Crustacean

(Group of Arthropods)

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Chapter 1

Crustacean

Crustacea Temporal range: 511–0 Ma Cambrian to Recent	

Abludomelita obtusata, an amphipod

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	**Crustacea** Brünnich, 1772

Classes & Subclasses

Thylacocephala
Branchiopoda

- Phyllopoda
- Sarsostraca

Remipedia
Cephalocarida
Maxillopoda

- Thecostraca
- Tantulocarida

Branchiura
Pentastomida
Mystacocarida
Copepoda

Ostracoda

Myodocopa
Podocopa

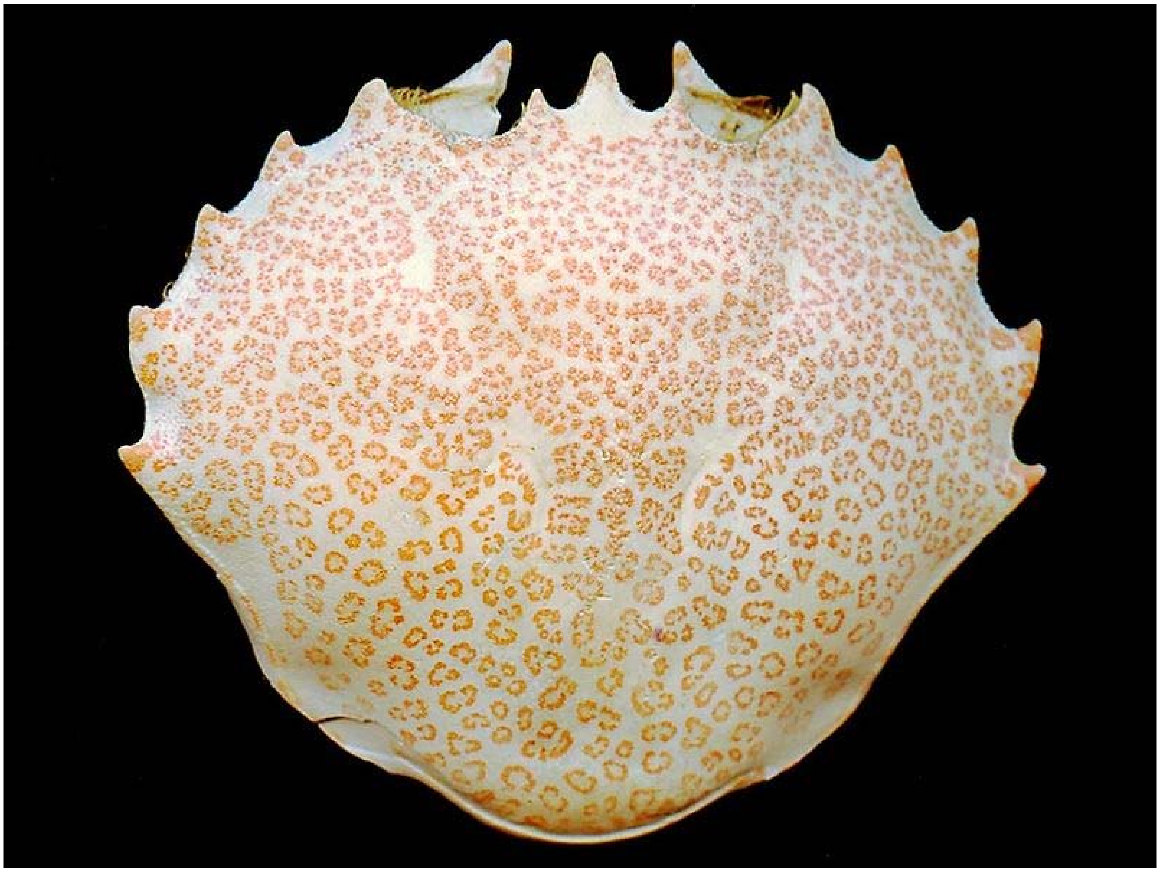
Malacostraca

Phyllocarida
Hoplocarida
Eumalacostraca

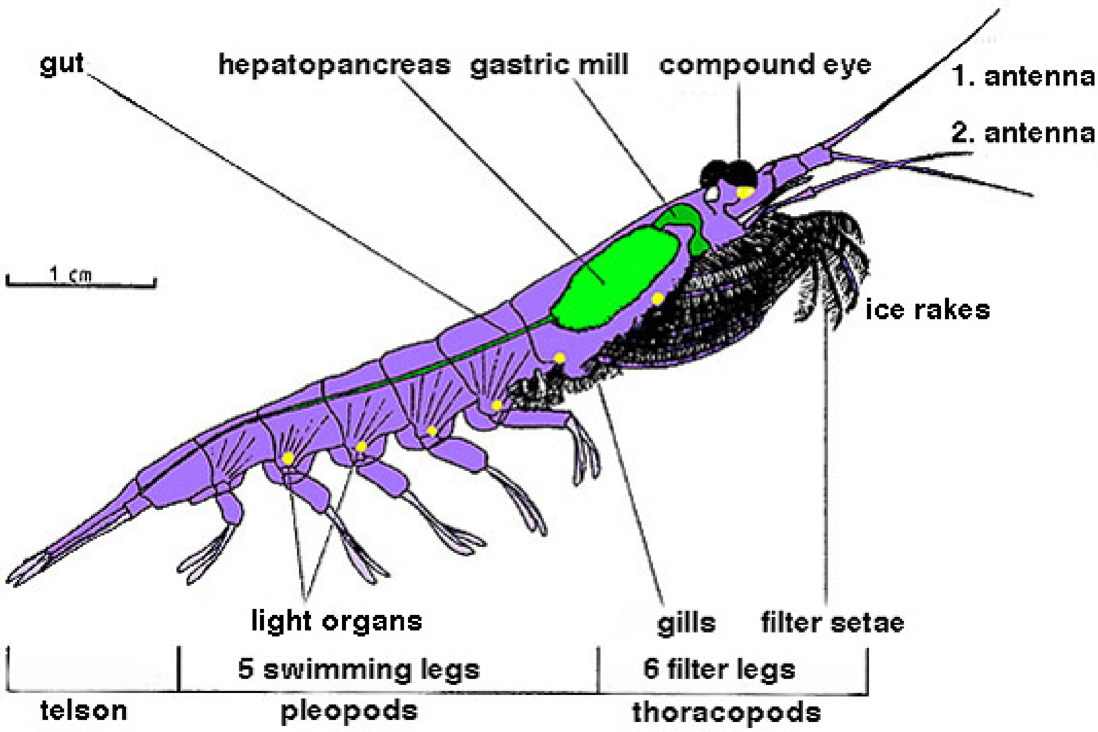
Crustaceans (**Crustacea**) form a very large group of arthropods, usually treated as a subphylum, which includes such familiar animals as crabs, lobsters, crayfish, shrimp, krill and barnacles. The 50,000 described species range in size from *Stygotantulus stocki* at 0.1 mm (0.004 in), to the Japanese spider crab with a leg span of up to 12.5 ft (3.8 m) and a mass of 44 lb (20 kg). Like other arthropods, crustaceans have an exoskeleton, which they moult to grow. They are distinguished from other groups of arthropods, such as insects, myriapods and chelicerates by the possession of biramous (two-parted) limbs, and by the nauplius form of the larvae.

Most crustaceans are free-living aquatic animals, but some are terrestrial (e.g. woodlice), some are parasitic (e.g. fish lice, tongue worms) and some are sessile (e.g. barnacles). The group has an extensive fossil record, reaching back to the Cambrian, and includes living fossils such as *Triops cancriformis*, which has existed apparently unchanged since the Triassic period. More than 10 million tons of crustaceans are produced by fishery or farming for human consumption, the majority of it being shrimps and prawns. Krill and copepods are not as widely fished, but may be the animals with the greatest biomass on the planet, and form a vital part of the food chain. The scientific study of crustaceans is known as carcinology (alternatively, malacostracology, crustaceology or crustalogy), and a scientist who works in carcinology is a carcinologist.

Structure



A shed carapace of a lady crab, part of the hard exoskeleton



Body structure of a typical crustacean - krill

The body of a crustacean is composed of body segments, which are grouped into three regions: the *cephalon* or head, the thorax, and the *pleon* or abdomen. The head and thorax may be fused together to form a cephalothorax, which may be covered by a single large carapace. The crustacean body is protected by the hard exoskeleton, which must be moulted for the animal to grow. The shell around each somite can be divided into a dorsal tergum, ventral sternum and a lateral pleuron. Various parts of the exoskeleton may be fused together.

Each somite, or body segment can bear a pair of appendages: on the segments of the head, these include two pairs of antennae, the mandibles and maxillae; the thoracic segments bear legs, which may be specialised as pereiopods (walking legs) and maxillipeds (feeding legs). The abdomen bears pleopods, and ends in a telson, which bears the anus, and is often flanked by uropods to form a tail fan. The number and variety of appendages in different crustaceans may be partly responsible for the group's success. Crustacean appendages are typically biramous, meaning they are divided into two parts; this includes the second pair of antennae, but not the first, which is uniramous. It is unclear whether the biramous condition is a derived state which evolved in crustaceans, or whether the second branch of the limb has been lost in all other groups. Trilobites, for instance, also possessed biramous appendages.

The main body cavity is an open circulatory system, where blood is pumped into the haemocoel by a heart located near the dorsum. The alimentary canal consists of a straight tube that often has a gizzard-like "gastric mill" for grinding food and a pair of digestive glands that absorb food; this structure goes in a spiral format. Structures that function as kidneys are located near the antennae. A brain exists in the form of ganglia close to the antennae, and a collection of major ganglia is found below the gut.

In many decapods, the first (and sometimes the second) pair of pleopods are specialised in the male for sperm transfer. Many terrestrial crustaceans (such as the Christmas Island red crab) mate seasonally and return to the sea to release the eggs. Others, such as woodlice, lay their eggs on land, albeit in damp conditions. In most decapods, the females retain the eggs until they hatch into free-swimming larvae.

Ecology

The majority of crustaceans are aquatic, living in either marine or fresh water environments, but a few groups have adapted to life on land, such as terrestrial crabs, terrestrial hermit crabs, and woodlice. Marine crustaceans are as ubiquitous in the oceans as insects are on land. The majority of crustaceans are also motile, moving about independently, although a few taxonomic units are parasitic and live attached to their hosts (including sea lice, fish lice, whale lice, tongue worms, and *Cymothoa exigua*, all of which may be referred to as "crustacean lice"), and adult barnacles live a sessile life – they are attached headfirst to the substrate and cannot move independently. Some branchiurans are able to withstand rapid changes of salinity and will also switch hosts from marine to non-marine species. Krill are the bottom layer and the most important part of the food chain in Antarctic animal communities. Some crustaceans are significant invasive species, such as the Chinese mitten crab and the Asian shore crab.

Life cycle

Eggs of *Potamon fluviatile*, a freshwater crab

Zoea larva of the European lobster, *Homarus gammarus*

Mating system

The majority of crustaceans have separate sexes, and reproduce sexually. A small number are hermaphrodites, including barnacles, remipedes, and Cephalocarida. Some may even change sex during the course of their life. Parthenogenesis is also widespread among crustaceans, where viable eggs are produced by a female without needing fertilisation by a male. This occurs in many brachiopods, some ostracods, some isopods, and certain "higher" crustaceans, such as the *Marmorkrebs* crayfish.

Eggs

In many groups of crustaceans, the fertilised eggs are simply released into the water column, while others have developed a number of mechanisms for holding on to the eggs until they are ready to hatch. Most decapods carry the eggs attached to the pleopods, while peracarids, notostracans, anostracans, and many isopods form a brood pouch from the carapace and thoracic limbs. Female Branchiura do not carry eggs in external ovisacs but attach them in rows to rocks and other objects. Most leptostracans and krill carry the eggs between their thoracic limbs; some copepods carry their eggs in special thin-walled sacs, while others have them attached together in long, tangled strings.

