to species).

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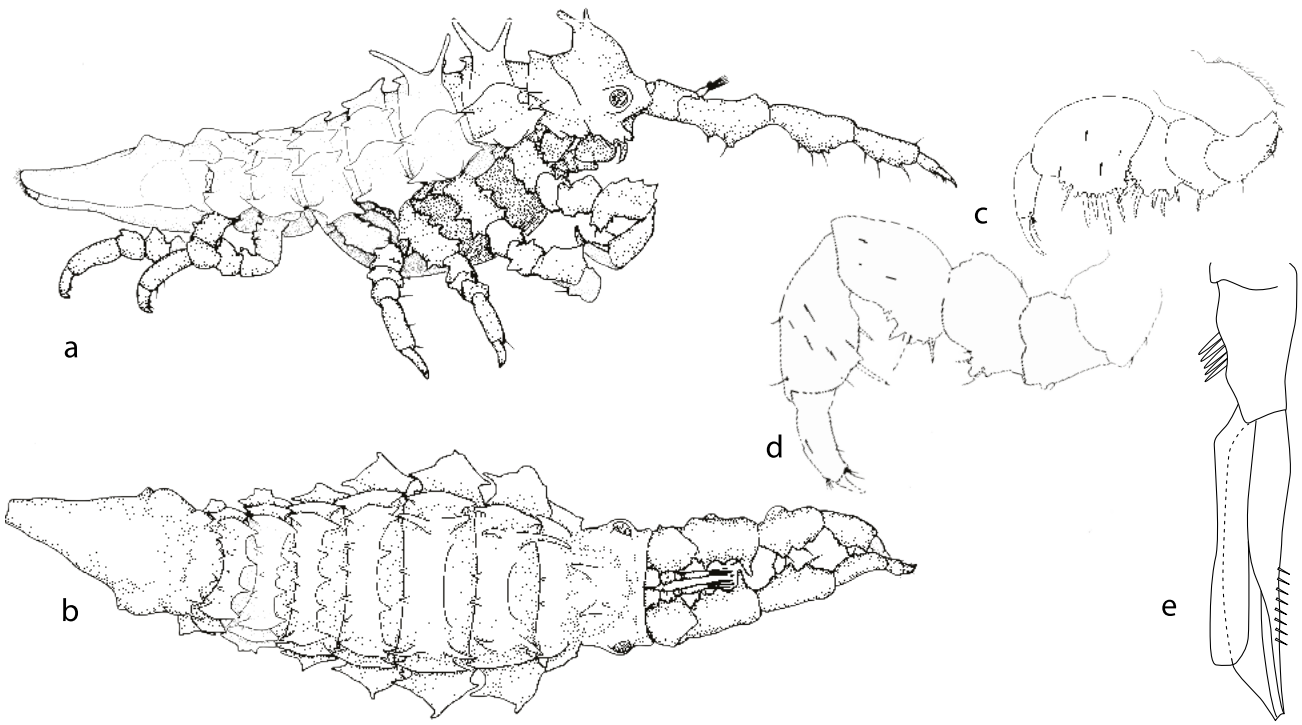


Figure 10.9. Pseudidotheidae, *Pseudidothea hoplites* Poore and Bardsley, 2004. a, b, habitus; c, pereopod 1; d, pereopod 2; e, male pleopod 1.

Rectarcturidae Poore, 2001

Figure 10.10

Rectarcturids are recognisable and distinguished from arcturids, antarcturids and austrarcturellids by their straight bodies and reduced setation of pereopods 2–4. The structure of the male pleopod 1 exopod separates rectarcturids from other "straight" families – the groove ends in a distolateral lobe separated from a distomesial lamina by a deep notch (Poore, 2013). Poore (2013) reviewed the family, described most species and provided a key to genera and species.

Diagnosis. Body more or less cylindrical, without coxal dorsal plates or pleonal epimera, straight, without flexion. Pereopod 1 gnathopod-like; pereopods 2–4 elongated, with pairs of stiff well-spaced setae, differentiated from ambulatory pereopods 5–7; with short dactyli, unguis longer and setiform. Uropodal exopod (smaller ramus) tapering (with terminal seta or setae only). Pleopod 1 peduncle more elongate than rami, longer than on other pleopods; exopod of male thickened and with groove on posterior face, ending distolaterally or laterally on simple margin.

Key to genera of Rectarcturidae

1. Antenna less than twice dorsal length of head+pereonite 1; article 4 subspherical, about as long as fused articles 1+2; article 5 at least twice as long as article 5 (fig. 10.10a, g, i, k). Pereopod 2 dactylus body+unguis 3 times as long as propodus (fig. 10.10l) 2

– Antenna at least 2.5 times dorsal length of head+pereonite 1; article 4 cylindrical, at least twice as long as fused articles 1+2; article 5 shorter than or at most 15 times as long as article 5 (fig. 10.10c, e, j). Pereopod 2 dactylus body+unguis shorter or at most 2.5 times as long as propodus (fig. 10.10m, n) 3

2. Head with paired submedian tubercles, pereonites with smooth transverse ridges, anterior pleonites barely elevated (fig. 10.10a, b). Antenna article 3 without ventrolateral flange (fig. 10.10i) ..... *Galathearcturus*

– Head, pereonites and anterior pereonites with paired blade-like submedian and sublateral tubercles/carinae, all secondarily tuberculate (fig. 10.10g, h). Antenna article 3 with ventrolateral teeth (fig. 10.10k) ..... *Tasmarcturus*

3. Head with paired submedian tubercles, pereonites with smooth transverse ridges (pereonite 3 with second ridge anterior to major one), anterior pleonites barely elevated (fig. 10.10c, d) ..... *Nowrarcturus*

– Head, pereonites and anterior pleonites with paired blade-like submedian and sublateral tubercles or carinae, smooth or barely secondarily ornamented (fig. 10.10e, f) ..... *Rectarcturus*

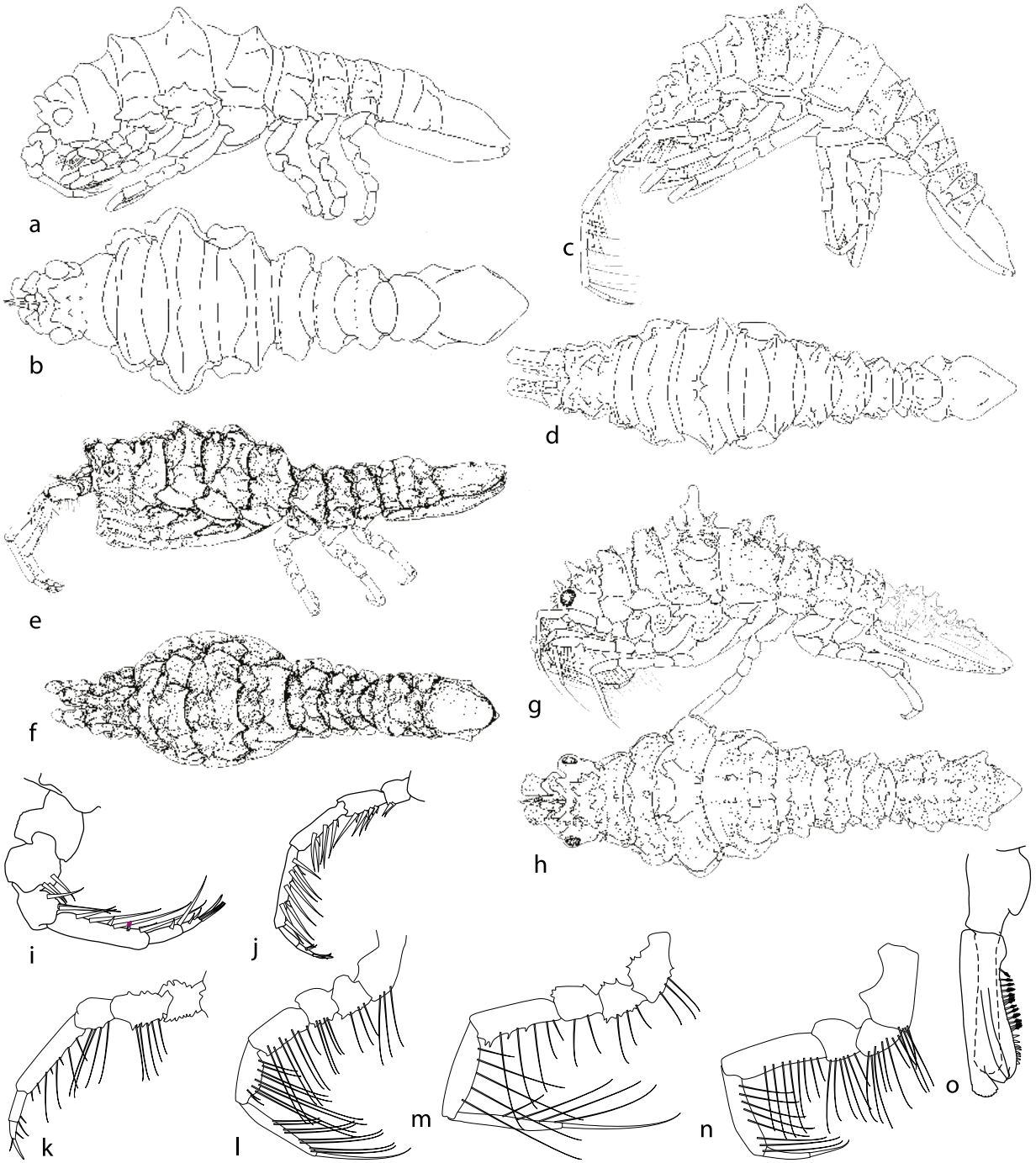


Figure 10.10. Rectarcturidae. a, b, *Galathearcturus antoniae* Poore, 2013; c, d, *Nowrarcturus jamesi* Poore, 2013; e, f, *Rectarcturus kophameli* (Ohlin, 1901); g, h, *Tasmarcturus simplicissimus* (Whitelegge, 1904). Antenna: i, *Galathearcturus*; j, *Nowrarcturus*; k, *Tasmarcturus*. Pereopod 2: l, *Galathearcturus*; m, *Nowrarcturus*; n, *Rectarcturus*. o, male pleopod 1, *Tasmarcturus*.

***Galathearcturus* Poore, 2013**

Diagnosis. Head with paired submedian tubercles, pereonites with smooth transverse ridges, anterior pleonites barely elevated. Antenna 1.5 times dorsal length of head+pereonite 1; article 3 cuboid, as long as deep, without ventrolateral flange; article 4 subspherical, about as long as fused articles 1–2; article 5 cylindrical, 2–2.5 times as long as article 4, 5 times as long as wide. Pereopod 2 propodus palm convex, denticulate; dactylus body+unguis 3 times as long as propodus; dactylus unguis setiform, as long or longer than dactylus body.

Shelf (86 m). Temperate E Australia. 1 species (Poore, 2013).

***Nowrarcturus* Poore, 2013**

Diagnosis. Head with paired submedian tubercles, pereonites with smooth transverse ridges (third with second ridge anterior to major one), anterior pleonites barely elevated. Antenna 2.5 times dorsal length of head+pereonite 1; article 3 cylindrical, twice as long as deep, without ventrolateral flange; article 4 cylindrical, more than twice as long as fused articles 1–2; article 5 cylindrical, 1.5 times as long as article 4, 5 times as long as wide. Pereopod 2 propodus palm convex, denticulate; dactylus body+unguis 2.5 times as long as propodus; dactylus unguis setiform, as long or longer than dactylus body.

Slope (990–1118 m). Temperate SE Australia. 1 species (Poore, 2013).

***Rectarcturus* Schultz, 1981**

Diagnosis. Head, pereonites and anterior pereonites with paired blade-like submedian and sublateral tubercles/carinae, smooth or barely secondarily ornamented. Antenna 2.5 times dorsal length of head+pereonite 1, or 3 times dorsal length of head+pereonite 1; article 3 cuboid, as long as deep, without ventrolateral flange; article 4 cylindrical, more than twice as long as fused articles 1–2; article 5 cylindrical, 0.7 length of article 4, 5 times as long as wide. Pereopod 2 propodus palm straight, smooth; dactylus body+unguis as long or little shorter than propodus; dactylus unguis setiform, shorter than dactylus body.

