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Chapter 2. Taxonomy of the Isopoda

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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

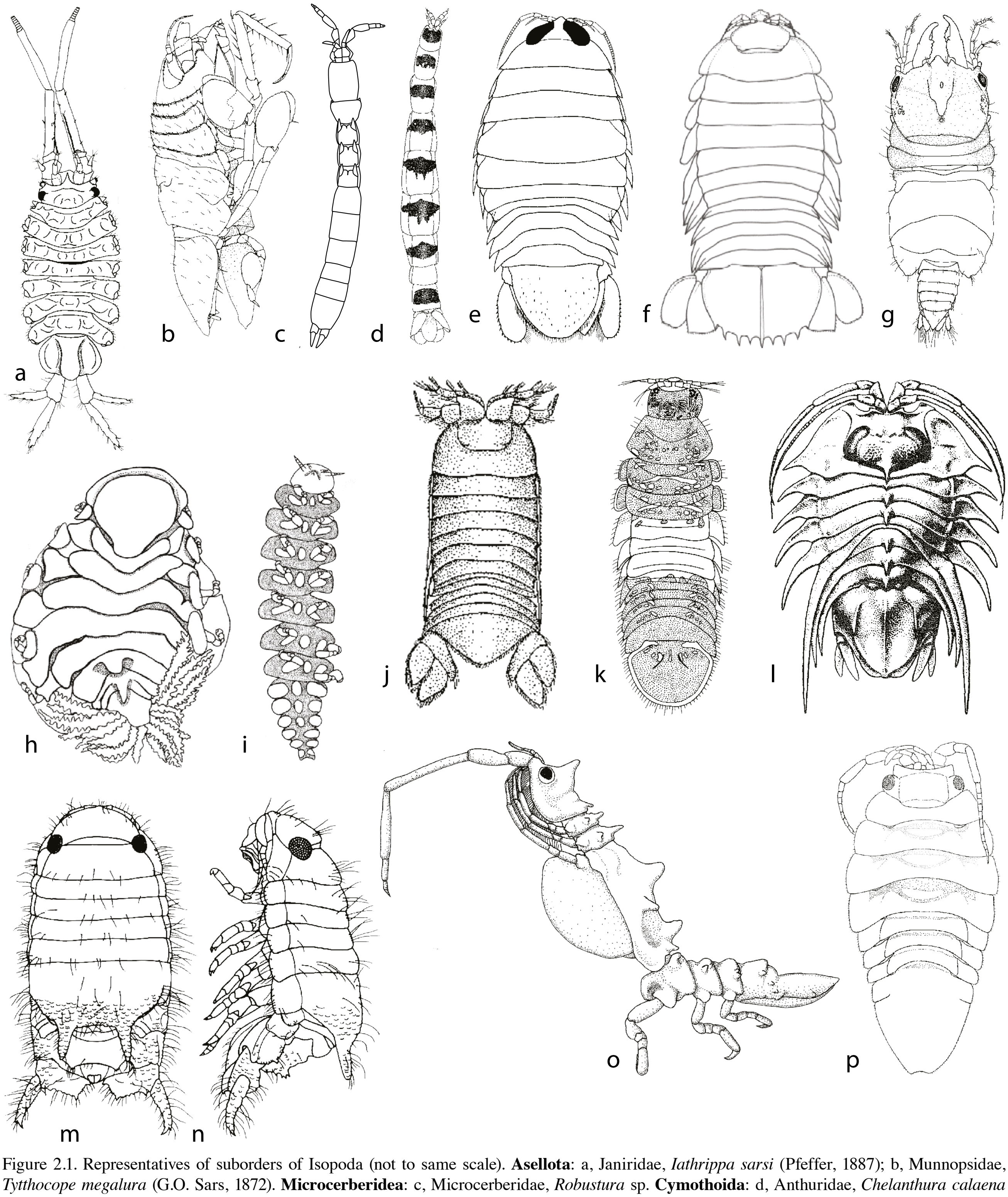

Figure 2.1. Representatives of suborders of Isopoda (not to same scale). **Asellota**: a, Janiridae, *Iathrippa sarsi* (Pfeffer, 1887); b, Munnopsidae, *Tytthocope megalura* (G.O. Sars, 1872). **Microcerberidea**: c, Microcerberidae, *Robustura* sp. **Cymothoida**: d, Anthuridae, *Chelanthura calaena* (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.