Larvae

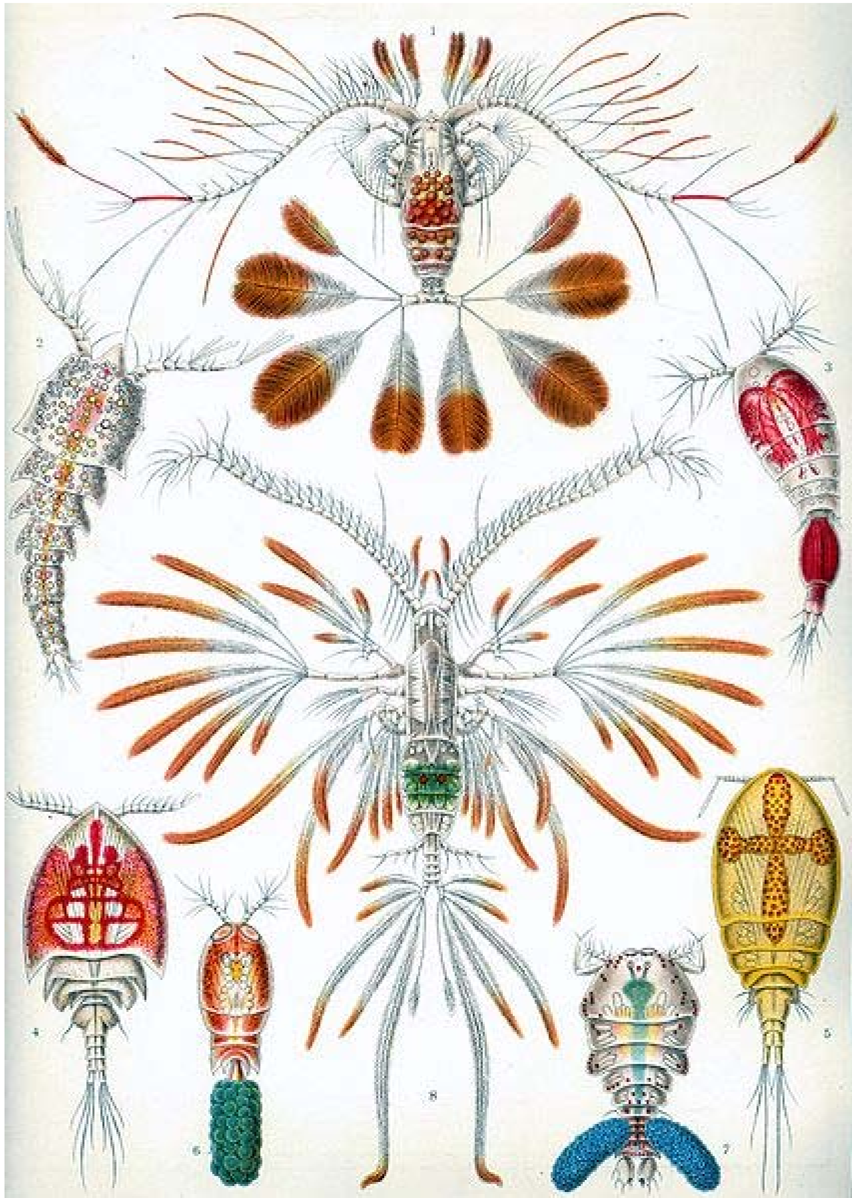
Crustaceans exhibit a number of larval forms, of which the earliest and most characteristic is the nauplius. This has three pairs of appendages, all emerging from the young animal's head, and a single naupliar eye. In most groups, there are further larval stages, including the zoea (pl. zoeæ or zoeas). This name was given to it when naturalists believed it to be a separate species. It follows the nauplius stage and precedes the post-larva. Zoea larvae swim with their thoracic appendages, as opposed to nauplii, which use cephalic appendages, and megalopa, which use abdominal appendages for swimming. It often has spikes on its carapace, which may assist these small organisms in maintaining directional swimming. In many decapods, due to their accelerated development, the zoea is the first larval stage. In some cases, the zoea stage is followed by the mysis stage, and in others, by the megalopa stage, depending on the crustacean group involved.

Classification

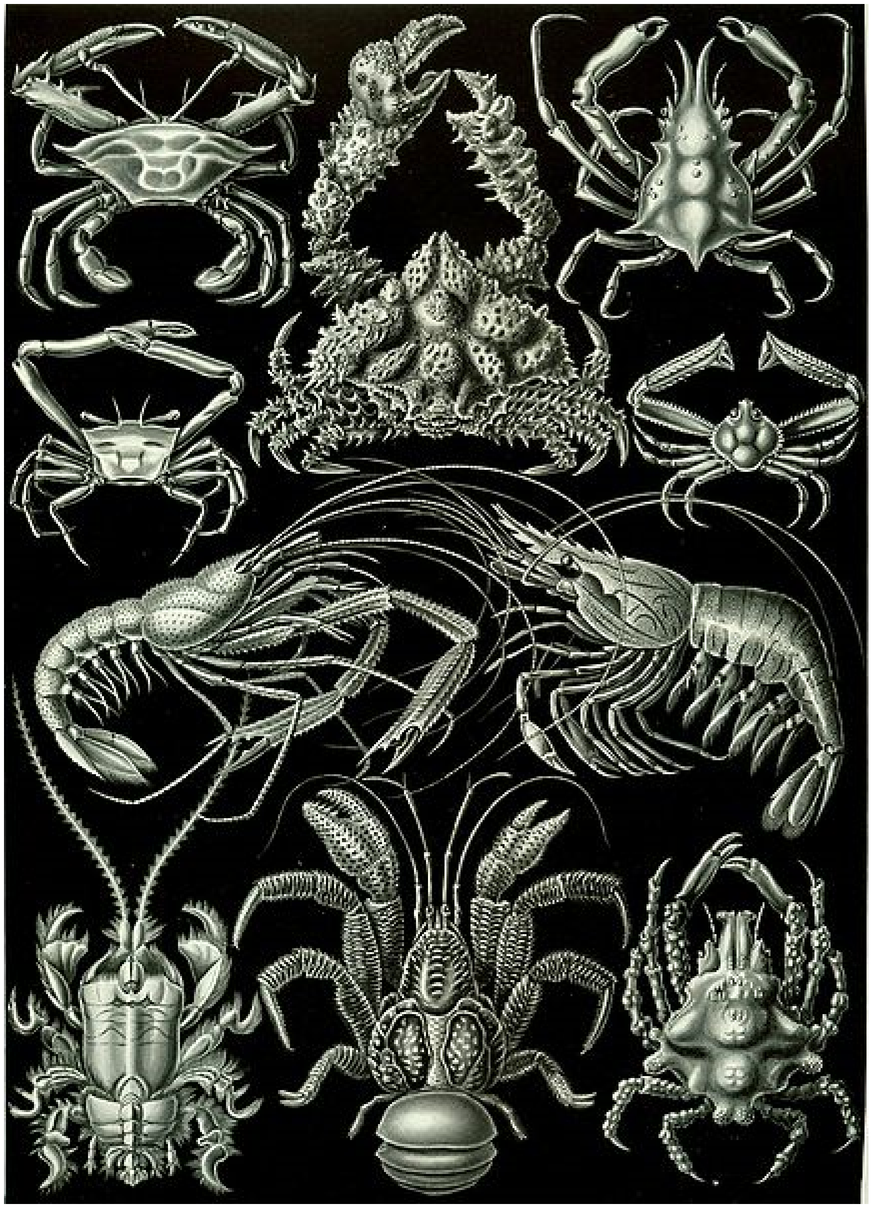
The name "crustacean" dates from the earliest works to describe the animals, including those of Pierre Belon and Guillaume Rondelet, but the name was not used by some later authors, including Carl Linnaeus, who included crustaceans among the "Aptera" in his *Systema Naturae*. The earliest nomenclaturally valid work to use the name "Crustacea" was Morten Thrane Brünnich's *Zoologiæ Fundamenta* in 1772, although he also included chelicerates in the group.

The subphylum Crustacea comprises almost 52,000 described species, although the number of undescribed species may be 10–100 times higher. Although most crustaceans are small, their morphology varies greatly and they include both the largest arthropod in the world – the Japanese spider crab with a leg span of 14 feet (4.3 m) – and the smallest – the 0.1 mm (0.004 in) long *Stygotantulus stocki*. Despite their diversity of form, crustaceans are united by the special larval form known as the nauplius.

The exact relationships of the Crustacea to other taxa are not yet entirely clear. Under the Pancrustacea hypothesis, Crustacea and Hexapoda (insects and allies) are sister groups. Studies using DNA sequences tend to show a paraphyletic Crustacea, with the insects (but not necessarily other hexapods) nested within that clade. Although the classification of crustaceans has been quite variable, the system used by Martin and Davis is the most authoritative, and largely supersedes earlier works. Mystacocarida and Branchiura, here treated as part of Maxillopoda, are sometimes treated as their own classes. Six classes are usually recognised:



Copepods, from Ernst Haeckel's 1904 work *Kunstformen der Natur*



Decapods, from Ernst Haeckel's 1904 work *Kunstformen der Natur*

Class	Members	Orders	Photo
Branchiopoda	brine shrimp Cladocera *Triops*	Anostraca Notostraca Laevicaudata Spinicaudata Cyclestherida Cladocera	 *Daphnia pulex* (Cladocera)
Remipedia		Nectiopoda	
Cephalocarida	horseshoe shrimp	Brachypoda	
Maxillopoda	barnacles copepods	Calanoida Pedunculata Sessilia *c.* 20 others	 *Chthamalus stellatus* (Sessilia)
Ostracoda	ostracods	Myodocopida Halocyprida Platycopida Podocopida	 Cylindroleberididae
Malacostraca	crabs lobsters shrimp krill mantis shrimp woodlice sandhoppers *etc.*	Decapoda Isopoda Amphipoda Stomatopoda *c.* 12 others	 *Gammarus roeseli* (Amphipoda)

Fossil record

Eryma mandelslohi, a fossil decapod from the Jurassic of Bissingen an der Teck, Germany

Crustaceans have a rich and extensive fossil record, which begins with animals such as *Canadaspis* and *Perspicaris* from the Middle Cambrian age Burgess Shale. Most of the major groups of crustaceans appear in the fossil record before the end of the Cambrian, namely the Branchiopoda, Maxillopoda (including barnacles and tongue worms) and Malacostraca; there is some debate as to whether or not Cambrian animals assigned to Ostracoda are truly ostracods, which would otherwise start in the Ordovician. The only classes to appear later are the Cephalocarida, which have no fossil record, and the Remipedia, which were first described from the fossil *Tesnusocaris goldichi*, but do not appear until the Carboniferous. Most of the early crustaceans are rare, but fossil crustaceans become abundant from the Carboniferous onwards.

Norway lobsters on sale at a Spanish market

Within the Malacostraca, no fossils are known for krill, while both Hoplocarida and Phyllopoda contain important groups that are now extinct as well as extant members (Hoplocarida: mantis shrimp are extant, while Aeschronectida are extinct; Phyllopoda: Canadaspidida are extinct, while Leptostraca are extant). Cumacea and Isopoda are both known from the Carboniferous, as are the first true mantis shrimp. In the Decapoda, prawns and polychelids appear in the Triassic, and shrimp and crabs appear in the Jurassic; however, the great radiation of crustaceans occurred in the Cretaceous, particularly in crabs, and may have been driven by the adaptive radiation of their main predators, bony fish. The first true lobsters also appear in the Cretaceous.

Consumption by man

Many crustaceans are consumed by humans, and nearly 10,700,000 tons were produced in 2007; the vast majority of this output is of decapod crustaceans: crabs, lobsters, shrimp, and prawns. Over 60% by weight of all crustaceans caught for consumption are shrimp and prawns, and nearly 80% is produced in Asia, with China alone producing nearly half the world's total. Non-decapod crustaceans are not widely consumed, with only 118,000 tons of krill being caught, despite krill having one of the greatest biomasses on the planet.

Chapter 2

Crustacean Larvae

Larval and adult prawns

Nauplius larva

Adult *Penaeus monodon*

Crustaceans may pass through a number of **larval and immature stages** between hatching from their eggs and reaching their adult form. Each of the stages is separated by a moult, in which the hard exoskeleton is shed to allow the animal to grow. The larvae of crustaceans often bear little resemblance to the adult, and there are still cases where it is not known what larvae will grow into what adults. This is especially true of crustaceans which live as benthic adults (on the sea bed), but where the larvae are planktonic and therefore more easily caught.

Many crustacean larvae were not immediately recognised as larvae when they were discovered, and were described as new genera and species. The names of these genera have become generalised to cover specific larval stages across wide groups of crustaceans, such as *zoea* and *nauplius*. Other terms described forms which are only found in particular groups, such as the *glaucothoe* of hermit crabs, or the *phyllosoma* of slipper lobsters and spiny lobsters.