Shelf, slope (10–3590 m). Temperate South America (Argentina). 3 species (Park and Wägele, 1995: species descriptions; Poore, 2013: rediagnosis, key to 2 species).

***Tasmarcturus* Poore, 2013**

Diagnosis. Head, pereonites and anterior pereonites with paired blade-like submedian and sublateral tubercles/carinae, all secondarily tuberculate. Antenna 1.7–2 times dorsal length of head+pereonite 1; article 3 cuboid, as long or little longer than deep, with ventrolateral teeth; article 4 subspherical, about as long as fused articles 1–2; article 5 cylindrical, 2–2.5 times as long as article 4, 5 times as long as wide. Pereopod 2 propodus palm convex, denticulate; dactylus body+unguis 3 times as long as propodus; dactylus unguis setiform, as long or longer than dactylus body.

Shelf, slope (26–1096 m). Temperate E Australia. 3 species (Poore, 2013: key to species).

References

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Thermoarcturidae Poore, 2015

Figure 10.11

Thermoarcturidae are a small family of three species from slope depths distinguished by their geniculate body and well-spaced stiff setae on pereopods 2–4 in place of the filter setae seen on similar Antarcturidae (Poore, 2015).

Diagnosis. Body more or less cylindrical, without coxal dorsal plates or pleonal epimera, flexed between pereonites 4 and 5, anterior segments held slightly erect. Pereopod 1 gnathopod-like; pereopods 2–4 elongated, with pairs of stiff well-spaced setae, differentiated from ambulatory pereopods 5–7; with prominent dactyli, unguis short (fig. 10.11k–m). Uropodal exopod (smaller ramus) triangular, similar to endopod (with terminal setae). Pleopod 1 peduncle more elongate than rami, longer than on other pleopods; exopod of male thickened and with groove on posterior face, ending on tapering distolateral apical extension or evident only as shallow proximal concavity.

Key to genera of Thermoarcturidae

1. Pleonite 3 with pair of long acute sublateral spines (fig. 10.11b). Male pleopod 2 exopod with area of fine setae about one third along, groove weakly defined (fig. 10.11h, i) ..... *Spinarcturus*

– Pleonite 3 without or with short tubercles. Male pleopod 2 exopod with well-defined groove running to subapical notch 2

2. Pereonites and pleonites with transverse rows of submedian, sublateral and lateral tubercles bearing bead-like spheres (fig. 10.11a). Male pleopod 2 exopod with groove opening at notch about three quarters along, without ventral keel or tooth (fig. 10.11g) ..... *Califarcturus*

– Pereonites with simple sublateral spines, pleotelson scarcely ornamented (fig. 10.11c, d). Male pleopod 2 exopod with groove opening at end of subdistal rounded lobe, with prominent keel ending in tooth on anterior (ventral) face (fig. 10.11j) ..... *Thermoarcturus*

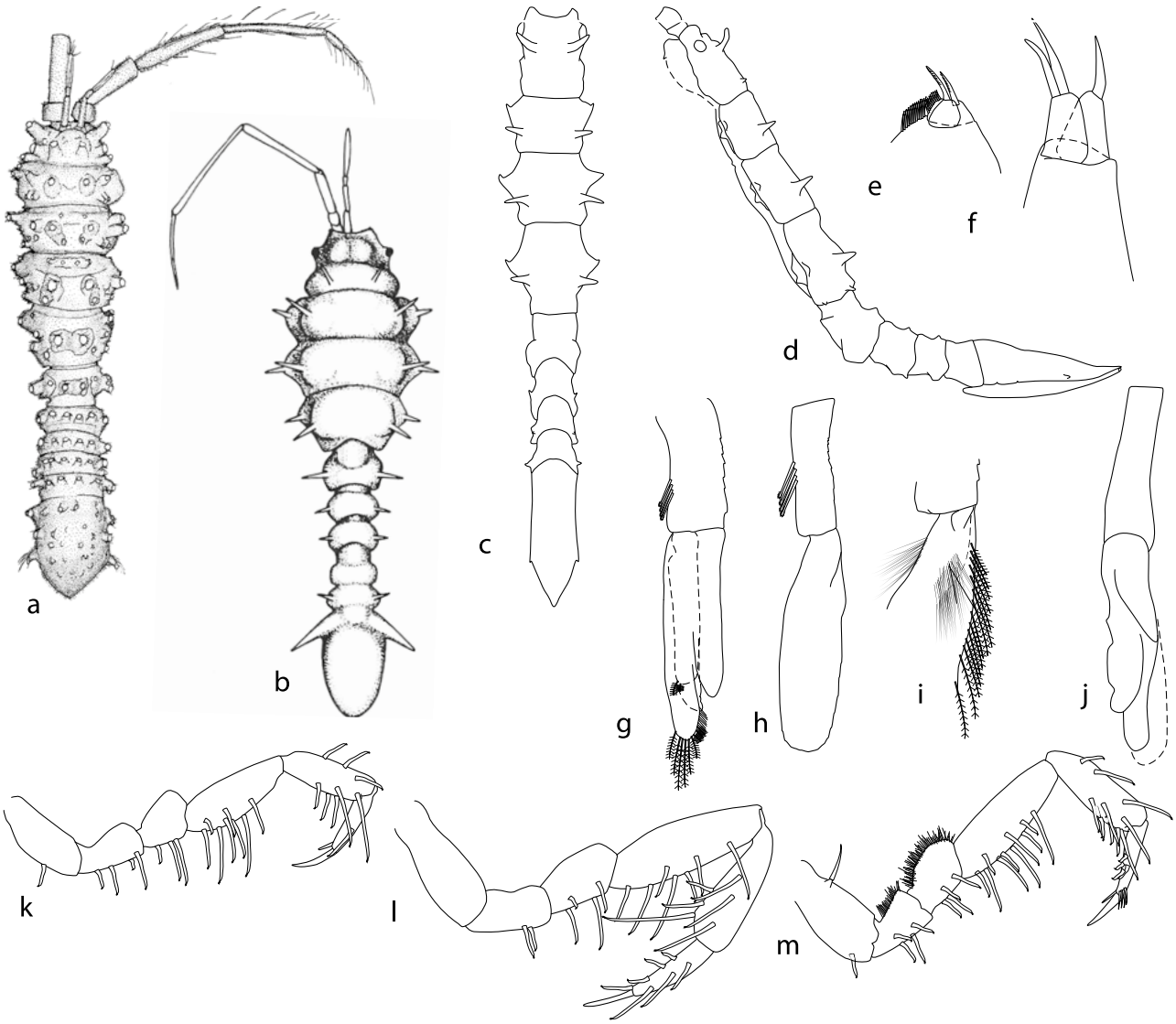


Figure 10.11. Thermoarcturidae. a, *Califarcturus tannerensis* (Schultz, 1966); b, *Spinarcturus natalensis* Kensley, 1978; c, d, *Thermoarcturus venezuelensis* Paul and Menzies, 1971. Uropodal rami: e, *Califarcturus*; f, *Spinarcturus*. Male pleopod 1: g, *Califarcturus*; h, i, *Spinarcturus* (with detail of base of exopod); j, *Thermoarcturus*. Pereopod 2: k, *Califarcturus*; l, *Spinarcturus*; m, *Thermoarcturus*.

Califarcturus Poore, 2015

Diagnosis. Head, pereonites and all pleonites each with transverse rows of submedian, sublateral and lateral tubercles bearing bead-like spheres. Pleotelson with short oblique lateral tubercles. Eyes absent. Male pleopod 1 exopod with well-defined anterior groove opening laterally at notch about three quarters along lateral margin, without ridge and tooth on anterior face. Male pleopod 2, appendix masculina slightly longer than endopod.

Slope (1300 m). Tropical Eastern Pacific. 1 species (Schultz, 1966: species description; Poore, 2015: species redescription, diagnosis).

Spinarcturus Kensley, 1978

Diagnosis. Pereonites 2–4 with prominent sublateral and lateral spines; pereonites 5–7 with prominent lateral spines; pleonite 3 with pair of acute sublateral spines, longer and stouter than other spines. Pleotelson unarmed. Eyes present. Male pleopod 1 exopod with area of fine setae about one third along on anterior face, without well-defined groove. Male pleopod 2, appendix masculina almost twice as long as endopod. Oostegites 5 a pair of small flaps on anterior margin of pereonite 5.

Slope (550 m). Temperate Southern Africa (Natal). 1 species (Kensley, 1978: species description; Poore, 2015: rediagnosis).

Thermoarcturus Paul and Menzies, 1971

Diagnosis. Head and pereonites 2–4 with simple sublateral spines, pleotelson scarcely ornamented; pereonites 5–7 and anterior pleon scarcely armed. Pleotelson with minute lateral wings. Eyes present. Male pleopod 1 exopod with well-defined groove opening laterally at end of rounded lobe, with prominent ridge-tooth on anterior face. Male pleopod 2, appendix masculina 1.3 times as long as endopod. Oostegites 5 a pair of small midventral ovoids covering oopores.

Slope (95–900 m). Tropical Atlantic. 1 species (Paul and Menzies, 1971: species description; Poore, 2015: rediagnosis).

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Xenarcturidae Sheppard, 1957

Figure 10.12

The Xenarcturidae is the only valviferan family in which pereopod 4 is one of the posterior ambulatory limbs. The single species, *Xenarcturus spinulosus* Sheppard, 1957, is confined to Patagonian Argentina; Park (1995) redescribed it in detail.

Diagnosis. Body more or less flattened or semicylindrical, coxae with expanded coxal dorsal plates, pleonites with expanded epimera, straight, without flexion. Pereopod 1 dactylus without unguis. Pereopod 1 gnathopod-like; pereopods 2–3 elongated, setose, differentiated from ambulatory pereopods 5–7, pereopod 4 different from pereopod 3, similar to pereopod 5; with prominent dactyli, unguis short. Uropodal exopod (smaller ramus) tapering (with terminal seta or setae only). Pleopod 1 peduncle more elongate than rami, longer than on other pleopods; exopod of male thickened and with groove on posterior face, ending on tapering distolateral apical extension.

Xenarcturus Sheppard, 1957

Shelf (150–256 m). Southern Ocean (Magellan Straits). 1 species (Sheppard, 1957; Park, 1995: redescription).

References

Park, J.-Y. 1995. *Xenarcturus spinulosus* Sheppard, 1957 (Crustacea, Isopoda, Valvifera): redescription of a specimen from the Strait of Magellan. *Bulletin Zoölogisch Museum, Universiteit van Amsterdam* 14: 145–152. http://www.repository.naturalis.nl/document/548940

Sheppard, E.M. 1957. Isopod Crustacea Part II. The sub-order Valvifera. Families: Idoteidae, Pseudidotheidae and Xenarcturidae fam. n. With a supplement to isopod Crustacea, Part 1. The family Serolidae. *Discovery Reports* 29: 141–197, pls 8, 9. http://biodiversitylibrary.org/page/5568877

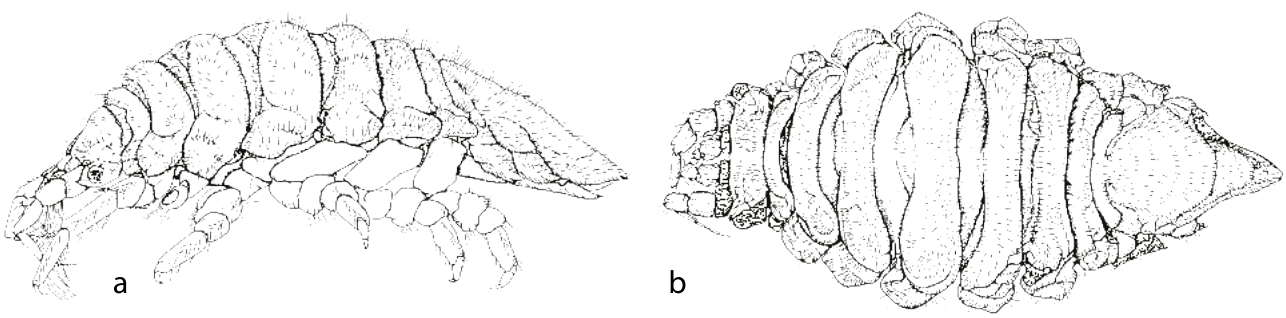


Figure 10.12. Xenarcturidae. *Xenarcturus spinulosus* Sheppard, 1957: a, b, lateral, dorsal views.