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

Elements in fig. 2.1 are reprinted directly with permission of the publisher and/or author or are in the public domain, as credited here: fig. 2.1a, Winkler (1993); b, Wilson (1981); c, Messana et 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)

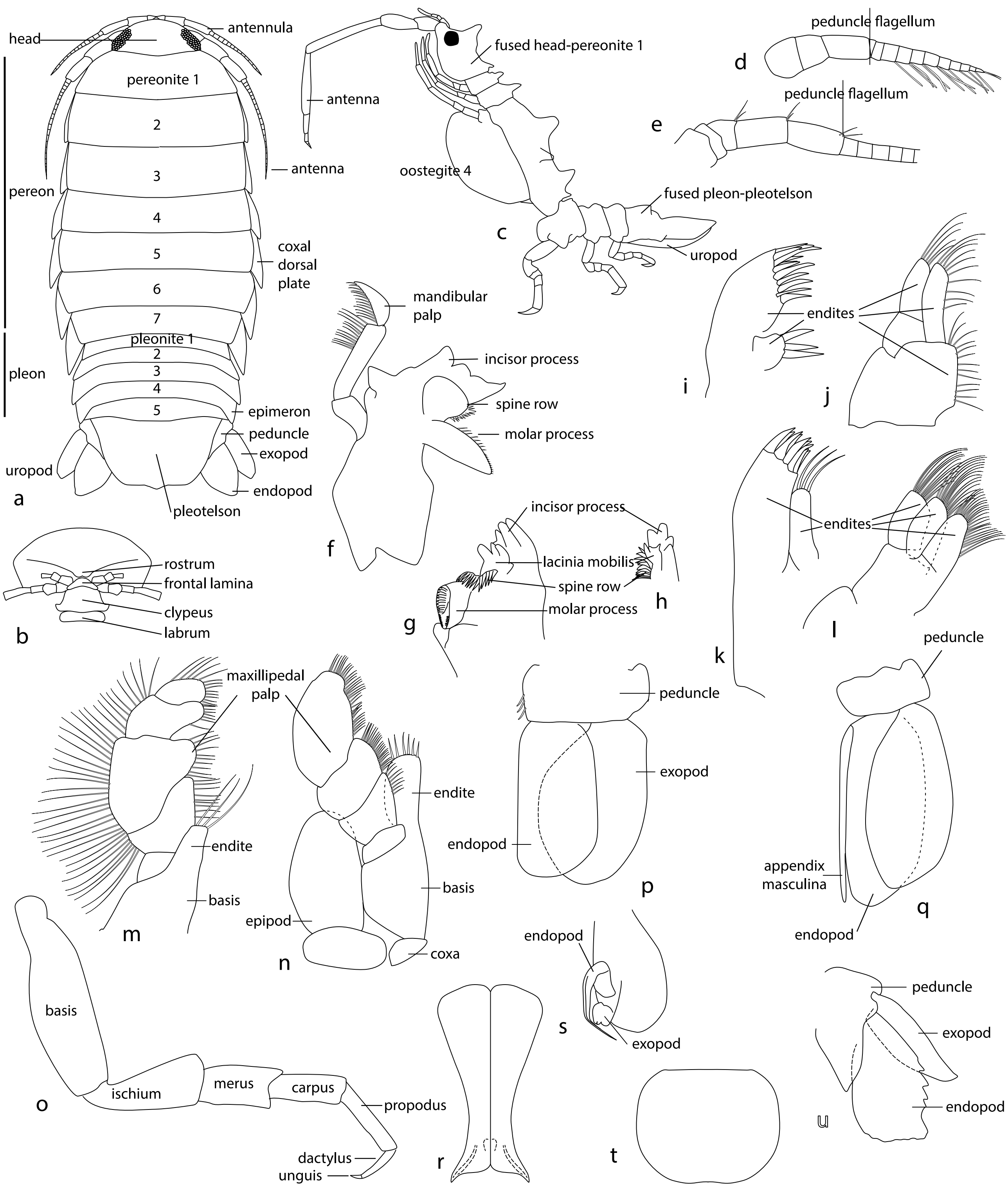

Figure 2.2. Illustrations of morphological terms used in isopod morphology. a, typical cymothoidan isopod; b, anterior view of cymothoidan head; c, lateral view of typical arcturid (Valvifera); d, typical cymothoidan antennula; e, typical cymothoidan antenna; f, typical cymothoidan mandible; g, right 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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