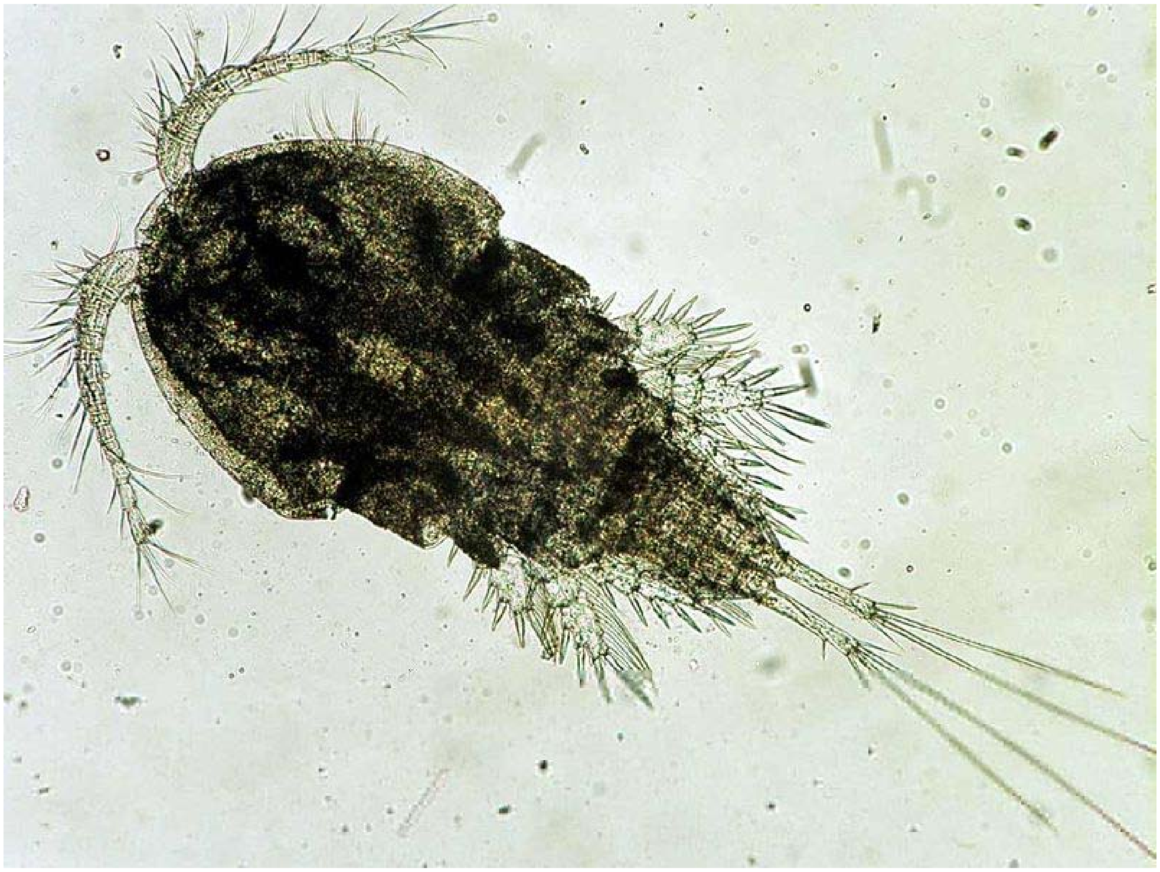
Life cycle

At its most complete, a crustacean's life cycle begins with an egg, which is usually fertilised, but may instead be produced by parthenogenesis. This egg hatches into a pre-larva or pre-zoea. Through a series of moults, the young animal then passes through various zoea stages, followed by a megalopa or post-larva. This is followed by metamorphosis into an immature form, which broadly resembles the adult, and after further moults, the adult form is finally reached. Some crustaceans continue to moult as adults, while for others, the development of gonads signals the final moult.

Any organs which are absent from the adults do not generally appear in the larvae, although there are a few exceptions, such as the vestige of the fourth pereiopod in the larvae of *Lucifer*, and some pleopods in certain Anomura and crabs.

***Cyclops* (Copepoda)**

Nauplius



Adult

History of the study of crustacean larva

Antonie van Leeuwenhoek was the first person to observe the difference between larval crustaceans and the adults when he watched the eggs of *Cyclops* hatching in 1699. Despite this, and other observations over the following decades, there was controversy among scientists about whether or not metamorphosis occurred in crustaceans, with conflicting observations presented, based on different species, some of which went through a metamorphosis, and some of which did not. This controversy persisted until the 1840s, and the first descriptions of a complete series of larval forms were not published until the 1870s (Sidney Irving Smith on the American lobster in 1873; Georg Ossian Sars on the European lobster in 1875, and Walter Faxon on the shrimp *Palaemonetes vulgaris* in 1879).

Larval stages

Close-up of an adult *Triops* (Notostraca), showing the naupliar eye between the two compound eyes

Nauplius

The genus name *Nauplius* was published posthumously by Otto Friedrich Müller in 1785 for animals now known to be the larvae of copepods. The nauplius stage (plural: *nauplii*) is characterised by the use of the appendages of the head (the antennae) for swimming. The nauplius is also the stage at which a simple, unpaired eye first appears. The eye is known for that reason as the "naupliar eye", and is often absent in later developmental stages, although it is retained into the adult form in some groups, such as the Notostraca.

Zoea

The genus *Zoea* was initially described by Louis Augustin Guillaume Bosc in 1802 for an animal now known to be the larva of a crab. The zoea stage (plural: *zoeas* or *zoeae*) is characterised by the use of the thoracic appendages for swimming.

Post-larva

The post-larva is characterised by the use of abdominal appendages (pleopods) for propulsion. The post-larva is usually similar to the adult form, and so many names have been erected for the stage in different groups. William Elford Leach erected the genus

Megalopa in 1813 for a post-larval crab; a shrimp post-larva is called a *parva*; hermit crab post-larva are called *glaucothoe*.

Larvae of crustacean groups

Branchiopoda

In the Branchiopoda, the most basal group of crustaceans, there is no metamorphosis; instead, the animal grows through a series of moults, with each moult adding segments to the body, but without any dramatic changes in form. Every other crustacean group with free larvae shows a metamorphosis, and this difference in the larvae is thought to reflect "a fundamental cleavage" of the crustaceans.

Cephalocarida

In the Mediterranean horseshoe shrimp *Lightiella magdalenina*, the young experience 15 metaneupliar stages and 2 juvenile stages, with each of the first six stages adding 2 trunk segments, and the last four segments being added singly.

Remipedia

The larvae of remipedes are lecithotrophic, consuming egg yolk rather than using external food sources. This characteristic, which is shared with malacostracan groups such as the Decapoda and Euphausiacea (krill) has been used to suggest a link between Remipedia and Malacostraca.

Malacostraca

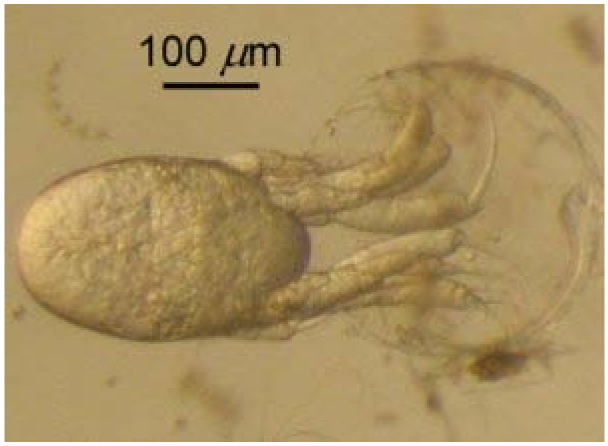
Amphipod hatchlings resemble the adults.

Young isopod crustaceans hatch directly into a *manca* stage, which is similar in appearance to the adult. The lack of a free-swimming larval form has led to high rates of endemism in isopods, but has also allowed them to colonise the land, in the form of the woodlice.

Stomatopoda

The larvae of many groups of mantis shrimp are poorly known. In the superfamily Lysiosquilloidea, the larvae hatch as *antizoea* larvae, with five pairs of thoracic appendages, and develop into *erichthus* larvae, where the pleopods appear. In the Squilloidea, a *pseudozoea* larva develops into an *alima* larva, while in Gonodactyloidea, a *pseudozoea* develops into an *erichthus*.

A single fossil stomatopod larva has been discovered, in the Upper Jurassic Solnhofen lithographic limestone.



A nauplius of *Euphausia pacifica* hatching, emerging backwards from the egg

Krill

The life cycle of krill is relatively well understood, although there are minor variations in detail from species to species. After hatching, the larvae go through several stages called *nauplius*, *pseudometanauplius*, *metanauplius*, *calyptopsis* and *furcilia* stages, each of which is sub-divided into several sub-stages. The *pseudometanauplius* stage is exclusive to the so-called "sac-spawners". Until the *metanauplius* stage, the larvae are reliant on the yolk reserves, but from the *calyptopsis* stage, they begin to feed on phytoplankton. During the *furcilia* stages, segments with pairs of swimmerets are added, beginning at the frontmost segments, with each new pair only becoming functional at the next moult. After the final furcilia stage, the krill resembles the adult.

Eggs being brooded by a female *Orconectes obscurus* crayfish: such large eggs are often indicative of abbreviated development.

Decapoda

Apart from the prawns of the suborder Dendrobranchiata, all decapod crustaceans brood their eggs on the female's pleopods. This has resulted in development in decapod crustaceans being generally abbreviated. There are at most 9 larval stages in decapods, as in krill, and both decapod nauplii and krill nauplii often lack mouthparts and survive on nutrients supplied in the egg yolk (lecithotrophy). In species with normal development, eggs are roughly 1% of the size of the adult; in species with abbreviated development, and therefore more yolk in the eggs, the eggs may reach 1/9 of the adult's size.

The post-larva of shrimp is called *parva*, after the species *Acanthephyra parva* described by Henri Coutière, but which was later recognised as the larva of *Acanthephyra purpurea*.

In the marine lobsters, there are three larval stages, all similar in appearance.

Freshwater crayfish embryos differ from those of other crustaceans in having 40 ectoteloblast cells, rather than around 19. The larvae show abbreviated development, and hatch with a full complement of adult appendages with the exceptions of the uropods and the first pair of pleopods.

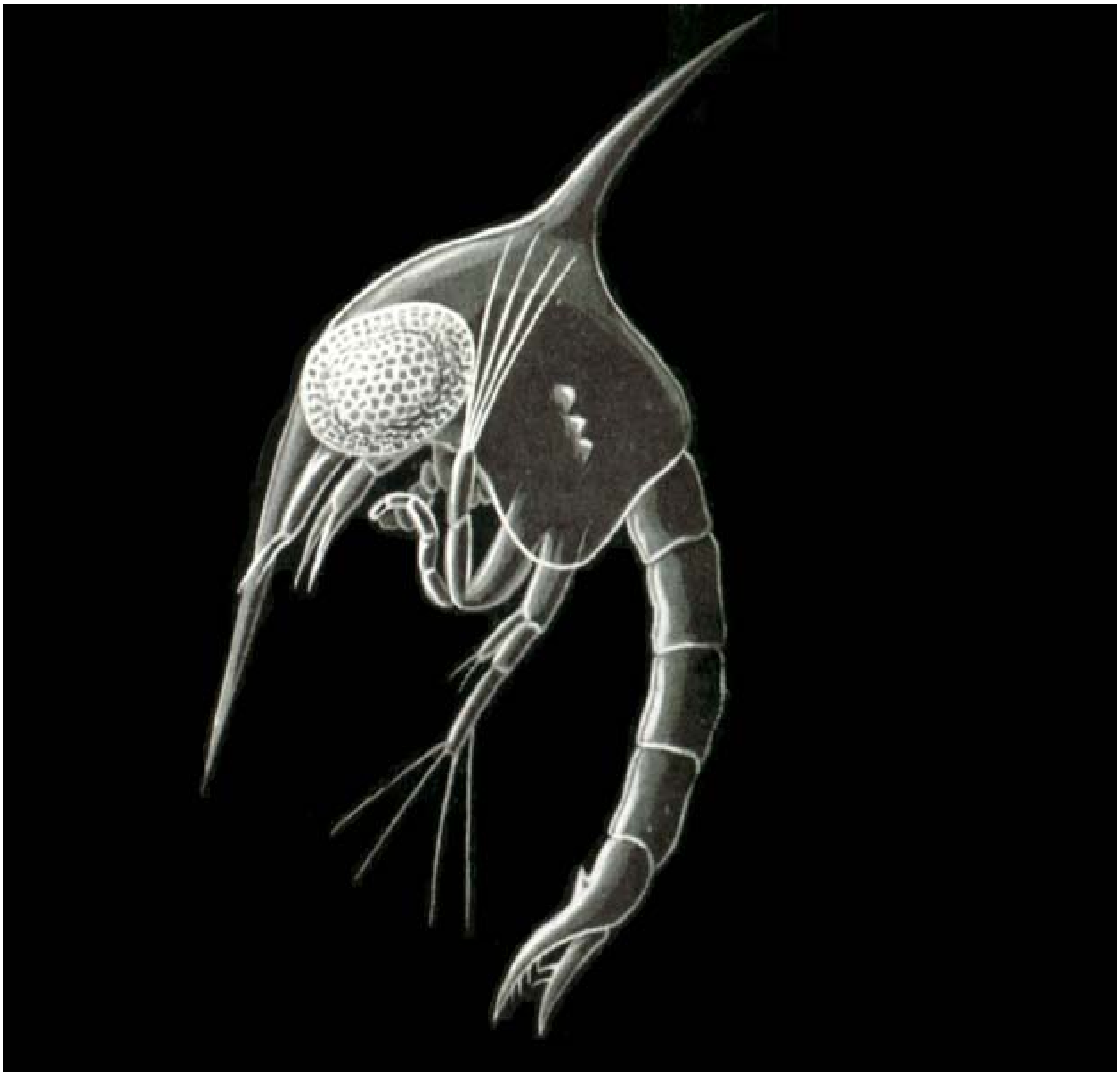
A phyllosoma larva of the spiny lobster *Palinurus elephas*, from Ernst Haeckel's *Kunstformen der Natur*

The larvae of the Achelata (slipper lobsters and spiny lobsters) are unlike any other crustacean larvae. The larvae are known as *phyllosoma*, after the genus *Phyllosoma* erected by William Elford Leach in 1817. They are flattened and transparent, with long legs and eyes on long eyestalks. After passing through 8–10 phyllosoma stages, the larva undergoes "the most profound transformation at a single moult in the Decapoda", when it develops into the so-called *puerulus* stage, which is an immature form resembling the adult animal.

The members of the traditional infraorder Thalassinidea can be divided into two groups on the basis of their larvae. According to Robert Gurney, the "homarine group" comprises the families Axiidae and Callianassidae, while the "anomuran group" comprises the families Laomediidae and Upogebiidae. This split corresponds with the division later confirmed with molecular phylogenetics.