Superfamily Idoteoidea Samouelle, 1819

Three families of Valvifera – Chaetiliidae, Hologнathidae and Idoteidae – are included in Idoteioidea. While Hologнathidae are probably monophyletic, having a shortened pereopod 4, relationships between the others are less clear. Idoteids have simple pereopods but those of chaetiliids are diverse; both families contain genera with plesiomorphic biramous uropods, suggesting both families are polyphyletic.

Diagnosis. Body more or less flattened or semicylindrical, coxae with expanded coxal dorsal plates, pleonites with expanded epimera. Head and pereonite 1 free, or fused (*Crabyzos*, *Lyidotea* only). Pereopod 1 subchelate; pereopods variously subchelate or ambulatory. Pleopod 1 peduncle shorter than or as long as rami (similar to pleopods 2 and 3); exopod of male laminar.

Chaetiliidae Dana, 1849

Figures 10.13, 10.14

The Chaetiliidae are a diverse family of largely flattened or vaulted isopods possessing both uropodal rami and diverse modifications of the pereopods. The most well studied are the large polar analogues, the Arctic species, *Saduria entomon* (Linnaeus, 1758) (e.g. Haahtela, 2000; Hagerman and Szaniawska, 1991; Svanbäck et al., 2011) and the Antarctic *Glyptonotus antarcticus* Eights, 1852 (e.g. Clarke, 1979; Meyer-Rochow and Suzuki, 1986). Most species are confined to the Southern Hemisphere, but a few occur on shelves and deeper water elsewhere. Species of *Macrochiridothea* and *Chiridotea* are inhabitants of sandy beaches.

The relationships between members of this family and those of Idoteidae are not clear. While most idoteids possess only a uropodal endopod, others have two rami; all have simple ambulatory pereopods 2–7.

Diagnosis. Body more or less flattened or vaulted, pereonites and/or coxae and pleonites with expanded epimera, straight, without flexion, tapering posteriorly. Head with prominent flat lateral lobes, sometimes with ocular notch. Pereopod 1 gnathopod-like; pereopods 2–7 ambulatory, similar, with marginal short robust setae or pereopods 1–3 subchelate, similar, differentiated from pereopod 4–7 or pereopods 1–6, similar, differentiated from pereopod 7; with prominent dactyli, unguis short. Uropodal exopod (smaller ramus) ovate, fringed with setae (if present). Pleopod 1 peduncle short (similar to other pleopods); exopod of male laminar.

Implicit generic attributes. Head without lateral ocular notches; body smooth or slightly sculptured; pereonite 7 little narrower than pereonite 6; coxal dorsal plates 2–4 fused with tergites, 5–7 separated by sutures visible in dorsal view from tergites; coxal dorsal plate 7 about as long as 6. Pleonite 2 approximately as wide as pleonite 3; pleotelson tapering more or less evenly to acute apex. Antennula flagellum aesthetascs marginal along clavate article. Antennal peduncle article 4 quadrate; flagellum multiarticulate. Pereopodal carpi 1–6 not produced; pereopods 4–5 ambulatory; pereopod 4 and 5 dactyli tapering; pereopods 6 and 7 with tapering dactyli. Uropodal rami short, broad, smaller exopod overlapped.

Key to genera of Chaetiliidae

1. Pereopod 1 subchelate, with propodus expanded; pereopods 2 and 3 with expanded articles (fig. 10.14e, g); pereopods 4–7 ambulatory 2
– Pereopods 1 or more subchelate (fig. 10.14f, h), others ambulatory 3
2. Antennal peduncle article 4 quadrate (fig. 10.14d). Pereopods 2 and 3 with minute subchelate dactyli (figs 10.13f, 10.14k) ..... *Macrochiridothea*
– Antennal peduncle article 4 with posterodistal lobe alongside article 5 (fig. 10.14c). Pereopods 2 and 3 without dactyli (figs 10.13d, 10.14i, j) ..... *Chiriscus*
3. Pereopods 1–6 subchelate; pereopods 2–6 carpi projected distally on lower margin; pereopod 7 ambulatory (figs 10.13m, 10.14o, q) ..... *Symmius*
– Fewer than first 6 pairs of pereopods subchelate, remaining pereopods ambulatory 4
4. Pereopods 1–5 subchelate, pereopods 6 and 7 ambulatory (figs 10.13b, 10.14f, n) ..... *Chaetilia*
– Pereopods 1 or 1–3 subchelate, pereopods 4–7 ambulatory 5
5. Coxal dorsal plates 2–4 fused with tergites, plates 5–7 separated from suture visible in dorsal view 6
– Coxal dorsal plates 2–7 separated from suture visible in dorsal view 9

6. Pereonites each with median and sublateral tubercles. Pleonites 1 and 2 articulating with each other and with remaining pleotelson (fig. 10.13k, l) ..... *Stegidotea*

– Pereonites each with median and sublateral tubercles. Pleonites 1–3 or 1–4 articulating with each other and with remaining pleotelson 7

7. Pleonites 1–3 articulating with each other and with fused pleotelson (fig. 10.13a). Antennula flagellum with aesthetascs on minute distal article only (fig. 10.14a) ..... *Austrochaetilia*

– Pleonites 1–4 articulating with each other and with fused pleotelson. Antennula flagellum with aesthetascs marginal along clavate article (fig. 10.14b) 8

8. Body vaulted, sculptured. Pleonite 2 narrower than pleonite 3 (fig. 10.13e) ..... *Glyptonotus*

– Body flat, smooth. Pleonite 2 about as wide as pleonite 3 (fig. 10.13g) ..... *Maoridotea*

9. Coxal dorsal plate 7 about as long as coxal dorsal plate 6 (fig. 10.13i, j) 10

– Coxal dorsal plate 7 clearly shorter than coxal dorsal plate 6 and pleonite 1 (fig. 10.13c, h) 11

10. Body vaulted. Pleonites 1–4 articulating with each other and with pleotelson (fig. 10.13i) ..... *Saduria*

– Body flattened. Pleonites 1–3 articulating with each other and with pleotelson (fig. 10.13j) ..... *Saduriella*

11. Pleonites 1–3 articulating with each other and with fused pleotelson (fig. 10.13c). Pereopods 4, 5 ambulatory (fig. 10.13l) ..... *Chiridotea*

– Pleonites 1, 2 articulating with each other and with fused pleotelson (fig. 10.13h). Pereopods 4, 5 natatory, broad (fig. 10.13m) ..... *Parachiridotea*

Austrochaetilia Poore, 1978

Diagnosis. Body vaulted; head without lateral ocular notches. Pleonites 1–3 articulating with each other and with fused pleotelson; pleonite 4 fused to pleotelson but indicated by lateral suture only; pleonite 1 narrower than pleonite 3. Antennula flagellum aesthetascs terminal only (on minute distal article). Pereopods 1–3 subchelate; pereopods 4–7 ambulatory.

Shelf. Temperate Australia. 1 species (Poore, 1978).

Chaetilia Dana, 1849

Diagnosis. Body flattened, coxal plates splayed; head with lateral ocular notches; pereonite 7 much narrower than pereonite 6, 6 times as wide as long; coxal dorsal plate 7 clearly shorter than 6 and pleonite 1. Pleonites 1–3 articulating with each other and with fused pleotelson; pleonite 4 not indicated; pleonite 1 narrower than pleonite 3. Pereopods 1–5 subchelate; pereopod 6 elongate; pereopod 7 ambulatory; 6 with long setose dactylus, 7 with minute obscure dactylus.

Subtidal. Temperate South America, Temperate Australasia. 4 species (Bastida and Torti, 1970; Poore, 1985: rediagnosis).

Chiridotea Harger, 1878

Diagnosis. Body flattened, coxal plates splayed; head with lateral ocular notches; coxal dorsal plates 2–7 separated by sutures visible in dorsal view from tergites; coxal dorsal plate 7 clearly shorter than 6 and pleonite 1. Pleonites 1–3 articulating with each other and with fused pleotelson; pleonite 4 fused to pleotelson but indicated by lateral suture only; pleonite 1 as wide as pleonite 3. Pereopods 1–3 subchelate; pereopods 4–7 ambulatory.

Subtidal, shelf. Temperate Northern W Atlantic. 5 species (Bastida and Torti, 1969; McDermott, 2001, 2005; King and Cawood, 2007: rediagnosis, key to species).

Chiriscus Richardson, 1911

Diagnosis. Body flattened, coxal plates splayed; head without lateral ocular notches; pereonite 7 much narrower than pereonite 6, 3 times as wide as long; coxal dorsal plate 7 clearly shorter than 6 and pleonite 1. Pleonites 1–3 articulating with each other and with fused pleotelson; pleonite 4 fused to pleotelson but indicated by complete suture; pleonite 1 narrower than pleonite 3. Antennal peduncle article 4 with posterodistal lobe alongside article 5. Pereopods 1 subchelate, propodus expanded; pereopods 2 and 3 with minute subchela; pereopods 4–7 ambulatory; 2 and 3 without dactyli; pereopod 4 and 5 dactyli minute or lost; 6 and 7 with minute dactylus.

Shelf. Tropical W Atlantic, Temperate South America (Atlantic coast). 2 species (Poore, 1984; Poore et al., 2009: rediagnosis, key to species).

Glyptonotus Eights, 1852

Diagnosis. Body vaulted; pereonite 7 little narrower than pereonite 6. Pleonites 1–4 articulating with each other and with fused pleotelson, others sometimes indicated but not articulating; pleonite 1 narrower than pleonite 3; pleonite 2 narrower than pleonite 3. Pereopods 1–3 subchelate; pereopods 4–7 ambulatory.

Subtidal, shelf. Southern Ocean (Antarctic shelf). 2 species (Wägele, 1991: rediagnosis; Held and Wägele, 2005).