Among the Anomura, there is considerable variation in the number of larval stages. In the South American freshwater genus *Aegla*, the young hatch from the eggs in the adult form. Squat lobsters pass through four, or occasionally five, larval states, which have a long rostrum, and a spine on either side of the carapace; the first post-larva closely resembles the adult. Porcelain crabs have two or three larval stages, in which the rostrum and the posterior spine on the carapace are "enormously long". Hermit crabs pass through around four larval stages. The post-larva is known as the *glaucothoe*, after a genus named by Henri Milne-Edwards in 1830. The glaucothoe is 3 millimetres (0.12 in) long in *Pagurus longicarpus*, but glaucothoe larvae up to 20 mm (0.79 in) are known, and were once thought to represent animals which had failed to develop correctly. Like the preceding stages, the glaucothoe is symmetrical, and although the glaucothoe begins as a free-swimming form, it often acquires a gastropod shell to live in; the coconut crab, *Birgus latro*, always carries a shell when the immature animal comes ashore, but this is discarded later.

Carcinus maenas **(Decapoda: Brachyura)**



Zoea

Juvenile

Although they are classified as crabs, the larvae of Dromiacea are similar to those of the Anomura, which led many scientists to place dromiacean crabs in the Anomura, rather than with the other crabs. Apart from the Dromiacea, all crabs share a similar and distinctive larval form. The crab zoea has a slender, curved abdomen and a forked telson, but its most striking features are the long rostral and dorsal spines, sometimes augmented by further, lateral spines. These spines can be many times longer than the body of the larva. Crab prezoea larvae have been found fossilised in the stomach contents of the Early Cretaceous bony fish *Tharrhias*.

Maxillopoda

Copepoda

Copepods have six naupliar stages, followed by a stage called the *copepodid*, which has the same number of body segments and appendages in all copepods. The copepodid larva has two pairs of unsegmented swimming appendages, and an unsegmented "hind-body" comprising the thorax and the abdomen. There are typically five copepodid stages, but parasitic copepods may stop after a single copepodid stage. Once the gonads develop, there are no further moults.

Facetotecta

The single genus in the Facetotecta, *Hansenocaris*, is only known from its larvae. They were first described by Christian Andreas Victor Hensen in 1887, and named "y-nauplia" by Hans Jacob Hansen, assuming them to be the larvae of barnacles. The adults are presumed to be parasites of other animals.

Chapter 3

Thylacocephala

Thylacocephala **Temporal range: Early Cambrian–Late Cretaceous**	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea?
Class:	**Thylacocephala** Pinna *et al.*, 1982
Orders	

- Concavicarida
- Conchyliocarida

The **Thylacocephala** (from the Greek *thylakos*, meaning "pouch", and *cephalon* meaning "head") are a unique group of extinct arthropods, with possible crustacean affinities. As a class they have a short research history, having been erected in the early 1980s . They typically possess a large, laterally flattened carapace that encompasses the entire body. The compound eyes tend to be large and bulbous, and occupy a frontal notch on the carapace. They possess three pairs of large raptorial limbs, and the abdomen bears a battery of small swimming limbs. The earliest thylacocephalan fossil is thought to date from the lower Cambrian , while the class has a definite presence in Lower Silurian marine communities . As a group, the Thylacocephala survived to the Upper Cretaceous . Beyond this, there remains much uncertainty concerning fundamental aspects of the thylacocephalan anatomy, mode of life, and relationship to the Crustacea, with whom they have always been cautiously aligned.

Research history

Ankitokazocaris

The Thylacocephala are relatively young as a class, yet species now included within the group were first described at the turn of the century . These were typically assigned to the phyllocarids despite an apparent lack of abdomen and appendages . In 1982/83, three research groups independently created higher taxa to accommodate new species. Based on a specimen from northern Italy, Pinna *et al.* designated a new class , Thylacocephala, while Secrétan – studying *Dollocaris ingens*, a species from the La Voulte-sur-Rhône konservat-lagerstätte in France - erected the class **Conchyliocarida** . Briggs & Rolfe, working on fossils from Australia's Devonian deposits were unable to attribute certain specimens to a known group, and created an order of uncertain affinities, the **Concavicarida**, to accommodate them . It was apparent the three groups were in fact working on a single major taxon (Rolfe noted disagreements over interpretation and taxonomic placement largely resulted from a disparity of sizes and differences in preservation). The group took the name Thylacocephala by priority, with **Concavicarida** and **Conchyliocarida** subjugated to orders, erected by Rolfe , and modified by Schram .

Taxonomy

Ostenocaris cypriformis

Researchers agree the Thylacocephala represent a class. Some efforts have been made at further classification: Schram split currently known taxa into two orders :

- **Concavicarida** (Briggs & Rolfe, 1983) which possesses:
  - A large, well developed optic notch
  - A discrete compound eye
  - A fused nostrum
  - 8 to 16 homonymous, well-demarcated trunk segments diminishing in height anteriorly and posteriorly
  - Order includes *Ainiktozoon* (Silurian), *Harrycaris* (Devonian), *Concavicaris* (Devonian to Carboniferous), *Dollocaris* (Jurassic).
- **Conchyliocarida** (Secrétan, 1983):
  - Lacks an optic notch
  - Eyes situated on a protrudant, sac-like cephalon
  - No rostrum.
  - Order includes *Convexicaris* (Carboniferous), *Yangzicaris* (Triassic), *Atropicaris*/*Austriocaris*/*Clausocaris*/*Kilianocaris*/*Ostenocaris*/*Paraosteni a* (Jurassic)

The accuracy of this scheme has been questioned in recent papers , as it stresses differences in the eyes and exoskeletal structure, which – in modern arthropods – tend to be a response to environmental conditions. Thus it has been suggested these features are too strongly controlled by external factors to be used alone to distinguish higher taxa. The problem is exacerbated by the limited number of thylacocephalan species known. More reliable anatomical indicators would include segmentation and appendage attachments (requiring the internal anatomy, currently elusive as a result of the carapace).

Anatomy

Based on Vannier , modified after Schram : The Thylacocephala are bivalved arthropods with morphology exemplified by three pairs of long raptorial (predatory) appendages and hypertrophied. They have a worldwide distribution. A laterally compressed, shield−like carapace encloses the entire body, and often has an anterior rostrum−notch complex and posterior rostrum. Its lateral surface can be externally ornamented, and evenly convex or with longitudinal ridges. Spherical or drop-shaped eyes are situated in the optic notches, and are often hypertrophied, filling the notches or forming a paired, frontal globular structure. No prominent abdominal features emerge from the carapace, and the cephalon is obscured. Even so, some authors have suggested the presence of five cephalic appendages, three of which could be the very long genticulate and chelate raptorials protruding beyond the ventral margin . Alternatively these could originate from three anterior trunk segments . The posterior trunk has a series of eight to twenty styliform, filamentous pleopod-like appendages, decreasing in size posteriorly. Most Thylacocephala have eight pairs of well developed gills, found in the trunk region.

Beyond this there is a lack of knowledge about even basic thylacocephalan anatomy, including the number of posterior segments, origin of the raptorials, number of cephalic appendages, shape and attachment of gills, character of mouth, stomach and gut. This results from the class's all–encompassing carapace, which prevents the study of their internal anatomy in fossils.

Affinities

It is universally accepted that the Thylacocephala are arthropods, yet the position within this phylum is debated. It has always been cautiously assumed that the class is a member of the Crustacea, but no conclusive proof exists. The strongest apomorphy aligning the class with other crustaceans is the carapace. As this feature has evolved independently numerous times within the Crustacea and other arthropods, it is not a very reliable pointer, and such evidence alone remains insufficient to align the class with the crustaceans .

Of the features which could prove crustacean affinities, the arrangement of mouthparts would be the easiest to find in the Thylacocephala. The literature features some mention of such a head arrangement, but none definitive. Schram reports the discovery of mandibles in the Mazon Creek thylacocephalan *Concavicaris georgeorum* . Secrétan also mentions — with caution — possible mandibles in serial sections of *Dollocaris ingens*, and traces of small limbs in the cephalic region (not well-preserved enough to assess their identity). Lange *et al.* report a new genus and species, *Thylacocephalus cymolopos*, from the Upper Cretaceous of Lebanon, which has two possible pairs of antennae, but note the possession of two pairs of antennae alone does not prove the class occupies a position in the crown-group Crustacea.

Despite a lack of evidence for a crustacean body plan, several authors have aligned the class with different groups of crustaceans. Schram provides an overview of possible affinities :

- Nothing in uniramia nor cheliceriformes likely.
- Conchostracans possible, no strong supporting evidence.
- Maxillopodan connection is possible. Largely considered due to the Italian researchers' insistence.
- Stomatopods show many parallels but have no comparison to cephalon or body regions.
- Remipedes show some parallels.
- Decapod-like gills suggest malacostracan affinities.

In these various interpretations, numerous different limb arrangements for the three raptorials have been proposed:

- antennules, antennae and mandibles
- antennules, antennae and maxillipeds
- thoracic (in keeping with stromatopod analogies)
- maxillules, maxillae, maxillipedes

Further work is necessary to provide any solid conclusions.

Disagreements

Numerous conflicts of opinion surround the Thylacocephala, of which the split between the "Italian school" and rest of the world is the most notable. Based on poorly preserved fossils from the Osteno deposits of Lombardy, Pinna *et al.* erected the class Thylacocephala . Based on inferred cirripede affinities the authors concluded the frontal lobed structure was not an eye, but a 'cephalic sac'. This opinion arose from the misinterpretation of the stomach as a reproductive organ (its contents included vertebral elements of fish, thought to be ovarian eggs). Such an arrangement is reminiscent of cirripede crustaceans, leading the authors to suggest a sessile, filter feeding mode of life, the 'cephalic sac' used to anchor the organism to the seabed. The researchers have since conceded it is highly improbable the ovaries are situated in the head, but maintain that the frontal structure is not an eye. Instead they suggest the 'cephalic sac' is covered with microsclerites, their arguments most recently presented in Alessandrello *et al.*

- The structure is complex and "presumably multipurpose" (pg 246)
- "Apart from a few features" it shows little affinity with a compound eye (pg 246)
- There is a close connection with stomach residues, sac muscular system and outer hexagonal layer
- Having a stomach between the eyes is unusual

- Sclerites that should correspond to rhabdoms in 'eye theory' are interstitial to the hexagons, not at centre as would be expected for individual ommatidium.
- Structural analogy with cirriped peduncle

Instead the authors suggest the sac is used to break down coarse chunks of food and reject indigestible portions.

All other parties interpret this as a large compound eye, the hexagons being preserved ommatidia (all researchers agree these are the same structure). This is supported by fossils of *Dollocaris ingens* which are so well preserved that individual retinula cells can be discerned. The preservation is so exceptional that studies have shown the species' numerous small ommatidia, distributed over the large eyes, could reduce the angle between ommatidia, thus improve their ability to detect small objects . Of the arguments above, it is posited by opponents that eyes are complex structures, and those in the Thylacocephala display clear and numerous affinities with compound eyes in other arthropod fossils, down to a cellular level of detail. The 'cephalic sac' structure itself is poorly preserved in Osteno specimens, a possible reason for interstitial 'sclerites'. The structural analogy with a cirripede peduncle lost supporting evidence when the 'ovaries' were shown to be alimentary residues , and the sac muscular system could be used to support the eyes. The unusual position of the stomach is thus the strongest inconsistency, but the Thylacocephala are defined by their unusual features, so this is not inconceivable. Further, Rolfe suggests the eyes' position can be explained if they have a large posterior area of attachment , while Schram suggests that the stomach region extending into the cephalic sac could result from an inflated foregut or anteriorly directed caecum .

Discussion of the matter has ceased in the last decade, and most researchers accept the anterior structure is an eye. Confusion is most likely the result of differing preservation in Osteno.

Mode of life

Numerous modes of life have been suggested for the Thylacocephala.

Secrétan suggested *Dollocaris ingens* was too large to swim , so inferred a predatory 'lurking' mode of life, lying in wait on the sea bed and then springing out to capture prey. The author also suggested it could be necrophagious, supported by Alessandrello *et al.* , who suggest they would have been incapable of directly killing the shark remains found in the Osteno specimens' alimentary residues. Instead they surmise the Thylacocephala could have ingested shark vomit which included such remains.

Vannier *et al.* note the Thylacocephala possess features which would suggest adaptations for swimming in dim-light environments - a thin, non-mineralized carapace, well-developed rostral spines for possible buoyancy control ins ome species, a battery of pleopods for swimming, and large prominent eyes . This is supported by the Cretaceous species from Lebanon, which show adaptations for swimming , and possibly schooling.

Rolfe provides many possibilities, but concludes a realistic mode of life is mesopelagic, by analogy with hyperiid amphipods . Further suggests floor-dwelling is also possible, and that the organism could rise to catch prey during the day and return to the sea floor at night. Another notable proposal is that, like hyperiids, the class could gain oil from their food source for buoyancy, an idea supported by their diet (known from stomach residues containing shark and coleoid remains, and other Thylacocephala).

Alessandrello *et al.* suggest a head-down, semi-sessile life on a soft bottom , in agreement with that of Pinna *et al.*, based on cirripede affinities. A necrophagious diet is suggested .

Briggs & Rolfe report that all the Gogo Thylacocephala are found in a reef formation, suggesting a shallow water environment . The authors speculate that due to the terracing of the carapace an infaunal mode of life is possible, or the ridges could provide more friction for hiding in crevices of rock.

Schram suggests a dichotomy in size of the class results from different environments ; larger Thylacocephala could have lived in a fluid characterized by turbulent flow, and relied on single power stroke of trunk limbs to position themselves. He suggests that smaller forms may have resided in a viscous medium, characterized by laminar flow, and used a lever to generate the speed necessary to capture prey.

With a wide variety of features and extended time range it more than possible the Thylacocephala employed more than a single mode of life, which is likely to have varied between species.

Chapter 4

Branchiopoda

Branchiopoda **Temporal range: Upper Cambrian–Recent**	

Triops, (Notostraca: Triopsidae)
left: dorsal view; right: ventral view

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	**Branchiopoda** Latreille, 1817

Orders

- ***Subclass Sarsostraca***

  Anostraca

- ***Subclass Phyllopoda***

  Lipostraca†

Notostraca
Infraclass Diplostraca
Laevicaudata
Spinicaudata
Cyclestherida
Cladocera

Branchiopoda is a class of crustaceans. It is the sister group to the remaining crustaceans, and comprises fairy shrimp, clam shrimp, Cladocera and Notostraca. They are mostly small, freshwater animals that feed on plankton and detritus, with the exception of the Cladocera, many of which are marine.

Description

Members of the Branchiopoda are unified by the presence of gills on many of the animal's appendages, including some of the mouthparts. This is also responsible for the name of the group (from the Greek: branchia, gills, akin to bronchos, windpipe; Greek: pous, foot). They generally possess compound eyes and a carapace, which may be a shell of two valves enclosing the trunk (as in most Cladocera), broad and shallow (as in the Notostraca), or entirely absent (as in the Anostraca). In the groups where the carapace prevents the use of the trunk limbs for swimming (Cladocera, clam shrimp and the extinct Lipostraca), the antennae are used for locomotion, as they are in the nauplius. Male fairy shrimp have an enlarged pair of antennae with which they grasp the female during mating, while the bottom-feeding Notostraca, the antennae are reduced to vestiges. The trunk limbs are beaten in a metachronal rhythm, causing a flow of water along the midline of the animal, from which it derives oxygen, food and, in the case of the Anostraca and Notostraca, movement.

Ecology

Among the branchiopods, only the cladocerans are found in the sea; all the other groups are found in fresh water, including temporary pools. Most branchiopodans eat floating detritus or plankton, which they take using the setae on their appendages.

Taxonomy

In early taxonomic treatments, the current members of the Branchiopoda were all placed in a single genus, *Monoculus*. The taxon Branchiopoda was erected by Pierre André Latreille in 1817, initially at the rank of order.

Anostraca

Artemia salina (Anostraca: Artemiidae)

The fairy shrimp of the order Anostraca are usually 6–25 mm (0.24–0.98 in) long (exceptionally up to 170 mm or 6.7 in). Most species have 20 body segments, bearing 11 pairs of leaf-like *phyllopodia* (swimming legs), and the body lacks a carapace. They live in vernal pools and hypersaline lakes across the world, including pools in deserts, in ice-covered mountain lakes and in Antarctica. They swim "upside-down" and feed by filtering organic particles from the water or by scraping algae from surfaces. They are an important food for many birds and fish, and are cultured and harvested for use as fish food. There are 300 species spread across 8 families.

Notostraca

The order Notostraca comprises the single family Triopsidae, containing the tadpole shrimp or shield shrimp. The two genera, *Triops* and *Lepidurus*, are considered living fossils, having not changed significantly in outward form since the Triassic. They have a broad, flat carapace, which conceals the head and bears a single pair of compound eyes. The abdomen is long, appears to be segmented and bears numerous pairs of flattened legs. The telson is flanked by a pair of long, thin caudal rami. Phenotypic plasticity within taxa makes species-level identification difficult, and is further compounded by variation in the mode of reproduction. Notostracans are omnivores living on the bottom of temporary pools and shallow lakes.

Laevicaudata, Spinicaudata and Cyclestherida

Clam shrimp are bivalved animals which have lived since at least the Devonian. The three groups are not believed to form a clade. They have 10–32 trunk segments, decreasing in size from front to back, and each bears a pair of legs which also carry gills. A strong muscle can close the two halves of the shell together.

Cladocera

Daphnia pulex (Cladocera: Daphniidae)

Cladocera is an order of small crustaceans commonly called water fleas. Around 620 species have been recognised so far, with may more undescribed. They are ubiquitous in inland aquatic habitats, but rare in the oceans. Most are 0.2–6.0 mm (0.0079–0.24 in) long, with a down-turned head, and a carapace covering the apparently unsegmented thorax and abdomen. There is a single median compound eye. Most species show cyclical parthenogenesis, where asexual reproduction is occasionally supplemented by sexual reproduction, which produces resting eggs that allow the species to survive harsh conditions and disperse to distant habitats.

Evolution

Branchiopods are considered the most primitive of the crustacean classes, and the sister group to the remaining crustaceans. The fossil record of branchiopods extends back at least into the Upper Cambrian and possibly further. The group is thought to be monophyletic, with the Anostraca having been the first group to branch off. It is thought that the group evolved in the seas, but was forced into temporary pools and hypersaline lakes by the evolution of bony fishes.

Chapter 5

Cladocera and Anostraca

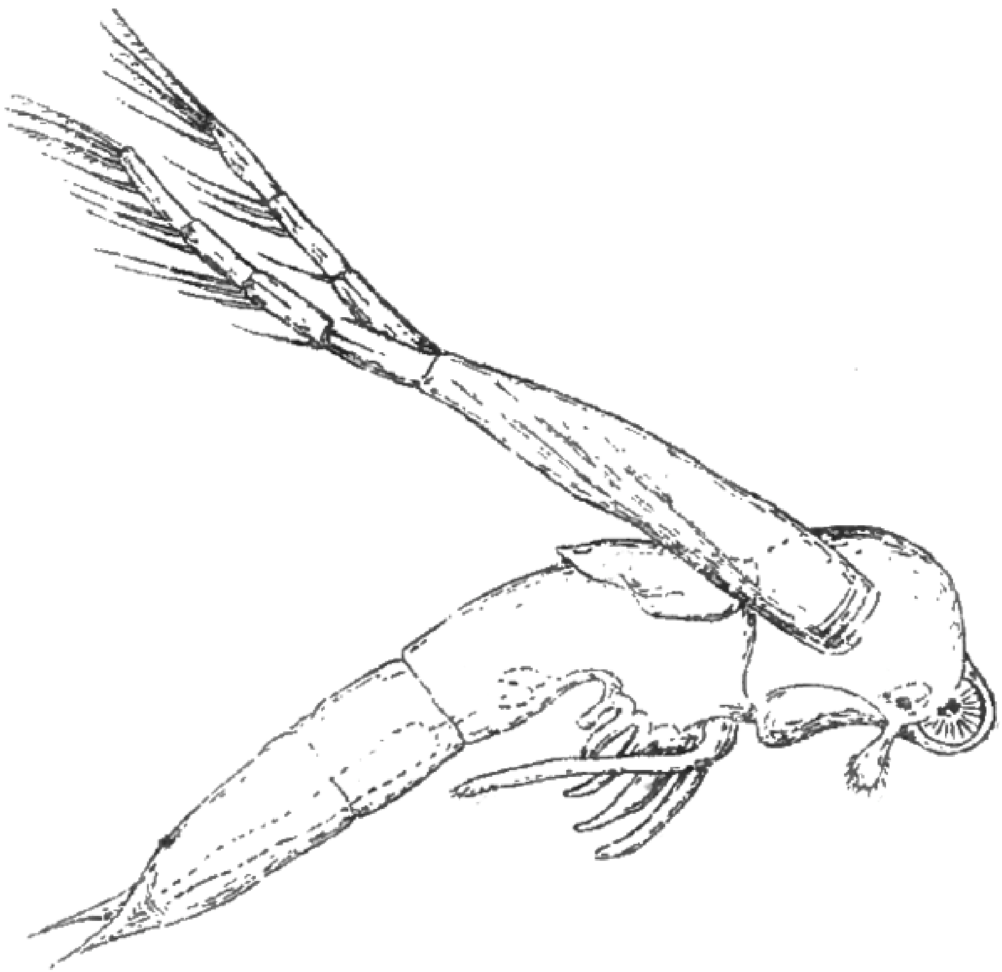
Cladocera

Cladocera	
	
Daphnia pulex	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Branchiopoda
Subclass:	Phyllopoda
Order:	**Cladocera** Latreille, 1829
Suborders	

- Anomopoda
- Ctenopoda
- Onychopoda
- Haplopoda

Cladocera is an order of small crustaceans commonly called **water fleas**. Around 620 species have been recognised so far, with many more undescribed. They are ubiquitous in inland aquatic habitats, but rare in the oceans. Most are 0.2–6.0 mm (0.0079–0.24 in) long, with a down-turned head, and a carapace covering the apparently unsegmented thorax and abdomen. There is a single median compound eye. Most species show cyclical parthenogenesis, where asexual reproduction is occasionally supplemented by sexual reproduction, which produces resting eggs that allow the species to survive harsh conditions and disperse to distant habitats.

Description



Leptodora kindtii is an unusually large cladoceran, at up to 18 mm long.

They are mostly 0.2–6.0 millimetres (0.008–0.236 in) long, with the exception of *Leptodora*, which can be up to 18 mm (0.71 in) long. The body is not obviosuly segmented and bears a folded carapace which covers the thorax and abdomen.

The head is angled downwards, and may separated from the rest of the body by a "cervical sinus" or notch. It bears a single black compound eye, located on the animal's midline, in all but two genera, and there is often a single ocellus. The head also bears two pairs of antennae – the first antennae are small unsegmented appendages, while the second antennae are large, segmented and branched, with powerful muscles. The first antennae bear olfactory setae, while the second are used for swimming by most species.

The pattern of setae on the second antennae is useful for identification; *Daphnia*. The part of the head which projects in front of the first antennae is known as the rostrum or "beak".

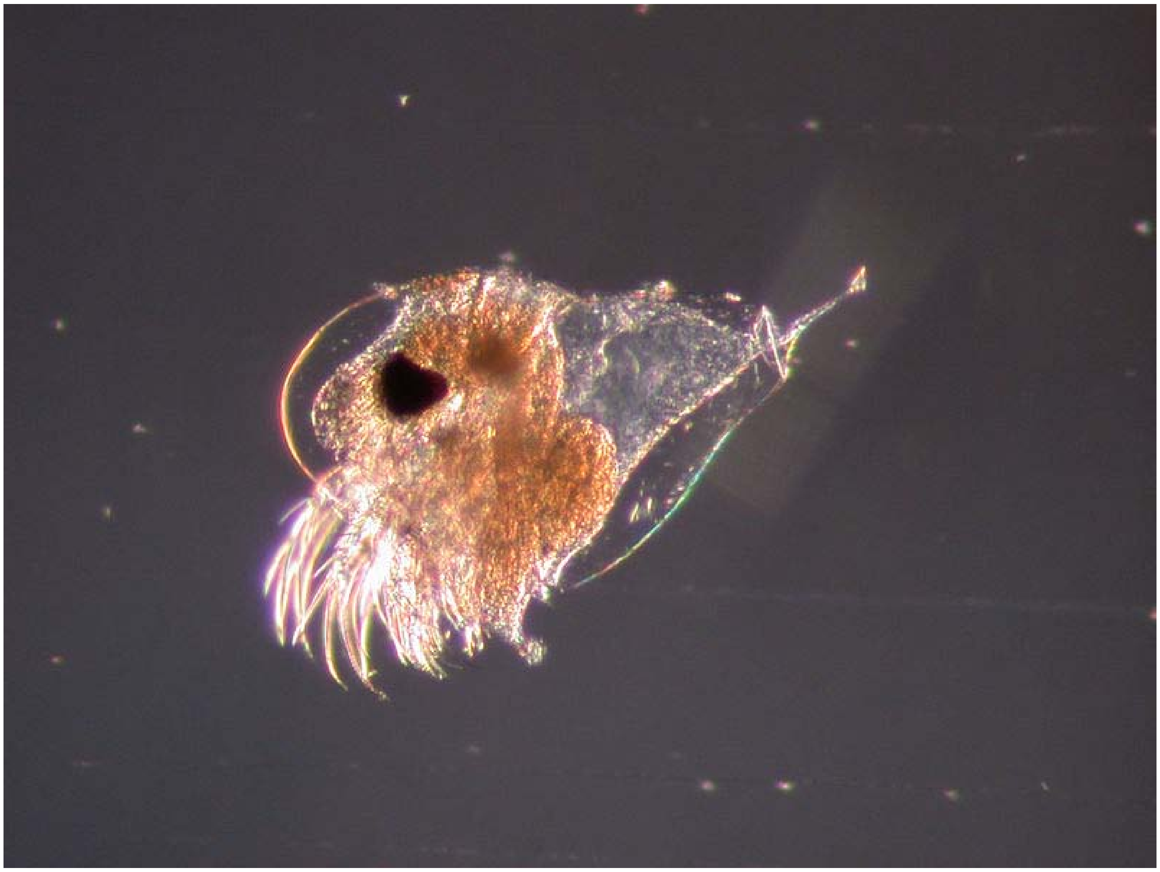
The mouthparts are small, and consist of an unpaired labrum, a pair of mandibles, a pair of maxillae, and an unpaired labium. They are used to eat "organic detritus of all kinds" and bacteria.