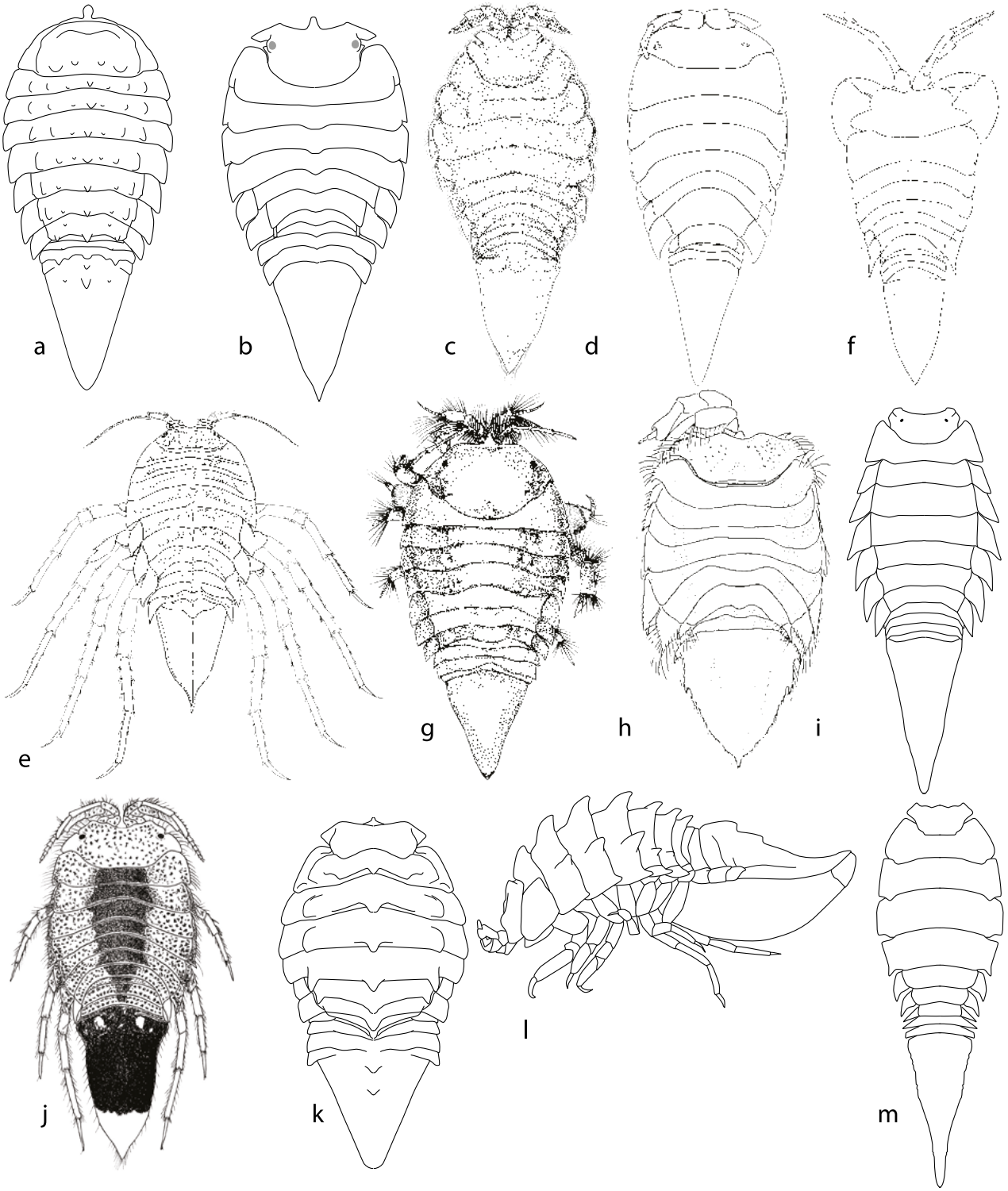


Figure 10.13. Chaetiliidae. a, *Austrochaetilia capeli* Poore, 1978; b, *Chaetilia tasmanica* Poore, 1985; c, *Chiridotea coeca* (Say, 1818); d, *Chiriscus australis* Richardson, 1911; e, *Glyptonotus antarcticus* Eights, 1852; f, *Macrochiridothea estuariae* Poore, Ramirez and Schiariti, 2009; g, *Maoridotea naylori* Jones and Fenwick, 1978; h, *Parachiridotea mediterranea* Roman, 1991; i, *Saduria entomon* (Linnaeus, 1758); j, *Saduriella losadai* Holthuis, 1964; k, l, *Stegidotea pinnata* Poore, 1985; m, *Symmius caudatus* Richardson, 1904.

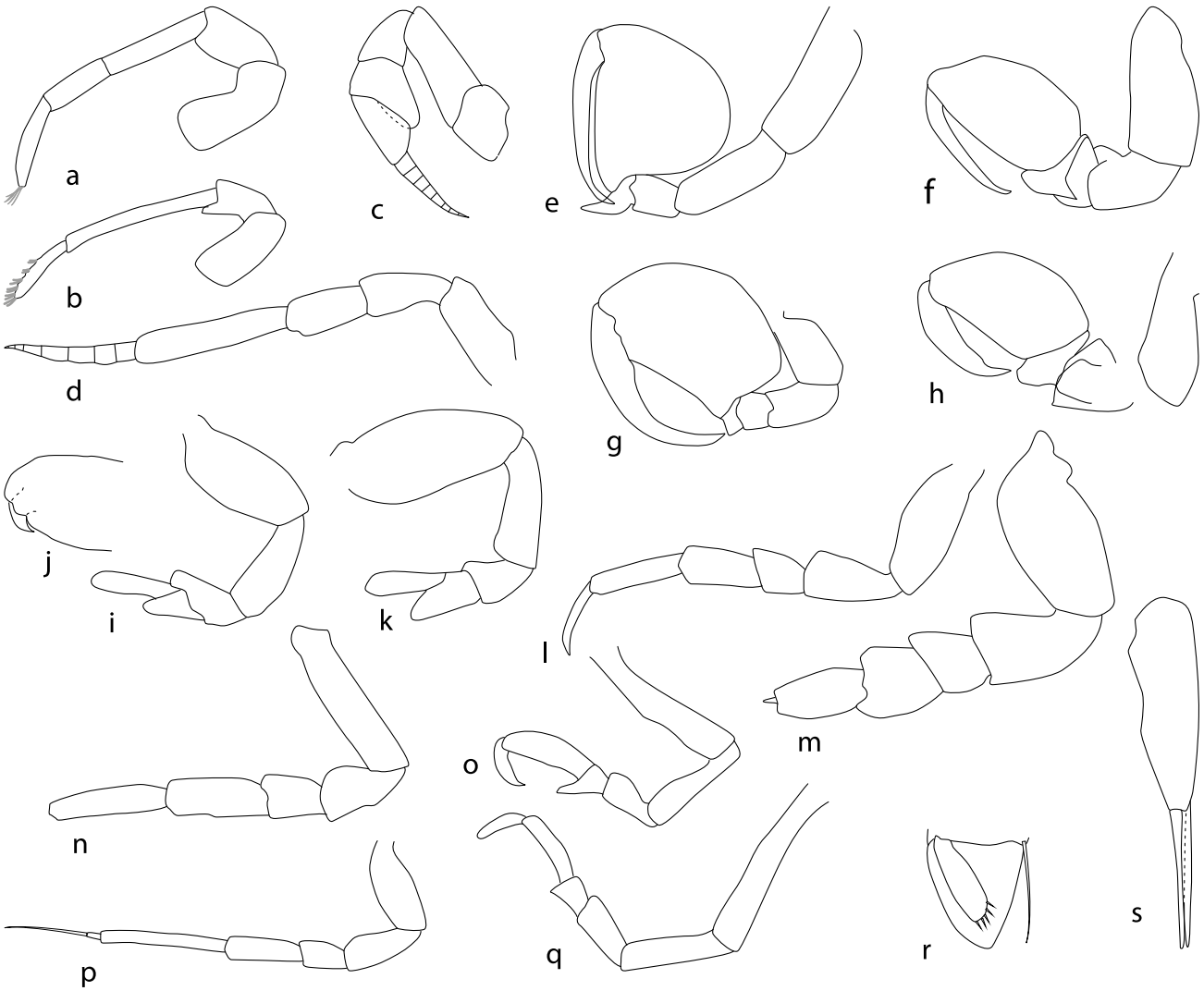


Figure 10.14. Chaetiliidae. Antennula: a, *Austrochaetilia*; b, *Maoridotea*. Antenna: c, *Chiriscus*; d, *Macrochiridothea*. Pereopod 1: e, *Chiriscus*; f, *Chaetilia*; g, *Macrochiridothea*; h, *Symmius*. Pereopod 2: i, j, *Chiriscus* (with detail of dactylus); k, *Macrochiridothea*. Pereopod 4: l, *Chiridotea*; m, *Parachiridotea*. Pereopod 6: n, *Chaetilia*; o, *Symmius*. Pereopod 7: p, *Macrochiridothea*; q, *Symmius*. Uropod: r, *Stegidotea* (rami only, internal view); s, *Symmius*.

Macrochiridothea Ohlin, 1901

Diagnosis. Body flattened, coxal plates splayed; head with lateral ocular notches; pereonite 7 much narrower than pereonite 6, 6 times as wide as long; coxal dorsal plate 7 clearly shorter than 6 and pleonite 1. Pleonites 1–3 articulating with each other and with fused pleotelson; pleonite 4 fused to pleotelson but indicated by complete suture; pleonite 1 narrower than pleonite 3. Pereopods 1 subchelate, propodus expanded; pereopods 2 and 3 with minute subchela; pereopods 4–7 ambulatory; 2 and 3 with minute subchelate dactyli; pereopod 4 and 5 dactyli minute or lost; 6 and 7 with minute dactylus.

Subtidal, shelf. Temperate South America, Temperate Australasia (New Zealand). 11 species (Carvacho, 1997; Poore et al., 2009: rediagnosis, key to species).

Maoridotea Jones and Fenwick, 1978

Diagnosis. Body flattened, coxal plates splayed; head without lateral ocular notches. Pleonites 1–4 articulating with each other and with fused pleotelson, others sometimes indicated but not articulating; pleonite 1 narrower than pleonite 3. Pereopods 1–3 subchelate; pereopods 4–7 ambulatory.

Subtidal. Temperate Australasia (New Zealand). 1 species (Jones and Fenwick, 1978).

Parachiridotea Daguerre de Hureaux and Elkaïm, 1972

Diagnosis. Body flattened, coxal plates splayed; head with lateral ocular notches (small anterior "horns"); pereonite 7 much narrower than pereonite 6, 3 times as wide as long; coxal

dorsal plates 2–7 separated by sutures visible in dorsal view from tergites; coxal dorsal plate 7 clearly shorter than 6 and pleonite 1. Pleonites 1 and 2 articulating with each other and with fused pleotelson; pleonite 3 fused to pleotelson but indicated by lateral suture only (slight); pleonite 4 not indicated; pleonite 1 as wide as pleonite 3; pleotelson lateral margins convex, with hook-like projections and acute apex. Pereopods 1–3 subchelate; pereopods 4–7 ambulatory; 4–5 natatory, broadened, with fringes of long setae; pereopod 4 and 5 dactyli minute or lost.

Subtidal. Temperate Northern E Atlantic. 2 species (Elkaïm and Daguerre de Hureaux, 1976; Guerao and Castelló, 2012; Roman, 1991).

Saduria Adams, 1852

Diagnosis. Body vaulted; head with lateral ocular notches; coxal dorsal plates 2–7 separated by sutures visible in dorsal view from tergites. Pleonites 1–4 articulating with each other and with fused pleotelson, others sometimes indicated but not articulating; pleonite 1 as wide as pleonite 3. Pereopods 1–3 subchelate; pereopods 4–7 ambulatory.

Estuarine and marine; subtidal–slope. Arctic, Temperate Northern Atlantic. 4 species (Kussakin, 1982: key to species as *Mesidotea*, junior synonym, in Russian; Lajus et al., 2003: variation; Svanbäck et al., 2011: predatory diet).

Saduriella Holthuis, 1964

Diagnosis. Body flattened, coxal plates splayed; head with lateral ocular notches; coxal dorsal plates 2–7 separated by sutures visible in dorsal view from tergites. Pleonites 1–3 articulating with each other and with fused pleotelson; pleonite 4 fused to pleotelson but indicated by lateral suture only; pleonite 1 as wide as pleonite 3. Pereopods 1–3 subchelate; pereopods 4–7 ambulatory.

Subtidal. Temperate Northern Atlantic (Spain). 1 species (Holthuis, 1964).

Stegidotea Poore, 1985

Diagnosis. Body vaulted; head without lateral ocular notches; strongly spinose with at least dorsal and dorsolateral pairs of spines, often dominated by pair near end of pleotelson; pereonite 7 little narrower than pereonite 6. Pleonites 1 and 2 articulating with each other and with fused pleotelson; pleonite 3 fused to pleotelson but indicated by lateral suture only; pleonite 4 fused to pleotelson but indicated by lateral suture only; pleonite 1 narrower than pleonite 3. Antennula flagellum aesthetascs terminal only (on minute distal article). Antennal flagellum of 2–3 articles without distal claw. Pereopods 1–3 subchelate; pereopods 4–7 ambulatory.

Shelf, slope. Central Indo-Pacific, Temperate Australasia. 6 species (Poore, 1985: description of 3 species; 1990: key to 3 Australian species; 1991).

Symmius Richardson, 1911

Diagnosis. Body vaulted; head with lateral ocular notches; pereonite 7 little narrower than pereonite 6; coxal dorsal plate 7 clearly shorter than 6 and pleonite 1. Pleonites 1 and 2 articulating with each other and with fused pleotelson; pleonite 3 fused to pleotelson but indicated by complete suture; pleonite 4 not indicated; pleonite 1 as wide as pleonite 3. Antennula flagellum aesthetascs terminal only (on minute distal article). Antennal flagellum of 2–3 articles without distal claw. Pereopods 1–6 subchelate; pereopods 2–6 carpi projected distally on lower margin; pereopod 7 ambulatory; pereopodal carpi 1–6 produced distally to oppose dactylus. Uropodal rami elongate, of equal length.

Shelf. Temperate Northern W Pacific. 5 species (Poore, 1984, 1991; Shimomura, 2008).

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Hologнathidae Thomson, 1904

Figure 10.15

The family Hologнathidae was erected for a single species, *Hologнathus stewarti* (Filhol, 1885), the only valviferan to possess a mandibular palp (Thomson, 1904). Other species are now included in the family. All possess a cylindrical shape and pereopod 4 shorter than other pereopods. Many are associated with seagrasses, and some use seagrass stems as homes (Poore and Lew Ton, 1990).