The thorax bears five or six pairs of lobed, leaf-like appendages, each with numerous hairs or setae. Carbon dioxide is lost, and oxygen taken up, through the body surface.

Life cycle

With the exception of a few purely asexual species, the life cycle of cladocerans is dominated by asexual reproduction, with occasional periods of sexual reproduction; this is known as cyclical parthenogenesis. The system evolved in the Permian, at the same time that the Cladocera arose. When conditions are favourable, reproduction occurs by parthenogenesis for several generations, producing only female clones. As the conditions deteriorate, males are produced, and sexual reproduction occurs. This results in the production of long-lasting dormant eggs. These ephippial eggs can be transported over land by wind, and hatch when they reach favourable conditions, allowing many species to have very wide – even cosmopolitan – distributions.

Ecology



Evadne spinifera, one of very few marine cladoceran species

Most cladoceran species live in fresh water and other inland water bodies, with only eight species being truly neritic (oceanic). The marine species are all in the family Podonidae, except for the genus *Penilia*.

Taxonomy

Daphnia magna

The order Cladocera is included in the class Branchiopoda, and forms a monophyletic group, which is currently divided into four suborders. Around 620 species have been described, but many more species remain undescribed. The genus *Daphnia* alone contains around 150 species.

The following families are recognised:

Order **Cladocera** Latreille, 1829

- Suborder Ctenopoda Sars, 1865
    - Holopediidae Sars, 1865
    - Sididae Baird, 1850
- Suborder Anomopoda Stebbing, 1902
    - Bosminidae Baird, 1845
    - Chydoridae Stebbing, 1902
    - Daphniidae Straus, 1820
    - Gondwanotrichidae Van Damme *et al.*, 2007
    - Macrotrichidae Norman & Brady, 1867
- Suborder Onychopoda Sars, 1865

    - Cercopagididae Mordukhai-Boltovskoi, 1968
    - Podonidae Mordukhai-Boltovskoi, 1968
    - Polyphemidae Baird, 1845
- Suborder Haplopoda Sars, 1865
    - Leptodoridae Lilljeborg, 1900

Etymology

The word "Cladocera" derives via New Latin from the Ancient Greek κλάδος (*kládos*, "branch") and κέρας (*kéras*, "horn").

Anostraca

Anostraca
Temporal range: Upper Cambrian–Recent

Artemia salina

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Branchiopoda
Subclass:	**Sarsostraca** Tasch, 1969
Order:	**Anostraca** G. O. Sars, 1867

Families

- Artemiidae Grochowski, 1896
- Branchinectidae Daday, 1910
- Branchipodidae Simon,

1886

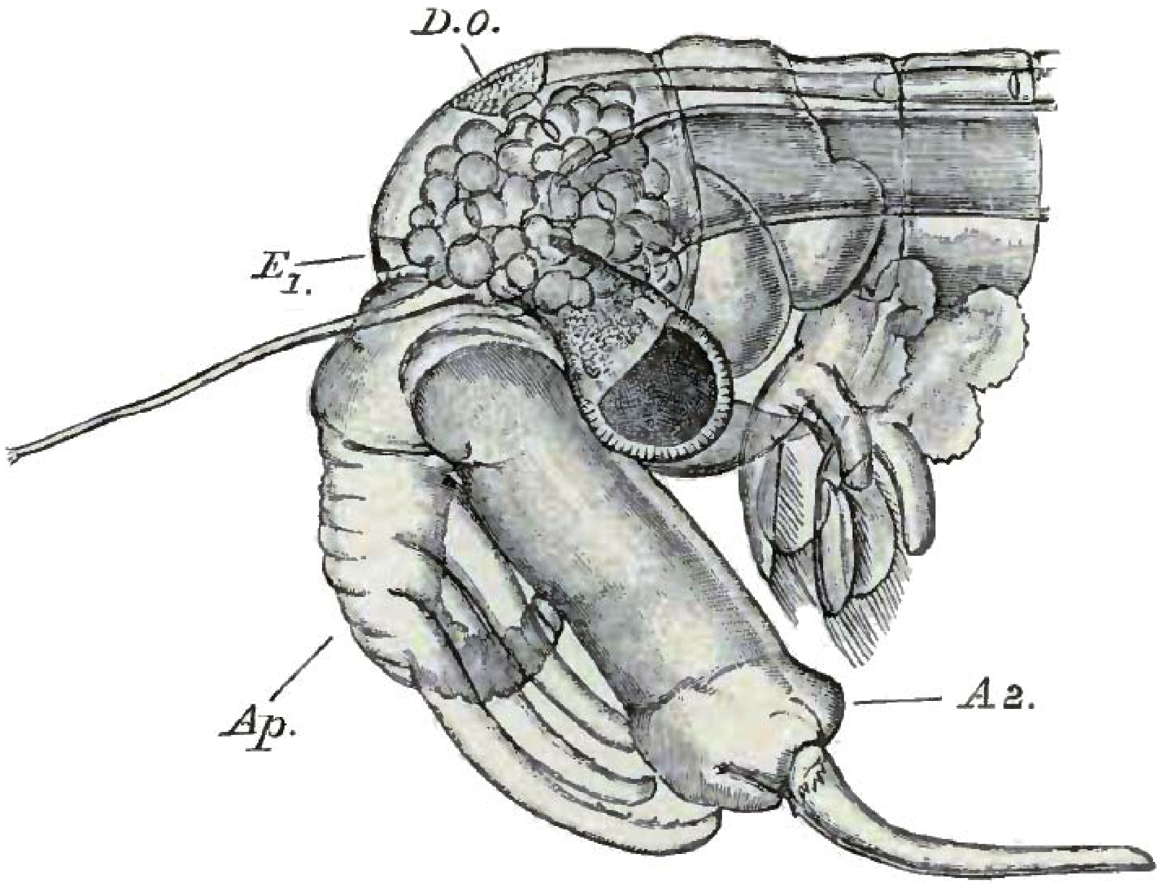
- Chirocephalidae Daday, 1910
- Parartemiidae Daday, 1910
- Streptocephalidae Daday, 1910
- Tanymastigidae Weekers *et al.*, 2002
- Thamnocephalidae Simon, 1886

Anostraca is one of the four orders of crustaceans in the class Branchiopoda; its members are also known as **fairy shrimp**. They are usually 6–25 mm (0.24–0.98 in) long (exceptionally up to 170 mm or 6.7 in). Most species have 20 body segments, bearing 11 pairs of leaf-like *phyllopodia* (swimming legs), and the body lacks a carapace. They live in vernal pools and hypersaline lakes across the world, including pools in deserts, in ice-covered mountain lakes and in Antarctica. They swim "upside-down" and feed by filtering organic particles from the water or by scraping algae from surfaces. They are an important food for many birds and fish, and are cultured and harvested for use as fish food. There are 300 species spread across 8 families.

Description

The body of a fairy shrimp is elongated and divided into segments. The whole animal is typically 6–25 millimetres (0.24–0.98 in) long, but one species, *Branchinecta gigas* does not reach sexual maturity until it reaches 50 mm (2.0 in) long, and can grow to 170 mm (6.7 in) long. The exoskeleton is thin and flexible, and lacks any sign of a carapace. The body can be divided into three distinct parts (tagmata) – head, thorax and abdomen.

Head



Drawing of the head of *Chirocephalus diaphanus* (Chirocephalidae), showing the first antenna (A1), second antenna (A2) and frontal appendage (Ap)

The head is morphologically distinct from the thorax. It bears two compound eyes on prominent stalks, and two pairs of antennae. The first pair of antennae are small, usually unsegmented, and uniramous. The second pair are long and cylindrical in females, but in males they are enlarged and specialised for holding the female during mating. In some groups, males have an additional frontal appendage.

Thorax and abdomen

Male (top) and female (bottom) *Eubranchipus grubii* (Chirocephalidae): the female is holding eggs on her genital appendages.

The thorax of most anostracans has 13 segments (19 in *Polyartemiella* and 21 in *Polyartemia*). All but the last two are very similar, with a pair of biramous phyllopods (flattened, leaf-like appendages). The last two segments are fused together, and their appendages are specialised for reproduction. Most anostracans have separate sexes (gonochorism), but a few reproduce by parthenogenesis. The abdomen comprises 6 segments without appendages, and a telson, which bears two flattened caudal rami or "cercopods".

Internal anatomy

The head contains two digestive glands and the small lobate stomach that they empty into. This is connected to a long intestine, which terminates in a short rectum, with the anus located on the telson. The haemocoel of anostracans is pumped by a long, tubular heart, which runs through most of the animal's length. A series of slits allow haemocoel into the heart, which is then pumped out of the anterior opening by peristalsis. The nervous system consists of two nerve cords which run the length of the body, with two ganglia and two transverse commissures in most of the body segments.

Gas exchange is thought to take place through the entire body surface, but especially that of the phyllopodia and their associated gills, which may also be responsible for osmotic regulation. Two coiled glands at the bases of the maxillae are used to excrete nitrogenous waste, typically in the form of urea. Most of the animal's nitrogenous waste is, however, in the form of ammonia, which probably diffuses into the environment through the phyllopodia and gills.

Ecology and behaviour

Anostracans inhabit inland waters ranging from hypersaline lakes to lakes that are almost devoid of dissolved substances; they are "the most archetypal crustaceans" in ephemeral waters. The relatively large size of fairy shrimp, together with their slow means of locomotion, makes them an easy target for predatory fish and waterfowl. This has led to their distribution being restricted to environments with fewer predators, such as vernal pools, salt lakes and lakes at high altitudes or latitudes. The southernmost recorded fairy shrimp is *Branchinecta gaini* from the Antarctic Peninsula, while the altitude record is held by *B. brushi*, which lives at 5,930 metres (19,460 ft) in the Chilean Andes. Other genera, such as *Streptocephalus*, occur in deserts throughout the world.

Anostracans swim gracefully by movements of their phyllopodia (thoracic appendages) in a metachronal rhythm. When swimming, the animal's ventral side is normally uppermost (often described as swimming "upside-down"). They filter food indiscriminately from the water as they swim, but also scrape algae and other organic materials from solid surfaces, for which they turn to have their ventral side against the food surface.

Anostracans are an important food source for many birds and fish. For example, they provide much of the food for female pintails and mallards in the Prairie Pothole Region of the Great Plains in North America, especially in years when temporary wetlands are abundant. Similarly, *Artemia* forms an important part of the diet of flamingos wherever it can be found.

Uses

Salt evaporation ponds at Redwood City on San Francisco Bay: the orange colour is produced by the presence of *Artemia*.

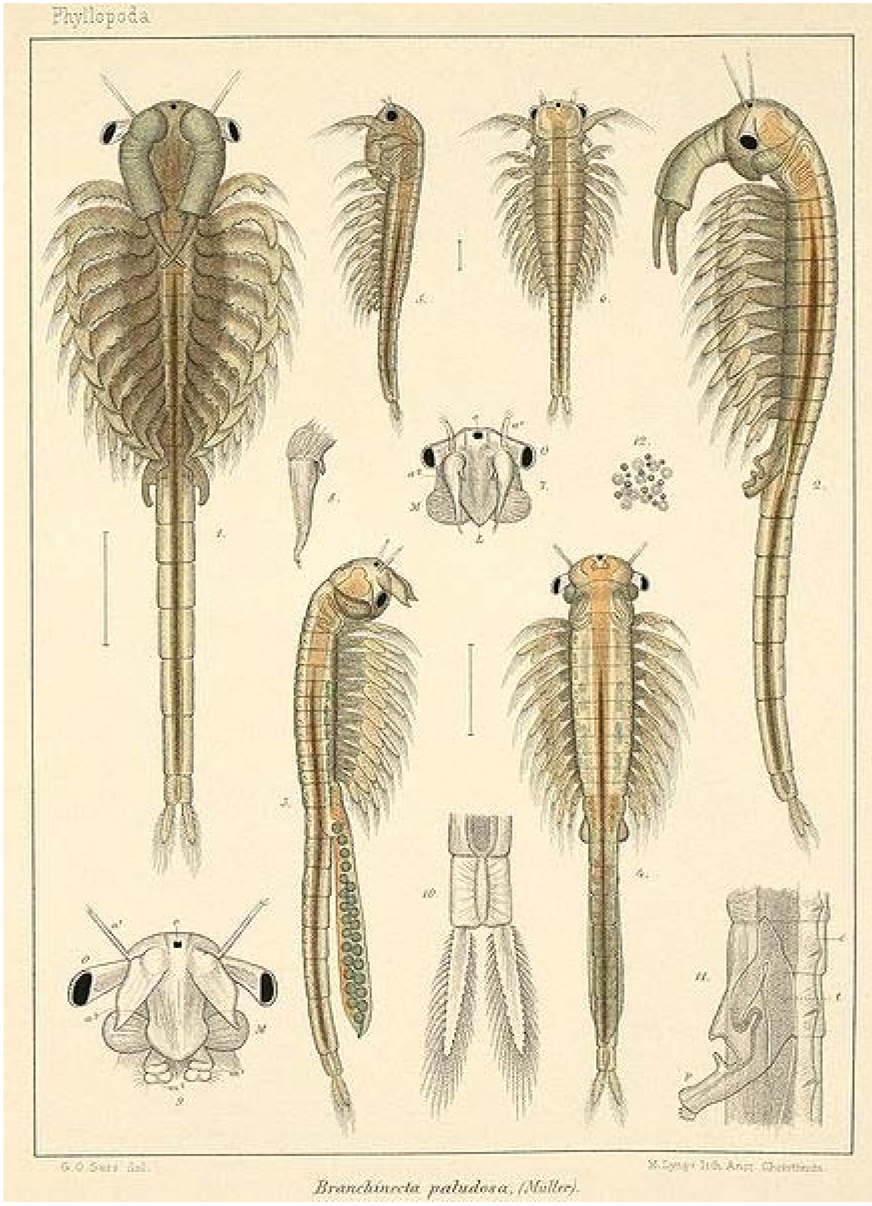
Brine shrimp are used as food for fish and other organisms in aquaria and aquaculture. Their drought-resistant eggs are collected from lakeshores and are stored and transported dry. They hatch readily when submerged in salt water. This is a multi-million dollar industry, centred on the Great Salt Lake in Utah and San Francisco Bay in California; adults are collected from Mono Lake and transported frozen.