Diagnosis. Body more or less flattened or semicylindrical, coxae with expanded coxal dorsal plates, pleonites with expanded epimera, straight, without flexion, parallel-sided over most of length. Head and pereonite 1 free. Head more or less semi-cylindrical. Pereopod 1 gnathopod-like; pereopods 2–7 ambulatory, similar, with marginal short robust setae, pereopod 4 shorter and more spinose than pereopods 3 and 5; with prominent dactyli, unguis short. Uropodal exopod (smaller ramus) ovate, fringed with setae (if present). Pleopod 1 peduncle shorter than or as long as rami (similar to other pleopods); exopod of male laminar.

Implicit generic attributes. Body parallel-sided over most of length; pereonite 1 little longer than pereonite 2. Eyes present. Mandibular palp present. Pereopods 5–7 articles about twice as long as deep.

Key to genera of Hologнathidae

1. Uropod with 2 rami (fig. 10.15q) 2
– Uropod with 1 ramus (endopod only) (fig. 10.15p) 3
2. Pleotelson with 4 pleonites marked dorsally (fig. 10.15i, j). Maxillipedal palp with article 4 lobed, article 5 long (fig. 10.15n) ..... *Hologнathus*
– Pleotelson with 2 or 3 pleonites marked dorsally (fig. 10.15a, b). Maxillipedal palp oval, article 5 shorter than wide (fig. 10.15m) ..... *Cleantis*
3. Antennal flagellum multiarticulate (fig. 10.15d). Maxillipedal palp article 3 lobed, article 4 elongate (fig. 10.15o) ..... *Zenobianopsis*

– Antennal flagellum clavate (fig. 10.15c). Maxillipedal palp oval, article 3 not lobed, article 4 short (fig. 10.15m) 4

4. Pleotelson parallel-sided, with rounded or slightly excavate apex (fig. 10.15g, h) ..... *Cleantioides*

– Pleotelson tapering dorsoventrally and laterally, with deeply notched apex (fig. 10.15e, f) ..... *Chongxidotea*

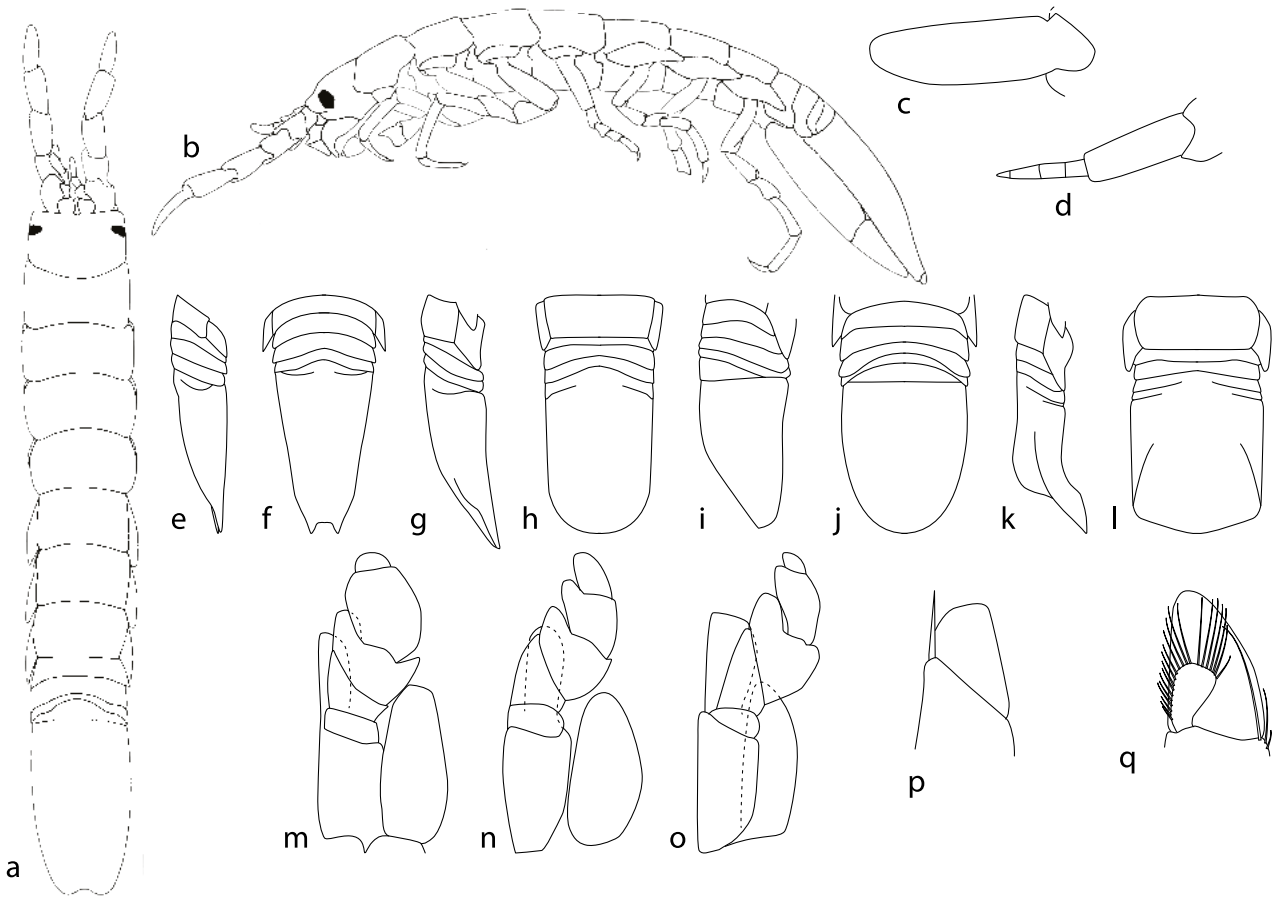


Figure 10.15. Hognathidae. a, b, *Cleantis phryganea* (Hale, 1924). Antennal flagellum: c, *Cleantis*; d, *Zenobianopsis*. Pereonite 7, pleotelson, lateral and dorsal: e, f, *Chongxidotea*; g, h, *Cleantioides*; i, j, *Hognathus*; k, l, *Zenobianopsis*. Maxilliped 3: m, *Cleantioides*; n, *Hognathus*; o, *Zenobianopsis*. Uropodal ramus/rami: p, *Chongxidotea*; q, *Cleantis*.

Chongxidotea Liu, Poore and Lu, 2010

Diagnosis. Body elongate oval, pleotelson tapering. Pleonite 1 articulating with fused pleotelson; pleonite 2 fused to pleotelson but indicated by complete suture; pleonite 3 fused to pleotelson, indicated by complete suture; pleonite 4 indicated by lateral suture; pleotelson deeply excavate, produced posterolaterally. Antennal flagellum clavate. Maxillipedal palp articles 1–5 free; article 3 scarcely lobed, article 4 elongate. Pereopod 4 dactylus with unguis differentiated from short proximal part. Pereopods 5–7 articles about 5 times as long as deep. Uropod with 1 ramus (endopod only).

Freshwater, estuarine, subtidal. Temperate Northern W Pacific (China, Korea). 1 species (Liu et al., 2010).

Cleantioides Kensley and Kaufman, 1978

Diagnosis. Pleonite 1 articulating with fused pleotelson; pleonite 2 fused to pleotelson but indicated by complete suture; pleonite 3 fused to pleotelson, indicated by complete or lateral suture; pleonite 4 indicated by lateral suture; pleotelson ending with oblique plane. Antennal flagellum clavate. Maxillipedal palp articles 2–3 fused (suture visible between); article 3 lobed, article 4 oval. Pereopod 4 dactylus reduced to unguis alone, or

with unguis differentiated from short proximal part. Uropod with 1 ramus (endopod only).

Subtidal (seagrass meadows). Tropical Atlantic, Temperate Northern W Pacific, Central Indo-Pacific, Tropical Eastern Pacific, Temperate Southern Africa, Temperate Australasia. 13 species (Poore and Lew Ton, 1990: rediagnosis).

Cleantis Dana, 1849

Diagnosis. Pleonites 1 and 2 articulating with each other and with fused pleotelson; pleonite 3 fused to pleotelson, indicated by complete or lateral suture; pleonite 4 indicated by lateral suture; pleotelson ending with oblique plane. Antennal flagellum clavate. Maxillipedal palp articles 2–3 fused (suture visible between); article 3 lobed, article 4 oval. Pereopod 4 dactylus with unguis differentiated from longer proximal part. Uropod with 2 rami (endopod and exopod fringed with setae).

Subtidal (seagrass, algae). Temperate Northern E Atlantic, including Mediterranean, Temperate South America, Temperate Australasia. 8 species (Poore and Lew Ton, 1990: rediagnosis).

Hologna thus Thomson, 1904

Diagnosis. Pereonite 1 twice as long as pereonite 2. Pleonites 1–3 articulating with each other and with fused pleotelson; pleonites 3, 4 fused to pleotelson, indicated by complete sutures; pleotelson domed posteriorly. Antennal flagellum clavate. Mandibular palp present or absent. Maxillipedal palp articles 1–5 free; articles 3 and 4 lobed mesially. Pereopod 4 dactylus with unguis differentiated from longer proximal part. Uropod with 2 rami (endopod and exopod fringed with setae).

Shelf (32–109 m; associated with sunken wood). Temperate Australasia. New Zealand. 2 species (Poore and Lew Ton, 1990).

Zenobianopsis Hale, 1946

Diagnosis. Pleonites 1 and 2 articulating with each other and with fused pleotelson; pleonites 3, 4 fused to pleotelson, indicated by lateral sutures; pleotelson ending with oblique plane. Eyes absent. Antennal flagellum of 10–12 articles. Maxillipedal palp articles 1–5 free; article 3 lobed mesially, article 4 elongate. Pereopod 4 dactylus with unguis differentiated from longer proximal part. Uropod with 1 ramus (endopod only).

Slope (386–1180 m). Central Indo-Pacific, Southern Ocean. 3 species (Hale, 1946; Kussakin, 1967; Poore and Lew Ton, 1990: rediagnosis; Poore, 2012).

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Idoteidae Samouelle, 1819

Figures 10.16–10.18

Idoteids are generally shallow-water valviferans recognisable from the generally elongated or somewhat oval dorsal aspect and the similarity of the walking legs, pereopods 2–7. Some are popularly referred to as sea-centipedes. They are distinguished from hologna thids by being less cylindrical and having pereopod 4 similar to the others. Most are associated with algal or seagrass communities and are principally herbivores (Salemaa, 1987; Sturaro et al., 2010). The association with algal substrates is taken to the extreme by the species of *Idotea* and *Synidotea*, which inhabit drift algae in oceanic environments (Poore, 2012; Thiel and Gutow, 2005a, 2005b; Thiel and Haye, 2006). Some species of *Synidotea* (Kussakin, 1982) and *Edotia* (Brandt and Bruce, 2006; Pereira and Doti, 2017) occurring in shelf or bathyal environments are not associated with algae. Most species prefer fully marine habitats, but species of *Austridotea* are estuarine (Chadderton et al., 2003), as are some species of *Idotea* (Salemaa, 1979, 1987).

The diagnoses of *Stenosoma* from the North Atlantic and *Euidotea* from southern Australasia are virtually identical. Song and Min's (2017) key to idoteid genera differentiates the two on the size of the lacinia mobilis, but differentiation of these two genera needs further investigation.

Diagnosis. Body more or less flattened or semicylindrical, coxae with expanded dorsal plates, pleonites with expanded epimera, straight, without flexion, tapering posteriorly. Head and pereonite 1 free, or fused (*Crabyzos*, *Lyidotea* only). Head more or less semi-cylindrical. Pereopod 1 gnathopod-like; pereopods 2–7 ambulatory, similar, with marginal short robust setae; with prominent dactyli, unguis short. Uropodal exopod

(smaller ramus) absent or ovate, fringed with setae (if present). Pleopod 1 peduncle shorter than or as long as rami (similar to pleopods 2 and 3); exopod of male laminar.

Implicit generic attributes. Body vaulted; head smooth; head and pereonite 1 free; smooth or slightly sculptured; parallel-sided over most of length. Pereonite 7 without ventral W-shaped ridge between pereopods. All pleonites fused into pleotelson. Antennal peduncle article 5 cylindrical. Mouthparts symmetrical. Mandibular lacinia mobilis accessory spine absent. Maxillula, inner lobe setose. Maxilla with 3 lobes. Uropod with endopod only. Penes fused basally as a penial plate but divided over most of length. Oostegites present on pereopods 1–5.

Key to genera of Idoteidae

1. Pleotelson with 1 or 2 free and articulating pleonites (figs 10.16a, m, 10.17f) 2
– Pleotelson without free and articulating pleonites, 1 or more completely or laterally indicated by sutures 4
2. Uropod with endopod only (fig. 10.18t) ..... *Idotea*
– Uropod with endopod and exopod (fig. 10.18s, u). New Zealand only 3
3. Smooth dorsally. Pleonites 1 and 2 articulating (fig. 10.16a). Maxillipedal palp articles 2, 3 free (fig. 10.18j) ..... *Austridotea*
– Median triangular dorsal tubercles, with sublateral and coxal ridges. Pleonite 1 articulating (fig. 10.17f). Maxillipedal palp articles 2, 3 fused (fig. 10.18r) ..... *Takereana*
4. Body cylindrical. Pleotelson fused to pereonite 7 (fig. 10.16n). Tropical Australia only ..... *Lyidotea*
– Body flat or vaulted. Pleotelson free from pereonite 7 5
5. Antennal flagellum multiarticulate (fig. 10.18a, d), sometimes with articles fused but identifiable by rings of short setae (fig. 10.18e) 6
– Antennal flagellum clavate, of 1 major article and minute terminal articles (fig. 10.18b, c) 19
6. Coxal dorsal plates 2–4 absent, sutures ventral, plates 5–7 present, sutures dorsal, completely traversing pereonites 7
– Coxal dorsal plates 2–7 visible in dorsal or lateral view, at least posteriorly, or absent 8
7. Body evenly oval, smooth dorsally. Dorsal sutures defining coxal plates 5–7 (fig. 10.16o) ..... *Moplisa*
– Body margin more or less irregular, pereonites expanded slightly or significantly laterally; smooth or ornamented dorsally. Dorsal sutures defining coxal plates 5–7 traversing tergites, visible or not (fig. 10.17c) ..... *Synidotea*
8. Coxal dorsal plates 2–7 absent, all sutures ventral. Head and body with longitudinal median ridge (fig. 10.17d, e) ..... *Synischia*
– Coxal dorsal plates 2–7 present at least on posterior pereonites, sutures more or less visible in dorsal or lateral view. Head and body usually smooth or rarely with anterior crest 9
9. Pereonite 1 fused to head. Pleonites not indicated by sutures; pleotelson especially elongate, acute (fig. 10.16e) ..... *Crabyzos*
– Pereonite and head free. Pleonite 1 or more indicated by lateral or complete sutures; pleotelson variously rounded or acute 10
10. Coxal dorsal plates 2–7 broad, similar, produced laterally over bases of pereopods 11
– Coxal dorsal plates 2–7 not visible dorsally or narrow, increasing in size posteriorly, not produced laterally over bases of pereopods 13
11. Coxal dorsal plates not contiguous (fig. 10.16g, h). Maxilliped with articles 2, 3 free, 4, 5 fused (fig. 10.18q) ..... *Engidotea*
– Some coxal dorsal plates more or less contiguous. Maxilliped with articles 1–5 free (fig. 10.18p) 12
12. Pleotelson apex excavate; pleonites 1 and 2 marked by lateral sutures only. Body with middorsal ridge (fig. 10.16l) ..... *Glyptidotea*

– Pleotelson apex acute; pleonites 1 and 2 marked by complete sutures. Body evenly vaulted (fig. 10.16s) ..... *Pentidotea*

13. Pleonite 1 indicated by lateral suture, pleonite 2 not indicated (fig. 10.16d) ..... *Colidotea*

– Pleonites 1 and 2 indicated as lateral or complete sutures 14

14. Maxilliped palp articles 1–5 free (fig. 10.18o, p) 15

– Maxilliped palp articles 2, 3 and/or 4, 5 fused 17

15. Pleotelson apex shallowly excavate (fig. 10.16b). Maxillula inner lobe reduced, without setae (fig. 10.18f). Maxilla a simple lobe (fig. 10.18h) ..... *Batedotea*

– Pleotelson apex acute or excavate. Maxillula of 2 lobes (fig. 10.18g). Maxilla of 3 lobes (fig. 10.18i) 16

16. Pereonite 7 with ventral W-shaped ridge between pereopods. Pleotelson apex blunt or excavate (fig. 10.17i) ..... *Paridotea*

– Pereonite 7 without ventral W-shaped ridge between pereopods. Pleotelson apex acute (fig. 10.16r) ..... *Pentias*

17. Maxilliped palp articles 2, 3 fused, 4, 5 free (fig. 10.18m) ..... *Koridotea*

– Maxilliped palp articles 2, 3 free or fused, 4, 5 fused (fig. 10.18n, q, r) 18

18. Pleonites 1, 2 indicated by complete or lateral suture, pleonite 3 indicated by lateral suture or not (figs 10.16j, 10.17g). Southern Australasia ..... *Euidotea*

– Pleonites 1–3 indicated laterally or ventrally only (fig. 10.17b). North Atlantic, Mediterranean ..... *Stenosoma*

19. Head and body with middorsal ridge. Pleonite 1 completely indicated (fig. 10.16c). Maxillipedal palp articles 1–5 free ..... *Cleantiella*

– Head and body smooth or variously sculptured, without middorsal ridge. Pleonite 1 not completely indicated. Maxillipedal palp articles 2, 3 usually free, 4, 5 fused 20

20. Pleotelson expanded posteriorly and then tapering to angular apex; pleonite 1 not indicated (fig. 10.16i) ..... *Erichsonella*

– Pleotelson evenly tapering; pleonite 1 indicated by lateral suture 21

21. Coxal dorsal plates 2–7 not visible, fused dorsally to tergites (fig. 10.17a). Antennal peduncle flattened (fig. 10.18c) ..... *Platidotea*

– Coxal dorsal plates 2–7 or 5–7 visible dorsally or laterally. Antennal peduncle cylindrical 22

22. Coxal dorsal plate 6 visible laterally, 7 produced laterally, separated from tergite by dorsal suture. Body evenly parallel-sided (fig. 10.16p) ..... *Parasymmerus*

– Coxal dorsal plates 5–7 well produced ventrolaterally, separated from tergite by dorsal suture. Body evenly or irregularly parallel-sided or ovate 23

23. Coxal dorsal plates 2–4 absent, tergite forming lateral margin; 5–7 well produced ventrolaterally, separated from tergite by dorsal suture traversing tergite (fig. 10.16f) ..... *Edotia*

– Coxal dorsal plates 2–5 not or scarcely visible dorsally; 6, 7 separated from tergite by oblique dorsal suture occupying posterior half of margin (fig. 10.16k) ..... *Eusymmerus*

Austridotea Poore, 2001

Diagnosis. Body widest in midpereon and tapering posteriorly. Coxal dorsal plates 2–7 produced ventrolaterally, sutures visible dorsally, more or less contiguous. Pleonites 1 and 2 articulating with each other and with fused pleotelson, pleonites 3, 4 indicated laterally only; pleotelson apex rounded. Antennal flagellum multiarticulate. Maxillipedal palp articles 1–5 free, or articles 2, 3 free, 4, 5 fused. Uropod with 2 short rami, exopod overlapped.

Freshwater, estuarine, intertidal. Temperate South America (S Argentina), Temperate Australasia (New Zealand). 4 species (Miers, 1881: figure of South American species; Nicholls, 1937: figures; Poore, 2001; Chadderton et al., 2003: ecology; McGaughran et al., 2006: genetics; Dufour et al., 2007: ecology).

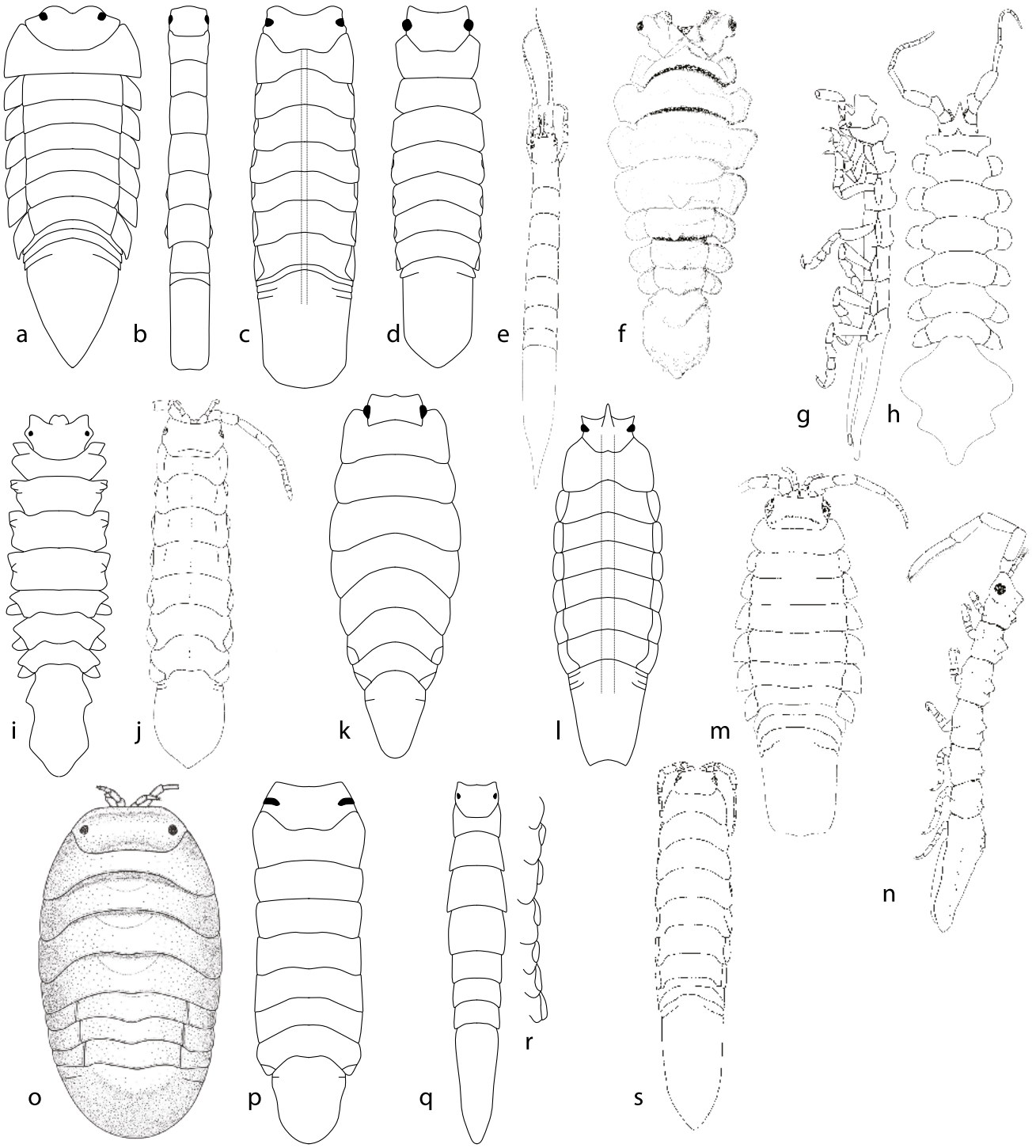


Figure 10.16. Idoteidae. a, *Austridotea annectans* Nicholls, 1937; b, *Batedotea elongata* (Miers, 1876); c, *Cleantiella isopus* (Miers, 1881); d, *Colidotea findleyi* Brusca and Wallerstein, 1977; e, *Crabyzos longicaudatus* Bate, 1863; f, *Edotia pulchra* Brandt, 1990; g, h, *Engidotea cristata* Poore and Lew Ton, 1993; i, *Erichsonella isabellensis* Menzies, 1951; j, *Euidotea bakeri* (Collinge, 1917); k, *Eusymmerus antennatus* Richardson, 1899; l, *Glyptidotea lichtensteini* (Krauss, 1843); m, *Idotea metallica* Bosc, 1802; n, *Lyidotea nodata* Hale, 1928; o, *Moplisa sphaeromiformis* (Mañe-Garzón, 1946); p, *Parasymmerus annamaryae* Brusca and Wallerstein, 1979; q, r, *Pentias hayi* Richardson, 1904 (dorsal, lateral pereon with coxal plates 2–7); s, *Pentidotea australis* Hale, 1924.