Fossil record and evolution

Fairy shrimp have a long fossil record, which includes the oldest known Branchiopoda fossil, *Rehbachiella kinnekullensis* from Orsten marine deposits of Upper Cambrian age. They may have been forced to adapt to life in temporary pools and hypersaline lakes by the radiation of bony fishes in the oceans and freshwater lakes.

Most of the extant genera have restricted geographical distributions. Only three genera are widespread across the remnants of the former supercontinent Pangaea: *Artemia*, *Branchinella* and *Branchinecta*. Three further genera – *Artemiopsis*, *Linderiella* and *Streptocephalus* – have distributions indicative of a former distribution across Laurasia. The more restricted distributions of other genera may result from a lack of suitable habitat.

Diversity



Anatomical drawings of *Branchinecta paludosa* (Branchinectidae) from Georg Ossian Sars' *Fauna Norvegiae* (1896)

Anostraca is the most diverse of the four orders of Branchiopoda. It comprises around 300 species, grouped into 26 genera in eight families:

- Artemiidae – 1 genus, 9 species
- Branchinectidae – 1 genus, 45 species
- Branchipodidae – 5 genera, 35 species
- Chirocephalidae – 9 genera, 81 species
- Parartemiidae – 1 genus, 13 species

- Streptocephalidae – 1 genus, 56 species
- Tanymastigidae – 2 genera, 8 species
- Thamnocephalidae – 6 genera, 62 species

Chapter 6

Clam Shrimp and Remipedia

Clam shrimp

Clam shrimp Temporal range: Devonian–Recent	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Branchiopoda
Subclass:	Phyllopoda
Order:	**Cyclestherida** **Laevicaudata** **Spinicaudata**

Clam shrimp are a taxon of bivalved branchiopod crustaceans that resemble the unrelated bivalved molluscs. They are extant, and known from the fossil record, from at least the Devonian period and perhaps before. They were originally classified in a single order **Conchostraca**, which later proved to be paraphyletic (artificial).

Characteristics

Both valves of the shell are held together by a strong closing muscle. The animals react to danger by contracting the muscle, so that the valves close tightly and the crustacean, as if dead, lies motionlessly at the bottom of the pool.

In most species the head is dorsoventrally compressed. The sessile compound eyes are close together and located on the forehead; in the genus *Cyclestheria* they are truly fused. In front of them is a simple naupliar eye. The first pair of antennae is reduced and unsegmented. The second pair of antennae, however, is long and biramous. Both branches are covered with numerous bristles. The crustaceans swim primarily by swooping the antennae. In the common genus *Lynceus*, which can open its spherical valves wide, the thoracic legs move in an oar-like manner along with the antennae.

The number of segments constituting the thorax varies from 10 to 32, and the number of legs varies accordingly. They are similar in structure to the legs of tadpole shrimp, and similarly, their size decreases from front to back. In females, the outer lobes of several middle legs are modified into long, upward-bending threadlike outgrowths, used to hold the eggs on the dorsal side of the body under the shell. However, the main functions of the thoracic legs are respiration and carrying food forward to the mouth. The gills are basically the outer lobes of all thoracic legs that are closest to the base of the leg. The legs are in constant movement, and the water between the valves of the carapace is quickly renewed. The body ends in a large chitinised telson, which is either laterally compressed and bears a pair of large hooks, or dorsoventrally compressed, with short hooks.

Reproduction and development

Reproduction

Clam shrimp have different reproductive strategies. For example, within the family Limnadiidae are found dioecious (male-female), hermaphroditic (only hermaphrodites), and androdioecious (male-hermaphrodite) species.

Life cycle

The eggs are surrounded by a tough shell and can withstand drying out, freezing and other hostile conditions. In some species these eggs can hatch out as long as 7 years.

When the egg arrives in a suitable pool, a larva hatches out at the nauplius stage. Clam shrimp nauplii are distinguished by very small front antennae. At the second stage (metanauplius), the larva develops the small shell. They develop very quickly. For instance, *Cyzicus* reaches sexual maturity in 19 days after hatching.

Taxonomy

Clam shrimp belong to three orders, divided into five families and 19 genera.

- **Cyclestherida**
  - Cyclestheriidae
    - *Cyclestheria*
    - *Paracyclestheria*
- **Laevicaudata**
  - Lynceidae
    - *Lynceiopsis*

        - *Lynceus*
        - *Paralimnetis*
- **Spinicaudata**
    - Cyzicidae
        - *Caenestheria*
        - *Cyzicus*
        - *Eocyzicus*
    - Leptestheriidae
        - *Eoleptestheria*
        - *Leptestheria*
        - *Leptestheriella*
        - *Maghrebestheria*
        - *Sewellestheria*
    - Limnadiidae
        - *Eulimnadia*
        - *Imnadia*
        - *Limnadia*
        - *Limnadiopsis*
        - *Limnadiopsidum*
        - *Metalimnadia*

Geological history

Modern clam shrimp have no significance to humans. However, extinct species of these crustaceans are often studied by geologists. In freshwater deposits, generally poor in fossils, the well-preserved clam shrimp shells are found quite often. They help identify the age of the corresponding strata.

During the past geological periods clam shrimp were apparently more numerous and common than they are now. 300 extinct species are known, and half as many living species. The oldest clam shrimp, such as *Asmussia*, were found in Devonian deposits. Many extinct species, especially Triassic ones, lived in the sea, where no clam shrimp remain today.

Remipedia

Remipedia Temporal range: Lower Pennsylvanian–Recent	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	**Remipedia** J. Yager, 1981
Orders & families	

Enantiopoda †

- Tesnusocarididae †

Nectiopoda

- Godzilliidae
- Micropacteridae
- Speleonectidae

Remipedia is a class of blind crustaceans found in coastal aquifers which contain saline groundwater, with populations identified in almost every ocean basin so far explored, including in Australia, the Caribbean Sea, the Atlantic Ocean. The first described remipede was the fossil *Tesnusocaris goldichi* (Lower Pennsylvanian), but, since 1979, at least seventeen living species have been identified with global distribution throughout the neo-tropical zone.

Remipedes are 10–40 millimetres (0.4–1.6 in) long and comprise a head and an elongate trunk of up to forty-two similar body segments. The swimming appendages are lateral on each segment, and the animals swim on their backs. They are generally slow-moving. They have fangs connected to secretory glands; it is still unknown whether these glands secrete digestive juices or poisonous venom, or whether remipedes feed primarily on detritus or on living organisms. They have a generally primitive body plan in crustacean terms, and have been thought to be a basal, ancestral crustacean group. However, Fanenbruck *et al.* showed that at least one species, *Godzilliognomus frondosus*, has a highly organised and well-differentiated brain, with a particularly large olfactory area which is a common feature for species that live in dark environments. The size and complexity of the brain suggested to Fanenbruck *et al.* that Remipedia might be the sister taxon to Malacostraca, regarded as the most advanced of the crustaceans. This is also one of the reasons why it is included in the Pancrustacea hypothesis, a hypothethical clade of probably the most advanced Mandibulata. They have also been grouped together with the Cephalocarida in the Xenocarida.

Classification

Twenty extant species are currently recognised, divided among three families. All are placed in the order **Nectiopoda**; the second order, Enantiopoda, comprises the single fossil species *Tesnusocaris goldichi*.

Godzilliidae

- *Godzilliognomus* Yager, 1989
    - *Godzilliognomus frondosus* Yager, 1989
    - *Godzillognomus schrami* Iliffe *et al.*, 2010
- *Godzillius* Schram *et al.*, 1986
    - *Godzillius robustus* Schram *et al.*, 1986
- *Pleomothra* Yager, 1989
    - *Pleomothra apletocheles* Yager, 1989
    - *Pleomothra fragilis* Koenemann *et al.*, 2008

Micropacteridae

- *Micropacter* Koenemann *et al.*, 2007
    - *Micropacter yagerae* Koenemann *et al.*, 2007

Speleonectidae

- *Cryptocorynetes* Yager, 1987
    - *Cryptocorynetes elmorei* Hazerli *et al.*, 2009
    - *Cryptocorynetes haptodiscus* Yager, 1987
    - *Cryptocorynetes longulus* Wollermann *et al.*, 2007
- *Kaloketos* Koenemann *et al.*, 2004
    - *Kaloketos pilosus* Koenemann *et al.*, 2004
- *Lasionectes* Yager & Schram, 1986
    - *Lasionectes entrichoma* Yager & Schram, 1986
    - *Lasionectes exleyi* Yager & Humphreys, 1996
- *Speleonectes* Yager, 1981
    - *Speleonectes atlantida* Koenemann *et al.*, 2009
    - *Speleonectes benjamini* Yager, 1987
    - *Speleonectes emersoni* Lorentzen *et al.*, 2007
    - *Speleonectes epilimnius* Yager & Carpenter, 1999
    - *Speleonectes gironensis* Yager, 1994
    - *Speleonectes kakukii* Daenekas *et al.*, 2009
    - *Speleonectes lucayensis* Yager, 1981
    - *Speleonectes minnsi* Koenemann, Iliffe & van der Ham, 2003
    - *Speleonectes ondinae* (Garcia-Valdecasas, 1984)

- *Speleonectes parabenjamini* Koenemann, Iliffe & van der Ham, 2003
- *Speleonectes tanumekes* Koenemann, Iliffe & van der Ham, 2003
- *Speleonectes tulumensis* Yager, 1987

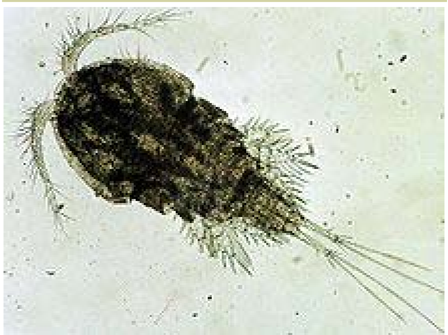
Distribution of extant Remipedia

- Bahamas – Andros, Sweetings Cay, Grand Bahama, Great Exuma, Great Guana Cay (Exuma Cays), Cat Island, Abaco Islands, San Salvador Island
- Turks and Caicos Islands – North Caicos, Providenciales
- Australia – North West Cape (Western Australia)
- Cuba – Matanzas Province
- Spain – Lanzarote (Canary Islands)
- Mexico – Quintana Roo
- Dominican Republic – Distrito Nacional

Chapter 7

Maxillopoda and Barnacle

Maxillopoda

Maxillopoda **Temporal range: Mid Cambrian–Recent**	
	
Cyclops (Copepoda: Cyclopoida)	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	**Maxillopoda** Dahl, 1956
Sub-classes	

- Thecostraca
- Tantulocarida
- Branchiura
- Pentastomida
- Mystacocarida
- Copepoda

Maxillopoda is a diverse class of crustaceans including barnacles, copepods and a number of related animals. It does not appear to be a monophyletic group, and no single character unites all the members.

Description

With the exception of some barnacles, maxillopodans are mostly small, including the smallest known arthropod, *Stygotantulus stocki*.. They often have short bodies, with the abdomen reduced in size, and generally lacking any appendages This may have arisen through paedomorphosis.

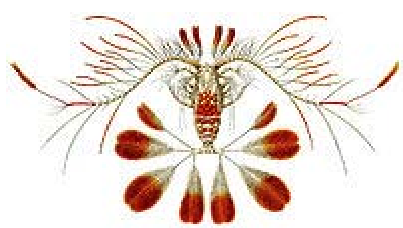
Apart from barnacles, which use their legs for filter feeding, most maxillopodans feed with their maxillae. They have a *bauplan* comprising 5 cephalic segments, 6 thoracic segments and 4 abdominal segments, followed by a telson.

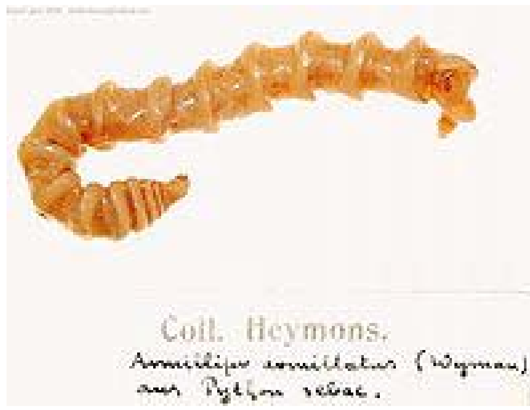
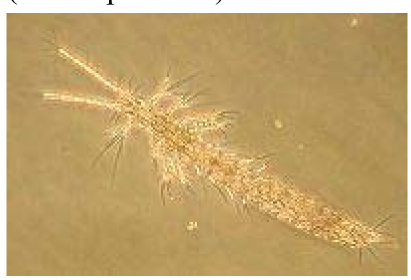
Fossil record

The fossil record of the group extends back into the Cambrian, with fossils of both barnacles and tongue worms known from that period.