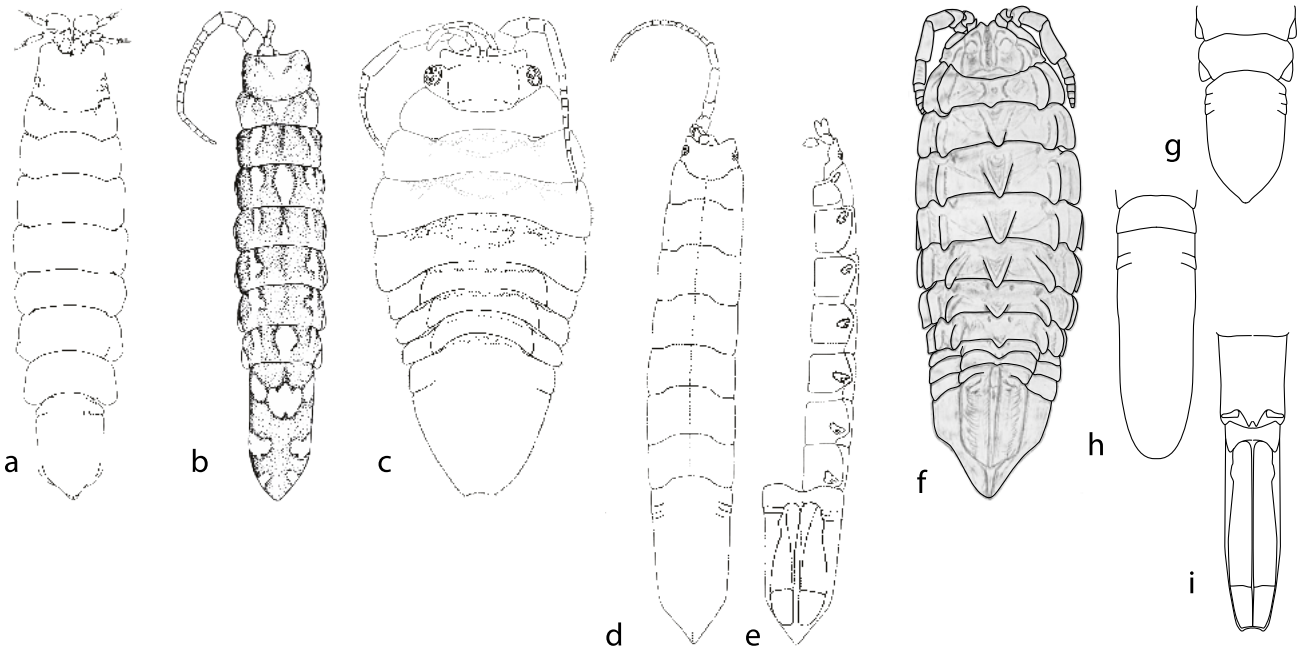


Figure 10.17. Idoteidae. a, *Platidotea magellanica* Park and Wägele, 1995; b, *Stenosoma stephenseni* Santos and Xavier, 2011; c, *Synidotea grisea* Poore and Lew Ton, 1993; d, e, *Synischia levidensis* Hale, 1924 (dorsal, ventral); f, *Takereana festiva* (Chilton, 1885). Pereonites 6, 7, pleotelson: g, *Euidotea*; h, *Koridotea*. i, pereonite 7, pleotelson, ventral, *Paridotea*.

Batedotea Poore and Lew Ton, 1993

Diagnosis. Coxal dorsal plates 2–7 visible only laterally, not contiguous (visible dorsally on posterior pereonites in male only). Pleonite 1 indicated by complete suture, pleonite 2 indicated laterally; pleotelson apex excavate; apical excavation slight. Antennal flagellum multiarticulate. Maxillula, inner lobe reduced, without setae. Maxilla with 1 lobe. Maxillipedal palp articles 1–5 free.

Subtidal. Temperate Australia. 1 species (Poore and Lew Ton, 1993).

Cleantiella Richardson, 1912

Diagnosis. Body flattened, coxal plates splayed; body with middorsal ridge. Coxal dorsal plates 2–7 produced laterally, not contiguous. Pleonite 1 indicated by complete suture, pleonites 2, 3 indicated laterally; pleotelson apex acute (broadly). Antennal flagellum clavate, of 1 major article with few minute terminal articles. Maxillipedal palp articles 1–5 free.

Subtidal. Temperate Northern W Pacific. 2 species (Kim and Kwon, 1988; Takahashi and Goshima, 2012).

Colidotea Richardson, 1899

Diagnosis. Body widest in midpereon and tapering posteriorly. Coxal dorsal plates 2–4 absent, tergite forming lateral margin; 5–7 well produced ventrolaterally, separated from tergite by dorsal suture traversing tergite. Pleonite 1 indicated laterally, or pleonites not indicated (probable); pleotelson apex rounded. Antennal flagellum multiarticulate. Maxillipedal palp articles 2, 3 free, 4, 5 fused.

Subtidal. Eastern Indo-Pacific, Tropical Eastern Pacific. 4 species (Brusca, 1983; Stebbins, 1988, 1989). *Synisoma wetzerae* Ormsby, 1991 is a probable member.

Crabyzos Bate, 1863

Diagnosis. Body cylindrical; head and pereonite 1 fused. Coxal dorsal plates 2–7 visible only laterally, not contiguous. Pleonites not indicated; pleotelson apex acute (extremely). Antennal flagellum multiarticulate. Mouthparts asymmetrical. Maxilla with 1 lobe. Maxillipedal palp articles 1–5 free.

Subtidal (seagrass). Temperate Australia. 1 species (Poore and Lew Ton, 1993).

Edotia Guérin-Méneville, 1843

Diagnosis. Head smooth, or with paired lobes or cones; body smooth or slightly sculptured, or nodulose; body widest in midpereon and tapering posteriorly. Coxal dorsal plates 2–4 absent, tergite forming lateral margin; 5–7 well produced ventrolaterally, separated from tergite by dorsal suture. Pleonite 1 indicated laterally; pleotelson apex acute. Antennal flagellum clavate, of 1 major article with few minute terminal articles. Maxillipedal palp articles 2, 3 free, 4, 5 fused. Penes fused as a single penial plate.

Intertidal–bathyal (0–3282 m). Tropical Atlantic, Eastern Indo-Pacific, Temperate South America, Southern Ocean. 20 species (Goeke and Heard, 1983; Brandt, 1990: description of 6 species; Brandt and Bruce, 2006; Pereira and Doti, 2017: key to 14 Southern Hemisphere species). Some species are symbionts of mussels (Zaixso et al., 2009).

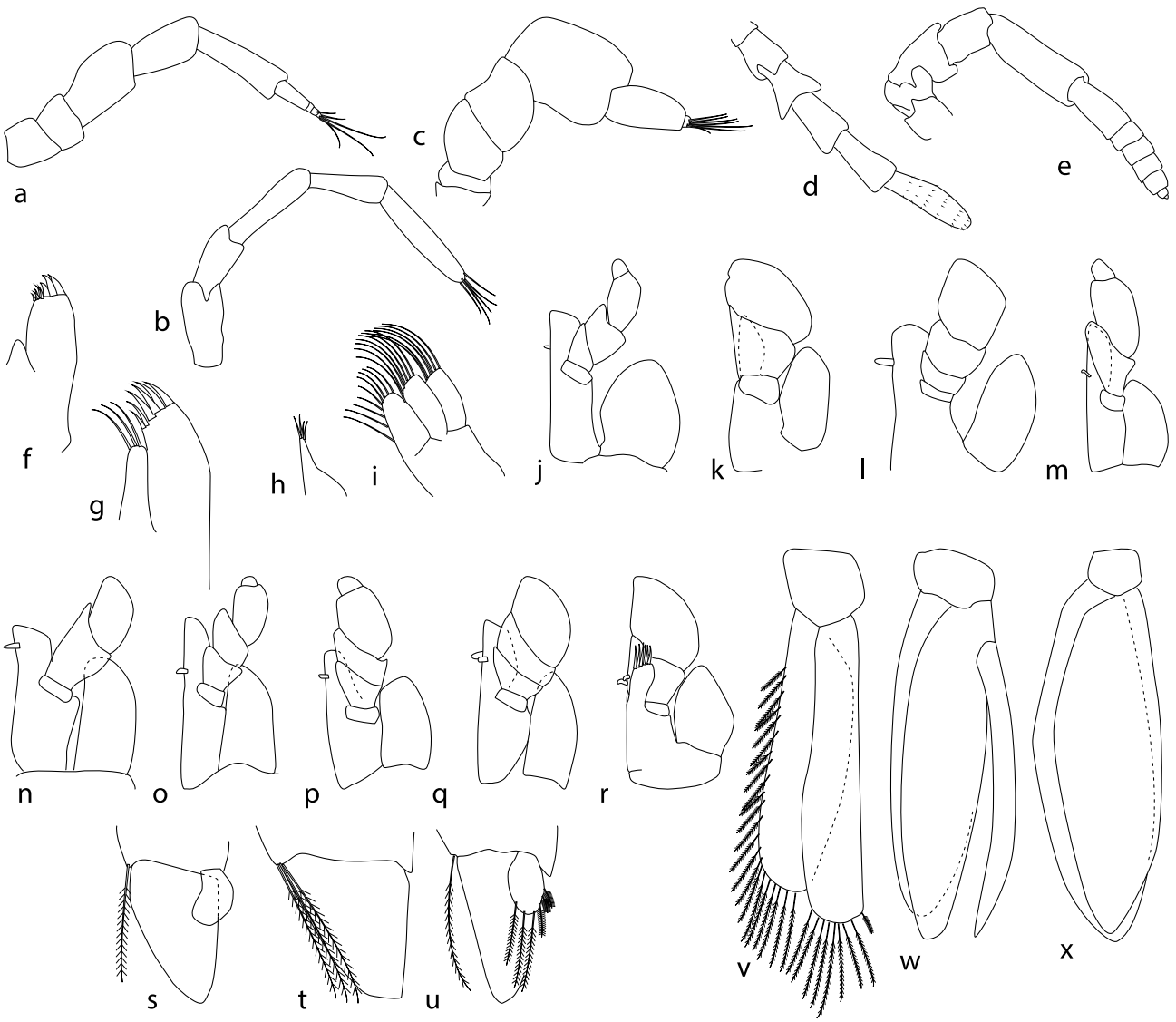


Figure 10.18. Idoteidae. Antenna: a, *Edotia*; b, *Eusymmerus*; c, *Platidotea*; d, e, *Stenosoma*. Maxillula: f, *Batedotea*; g, *Euidotea*. Maxilla: h, *Batedotea*; i, *Euidotea*. Maxilliped: j, *Austridotea*; k, *Edotia*; l, *Eusymmerus*; m, *Koridotea*; n, *Parasymmerus*; o, *Pentias*; p, *Pentidotea*; q, *Stenosoma*; r, *Takereana*. Uropodal ramus/rami: s, *Austridotea*; t, *Synidotea*; u, *Takereana*. v–x, male pleopods 1–3, *Euidotea*.

Engidotea Barnard, 1914

Diagnosis. Body flattened, coxal plates splayed; head smooth, or with a crest or lobe; body with middorsal ridge (anteriorly); parallel-sided over most of length (excavated between coxal plates). Coxal dorsal plates 2–7 well produced laterally, not contiguous. Pleonite 1 indicated by complete or lateral suture; pleotelson apex rounded, or apex excavate. Antennal flagellum multiarticulate. Maxilla with 2 lobes. Maxillipedal palp articles 2, 3 free, 4, 5 fused.

Subtidal. Temperate Southern Africa, Temperate Australasia. 2 species (Kensley, 1978; Poore and Lew Ton, 1993).

Erichsonella Benedict *in* Richardson, 1901

Diagnosis. Body cylindrical; head with paired lobes or cones; smooth or slightly sculptured, or pereonites with dorsal spines. Coxal dorsal plates 2–7 visible laterally and dorsally on all or only posterior pereonites, not contiguous. Pleonites not indicated; pleotelson expanded and widest posteriorly. Antennal flagellum clavate, of 1 major article with few minute terminal articles. Maxillipedal palp articles 2, 3 free, 4, 5 fused.

Intertidal–shelf (seagrasses, algae). Temperate Northern and Tropical Atlantic, Temperate Northern and Tropical Eastern Pacific. 7 species (Brusca, 1983; Brusca and Wallerstein, 1977; Pires, 1984: rediagnosis, key to 6 species).

Euidotea Collinge, 1917

Diagnosis. Coxal dorsal plates 2–7 visible laterally and dorsally on all or only posterior pereonites, not contiguous. Pleonites 1, 2 indicated by complete or lateral suture, pleonite 3 indicated by lateral suture or not; pleotelson apex rounded, or apex acute. Antennal flagellum multiarticulate. Maxillipedal palp articles 2, 3 fused, 4, 5 fused (rare), or articles 2, 3 free, 4, 5 fused.

Subtidal. Temperate Australasia. 7 species (Poore and Lew Ton, 1993: rediagnosis, key to species). *Idotea distincta* Guérin-Méneville, 1843 from South Africa, synonymised with *E. peronii* by Miers (1881) has not been seen since its description (Kensley, 1978) and is not included.

Eusymmerus Richardson, 1899

Diagnosis. Head with paired lobes or cones; body smooth or sculptured slightly, or body with middorsal ridge; body widest in midpereon and tapering posteriorly. Coxal dorsal plates 2–5 not or scarcely visible dorsally; 6, 7 separated from tergite by oblique dorsal suture occupying posterior half of margin. Pleonite 1 indicated laterally; pleotelson apex rounded. Antennal flagellum clavate, of 1 major article with few minute terminal articles. Maxillipedal palp articles 2, 3 free, 4, 5 fused.

Subtidal. Tropical Eastern Pacific. 2 species (Brusca and Wallerstein, 1977: rediagnosis; 1979a: distribution; 1979b: phylogeny; Brusca, 1984: phylogeny).

Glyptidotea Stebbing, 1902

Diagnosis. Head with middorsal crest and longitudinal ridge; body with middorsal ridge; body widest in midpereon and tapering posteriorly. Coxal dorsal plates 2–7 produced ventrolaterally, sutures visible dorsally, more or less contiguous. Pleonites 1–3 indicated laterally or ventrally only; pleotelson apex excavate; apical excavation slight. Antennal flagellum multiarticulate. Maxillipedal palp articles 1–5 free.

Intertidal. Temperate Southern Africa. 1 species (Stebbing, 1902; Kensley, 1978: redescription).

Idotea Fabricius, 1798

Diagnosis. Head smooth, or with paired lobes or cones (obscure if present). Coxal dorsal plates 2–7 produced ventrolaterally, sutures visible dorsally, more or less contiguous. Pleonites 1 and 2 articulating with each other and with fused pleotelson, others sometimes indicated but not articulating; pleotelson apex rounded, or apex acute, or apex truncate, or with prominent apical lobe. Antennal flagellum multiarticulate. Maxillipedal palp articles 2, 3 free, 4, 5 fused. Penes paired (adjacent).

Subtidal and pelagic. Cosmopolitan, mostly Northern Hemisphere (Rafi and Laubitz, 1990). *Idotea metallica* Bosc, 1802 has been recorded in most oceans associated with drifting kelp (Clarkin et al., 2012; Gutow and Franke, 2003; Thiel and Gutow, 2005a). *Idotea balthica* (Pallas, 1772) is one of the best studied of all marine isopods (Bell and Sotka, 2012; Zaabar et al., 2014).

Koridotea Song and Min, 2017

Diagnosis. Body cylindrical. Coxal dorsal plates 2–7 visible only laterally, not contiguous. Pleonite 1 indicated by complete suture, pleonites 2, 3 indicated laterally; pleotelson apex acute. Antennal flagellum multiarticulate. Maxillipedal palp articles 2, 3 fused, 4, 5 free.

Subtidal. Temperate Northern W Pacific. 1 species (Song and Min, 2017).

Lyidotea Hale, 1929

Diagnosis. Body cylindrical; head with paired lobes or cones; head and pereonite 1 fused; with median triangular tubercles, with sublateral and coxal ridges. Coxal dorsal plates 2–7 absent, tergite forming lateral margin. All pleonites fused to pereonite 7, none indicated laterally; pleotelson apex rounded. Antennal flagellum clavate, of 1 major article with minute claw. Maxillipedal palp articles 2, 3 fused, 4, 5 free. Penes paired, elongate (adjacent).

Subtidal, shelf (0–140 m). Central Indo-Pacific (N Australia). 1 species (King and Poore, 2001: rediagnosis, redescription of only species).

Moplisa Moreira, 1974

Diagnosis. Body flattened, coxal plates splayed; widest in midpereon and tapering posteriorly. Coxal dorsal plates 2–4 absent, tergite forming lateral margin; 5–7 well produced ventrolaterally, separated from tergite by dorsal suture. Pleonite 1 indicated laterally; pleotelson apex rounded. Antennal flagellum multiarticulate. Maxillipedal palp articles 2, 3 fused, 4, 5 fused.

Shelf (4.5–32 m). Temperate South America (Uruguay, Brazil). 1 species (Moreira, 1974).

Parasymmerus Brusca and Wallerstein, 1979

Diagnosis. Body flattened, coxal plates splayed. Coxal dorsal plates 2–4 absent, tergite forming lateral margin; 6 visible laterally, 7 produced laterally, separated from tergite by dorsal suture. Pleonite 1 indicated laterally; pleotelson apex acute (broadly). Antennal flagellum clavate, of 1 major article with few minute terminal articles. Maxillipedal palp articles 2, 3 free, 4, 5 fused.

Subtidal. Tropical Eastern Pacific. 1 species (Brusca and Wallerstein, 1979b).

Paridotea Stebbing, 1900

Diagnosis. Body flattened, coxal plates splayed (somewhat), or cylindrical. Coxal dorsal plates 2–7 produced ventrolaterally, sutures not or scarcely visible dorsally, contiguous only posteriorly (if at all). Pereonite 7 with ventral W-shaped ridge between pereopods. Pleonites 1, 2 indicated by complete or lateral suture, pleonite 3 indicated by lateral suture or not; pleotelson apex blunt or excavate; apical excavation almost as deep as wide, or slight. Antennal flagellum multiarticulate. Maxillipedal palp articles 1–5 free.

Subtidal. Temperate Northern W Pacific, Temperate Southern Africa, Temperate Australasia. 13 species (Kensley, 1978: key to 5 species; Poore and Lew Ton, 1993: rediagnosis, key to 6 species).

Pentias Richardson, 1904

Diagnosis. Coxal dorsal plates 2–7 produced ventrolaterally, sutures not or scarcely visible dorsally, contiguous only posteriorly (if at all). Pleonites 1–3 indicated laterally or ventrally only, or pleonites not indicated (probable); pleotelson apex acute. Antennal flagellum multiarticulate. Maxillipedal palp articles 1–5 free.

Subtidal. Temperate Northern W Pacific (Japan). 4 species (Rafi, 1973: 3 species compared; Nunomura, 2006). *Synisoma pacificum* Nunomura, 1974 is a probable member.

Pentidotea Richardson, 1905

Diagnosis. Coxal dorsal plates 2–7 produced ventrolaterally, sutures not or scarcely visible dorsally, contiguous only posteriorly (if at all). Pleonites 1, 2 indicated by complete suture, pleonite 3 indicated laterally; pleotelson apex acute. Antennal flagellum multiarticulate. Maxillipedal palp articles 1–5 free.

Intertidal, subtidal. Temperate Northern W Pacific, Temperate Australasia. 11 species (Brusca and Wallerstein, 1977, 1979a; Poore and Lew Ton, 1993).

Platidotea Park and Wägele, 1995

Diagnosis. Body flattened, coxal plates splayed. Coxal dorsal plates 2–7 produced ventrolaterally, sutures not or scarcely visible dorsally, contiguous only posteriorly (if at all). Pleonite 1 indicated laterally; pleotelson apex acute. Antennal peduncle article 5 flattened and broad. Antennal flagellum clavate, of 1 major article with few minute terminal articles. Maxillipedal palp articles 2, 3 fused, 4, 5 fused.

Shelf (21 m). Temperate South America. Magellan Strait. 1 species (Park and Wägele, 1995).

Stenosoma Leach, 1814

Diagnosis. Coxal dorsal plates 2–7 produced ventrolaterally, sutures not or scarcely visible dorsally, contiguous only posteriorly (if at all). Pleonites 1–3 indicated laterally or ventrally only; pleotelson apex acute. Antennal flagellum multiarticulate, or of up to 10 fused articles surrounded by short setae. Maxillipedal palp articles 2, 3 free, 4, 5 fused.

Intertidal–shelf (0–118 m). Temperate Northern Atlantic. 16 species (Rezig, 1989: illustrations; Castellanos and Junoy, 2005: key to 13 species; Santos et al., 2011: key to 14 species; Artüz and Kubanç, 2015: key to 16 species). *Stenosoma* is confined here to species from the North Atlantic and Mediterranean. *Stenosoma* has a complex taxonomy, many species having been described as members of *Synisoma* Collinge, 1917 (Santos et al., 2011). The keys to species cited above differentiate three species as possessing a “clavate” antennal flagellum. Their flagellum comprises fused articles surrounded by short setae, not homologous to the clavate form where the flagellum is one large article and few minute terminal articles (Brusca, 1984).

Leptosoma Risso, 1827 is a junior subjective synonym without type species (Risso, 1827). *Leptosoma appendiculata* Risso, 1827 is herein designated as its type species.

Two species from the northern Pacific, both without pleonal sutures, probably belong in other genera in the region. The maxillipedal palp of *Synisoma pacificum* Nunomura, 1974 is narrow like that of *Pentias*, while that of *Synisoma wetzerae* Ormsby, 1991 resembles that of *Colidotea*. Pleonal sutures are visible laterally in both these genera.

Synidotea Harger, 1878

Diagnosis. Head smooth, or with paired lobes or cones; body smooth or sculptured slightly, or nodulose; body widest in midpereon and tapering posteriorly. Coxal dorsal plates 2–4 absent, tergite forming lateral margin; 5–7 well produced ventrolaterally, separated from tergite by dorsal suture (sometimes fused). Pleonite 1 indicated laterally; pleotelson apex rounded, acute, truncate or excavate; apical excavation slight. Antennal flagellum multiarticulate. Mandibular lacinia mobilis accessory spine present. Maxillipedal palp articles 2, 3 fused, 4, 5 fused. Penes fused as a single penial plate. Oostegites present on pereopods 1–4, as vestigial lobes on 5.

Intertidal–slope. Cosmopolitan. 61 species (Kussakin, 1982; Menzies and Miller, 1972; Poore, 2012; Rafi and Laubitz, 1990; Schotte and Heard, 2004). *Synidotea laticauda* Benedict, 1897, described from San Francisco Bay, has become widespread in harbours throughout the world (Poore, 1996; Soors et al., 2010).

Synischia Hale, 1924

Diagnosis. Body flattened, coxal plates splayed or cylindrical; head with longitudinal ridge; body with middorsal ridge. Coxal dorsal plates 2–7 absent, tergite forming lateral margin. Pleonites 1–3 indicated laterally or ventrally only; pleotelson apex acute. Antennal flagellum multiarticulate. Maxillipedal palp articles 1–5 free.

Subtidal. Temperate Australia. 2 species (Poore and Lew Ton, 1993).

Takereana Poore and Hurley, 2015

Diagnosis. Head with middorsal crest; body with median triangular tubercles, with sublateral and coxal ridges; body widest in midpereon and tapering posteriorly. Coxal dorsal plates 2–7 produced ventrolaterally, sutures visible dorsally, more or less contiguous. Pleonite 1 articulating with fused pleotelson; pleotelson apex acute. Antennal flagellum multiarticulate. Maxillipedal palp articles 2, 3 fused, 4, 5 fused. Uropod with 2 short rami, exopod overlapped.

Subtidal. Temperate Australasia (New Zealand). 1 species (Poore and Hurley, 2015).

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