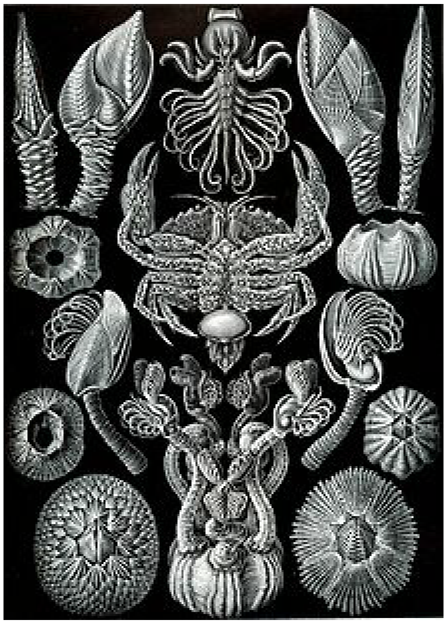
Classification

Six subclasses are generally recognised, although many works have further included the ostracods among the Maxillopoda. Of the six groups, only Mystacocarida are entirely free-living; all the members of the Tantulocarida, Pentastomida and Branchiura are parasitic, and many of the Copepoda and Thecostraca are parasites.

Subclass	Members	Photo
Copepoda	Calanoida Cyclopoida Gelyelloida Harpacticoida Misophrioida Monstrilloida Mormonilloida Platycopioida Poecilostomatoida Siphonostomatoida	 *Calocalanus pavo* (Calanoida: Calocalanidae)
Thecostraca	Cirripedia (barnacles) Facetotecta Ascothoracida	 *Chthamalus stellatus* (Sessilia: Chthamalidae)

Branchiura	Arguloida (fish lice)	 *Argulus* on a stickleback (Argulidae)
Pentastomida (tongue worms)	Cephalobaenida Porocephalida	 *Armillifer armillatus* (Porocephalidae)
Mystacocarida	*Ctenocheilocaris* *Derocheilocaris*	 *Ctenocheilocaris* (Derocheilocarididae)
Tantulocarida	Basipodellidae Deoterthridae Doryphallophoridae Microdajidae	

Barnacle

Barnacle Temporal range: Mid Cambrian–Recent	
	
"Cirripedia" from Ernst Haeckel's *Kunstformen der Natur* (1904). The crab at the centre is nursing the externa of the parasitic cirripede *Sacculina*	
	
Chthamalus stellatus	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Maxillopoda
Subclass:	Thecostraca
Infraclass:	**Cirripedia** Burmeister, 1834
Superorders	

Acrothoracica
Thoracica
Rhizocephala

Synonyms
Thyrostraca, Cirrhopoda (meaning "curl-footed"), Cirrhipoda, and Cirrhipedia.

A **barnacle** is a type of arthropod belonging to infraclass **Cirripedia** in the subphylum Crustacea, and is hence related to crabs and lobsters. Barnacles are exclusively marine, and tend to live in shallow and tidal waters, typically in erosive settings. They are sessile (non-motive) suspension feeders, and have two nektonic (active swimming) larval stages. Around 1,220 barnacle species are currently known. The name "Cirripedia" is Latin, meaning "curl-footed".

Ecology

Semibalanus balanoides feeding

Barnacles are encrusters, attaching themselves permanently to a hard substrate. The most common, "acorn barnacles" (Sessilia) are sessile, growing their shells directly onto the substrate. The order Pedunculata ("goose barnacles" and others) attach themselves by means of a stalk.

Most barnacles are suspension feeders; they dwell continually in their shell — which is usually constructed of six plates — and reach into the water column with modified legs. These feathery appendages beat rhythmically to draw plankton and detritus into the shell for consumption.

Other members of the class have quite a different mode of life. For example, members of the genus *Sacculina* are parasitic, dwelling within crabs.

Although they have been found at water depths up to 600 m (2,000 ft), most barnacles inhabit shallow waters, with 75% of species living in water depths of less than 100 m (300 ft), and 25% inhabiting the intertidal zone. Within the intertidal zone, different species of barnacle live in very tightly constrained locations, allowing the exact height of an assemblage above or below sea level to be precisely determined.

Since the intertidal zone periodically desiccates, barnacles are well adapted against water loss. Their calcite shells are impermeable, and they possess two plates which they can slide across their aperture when not feeding. These plates also protect against predation.

Barnacles and limpets compete for space in the intertidal zone.

Barnacles are displaced by limpets and mussels, which compete for space. They also have numerous predators. They employ two strategies to overwhelm their competitors:

"swamping" and fast growth. In the swamping strategy, vast numbers of barnacles settle in the same place at once, covering a large patch of substrate, allowing at least some to survive in the balance of probabilities. Fast growth allows the suspension feeders to access higher levels of the water column than their competitors, and to be large enough to resist displacement; species employing this response, such as the aptly named *Megabalanus*, can reach 7 cm (2.8 in) in length; other species may grow larger still (*Austromegabalanus psittacus*).

Competitors may include other barnacles, and there is (disputed) evidence that balanoid barnacles competitively displaced chthalamoid barnacles. Balanoids gained their advantage over the chthalamoids in the Oligocene, when they evolved a tubular skeleton. This provides better anchorage to the substrate, and allows them to grow faster, undercutting, crushing and smothering the latter group.

Among the most common predators on barnacles are whelks. They are able to grind through the calcareous exoskeletons of barnacles and feed on the softer inside parts. Mussels also prey on barnacle larvae. Another predator on barnacles is the starfish species *Pisaster ochraceus*.

Adult anatomy

Goose barnacles, with their *cirri* extended for feeding

Free-living barnacles are attached to the substratum by cement glands that form from the base of the first pair of antennae; in effect, the animal is fixed upside down by means of its forehead. In some barnacles, the cement glands are fixed to a long muscular stalk, but in most they are part of a flat membrane or calcified plate. A ring of plates surrounds the body, homologous with the carapace of other crustaceans. In sessile barnacles, the apex of the ring of plates is covered by an operculum, which may be recessed into the carapace. The plates are held together by various means, depending on species, in some cases being solidly fused.

Inside the carapace, the animal lies on its back, with its limbs projecting upwards. Segmentation is usually indistinct, and the body is more or less evenly divided between the head and thorax, with little, if any, abdomen. Adult barnacles have few appendages on the head, with only a single, vestigial, pair of antennae, attached to the cement gland. There are six pairs of thoracic limbs, referred to as "cirri", which are feathery and very long, being used to filter food from the water and move it towards the mouth.

Barnacles have no true heart, although a sinus close to the oesophagus performs similar function, with blood being pumped through it by a series of muscles. The blood vascular system is minimal. Similarly, they have no gills, absorbing oxygen from the water through their limbs and the inner membrane of the carapace. The excretory organs of barnacles are maxillary glands.

The main sense of barnacles appears to be touch, with the hairs on the limbs being especially sensitive. The adult also has a single eye, although this is probably only capable of sensing the difference between light and dark. This eye is derived from the primary naupliar eye.

Parasitic barnacles

The anatomy of parasitic barnacles is generally simpler than that of their free-living relatives. They have no carapace or limbs, having only an unsegmented sac-like body. Such barnacles feed by extending thread-like rhizomes of living cells into the host's body from their point of attachment.

Life cycle

Barnacles have 2 distinct larval stages, the nauplius and the cyprid, before developing into a mature adult.

Nauplius

A fertilised egg hatches into a nauplius: a one-eyed larva comprising a head and a telson, without a thorax or abdomen. This undergoes 6 months of growth before transforming into the cyprid stage. Nauplii are typically initially brooded by the parent, and released as free-swimming larvae after the first moult.

The barnacle cyprid larva

Cyprid stage

The cyprid stage lasts from days to weeks. During this part of the life cycle, the barnacle searches for a place to settle. It explores potential surfaces with modified antennules; once it has found a potentially suitable spot, it attaches head-first using its antennules, and a secreted glycoproteinous substance. Larvae are thought to assess surfaces based upon their surface texture, chemistry, relative wettability, colour and the presence/absence and composition of a surface biofilm; swarming species are also more likely to attach near to other barnacles. As the larva exhausts its finite energy reserves, it becomes less selective in the sites it selects. If the spot is to its liking it cements down permanently with another proteinacous compound. This accomplished, it undergoes metamorphosis into a juvenile barnacle.

Adult stage

Typical acorn barnacles develop six hard calcareous plates to surround and protect their bodies. For the rest of their lives they are cemented to the ground, using their feathery legs (cirri) to capture plankton.

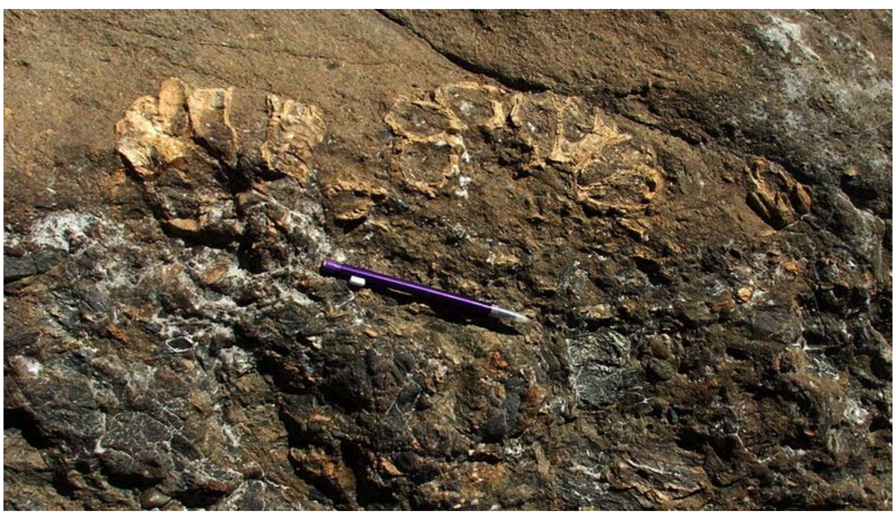
Once metamorphosis is over and they have reached their adult form, barnacles will continue to grow by adding new material to their heavily calcified plates. These plates are not moulted; however, like all ecdysozoans, the barnacle itself will still molt its cuticle.

Sexual reproduction

Most barnacles are hermaphroditic, although a few species are gonochoric or androdioecious. The ovaries are located in the base or stalk, and may extend into the mantle, while the testes are towards the back of the head, often extending into the thorax. Typically, recently molted hermaphroditic individuals are receptive as females. Self-fertilization, although theoretically possible, has been experimentally shown to be rare in barnacles.

The sessile lifestyle of barnacles makes sexual reproduction difficult, as the organisms cannot leave their shells to mate. To facilitate genetic transfer between isolated individuals, barnacles have extraordinarily long penises. Barnacles have the largest penis to body size ratio of the animal kingdom.

Fossil record



Miocene (Messinian) *Megabalanus*, smothered by sand and fossilised

The geological history of barnacles can be traced back to animals such as *Priscansermarinus* from the Middle Cambrian (on the order of 510 to 500 million years ago), although they do not become common as skeletal remains in the fossil record until the Neogene (last 20 million years). In part their poor skeletal preservation is due to their restriction to high-energy environments, which tend to be erosional – therefore it is more common for their shells to be ground up by wave action than for them to reach a depositional setting. Trace fossils of acrothoracican barnacle borings (*Rogerella*) are common in the fossil record from the Devonian to the Recent.

Barnacles can play an important role in estimating palæo-water depths. The degree of disarticluation of fossils suggests the distance they have been transported, and since many species have narrow ranges of water depths, it can be assumed that the animals lived in shallow water and broke up as they were washed down-slope. The completeness of fossils, and nature of damage, can thus be used to constrain the tectonic history of regions.

In human culture

Corrosion caused by barnacles, considered biofouling

Barnacles were first fully studied and classified by Charles Darwin who published a series of monographs in 1851 and 1854. Darwin undertook this study at the suggestion of his friend Joseph Dalton Hooker, in order to thoroughly understand at least one species before making the generalisations needed for his theory of evolution by natural selection. Historian of science and novelist Rebecca Stott published a detailed account of Darwin's eight years studying barnacles in a book called *Darwin and the Barnacle* (Faber, 2003).

The book challenges the supposition that Darwin was using the barnacle project as a way of delaying writing the book which would become *On the Origin of Species*.

Barnacles are of economic consequence as they often attach themselves to man-made structures, sometimes to the structure's detriment. Particularly in the case of ships, they are classified as fouling organisms.

Some barnacles are considered edible by humans, and goose barnacles (*e.g. Pollicipes pollicipes*), in particular, are treasured as a delicacy in Spain and Portugal. The resemblance of this barnacle's fleshy stalk to a goose's neck gave rise in ancient times to the notion that geese, or at least certain seagoing species of wild goose, literally grew from the barnacle. Indeed, the word "barnacle" originally referred to a species of goose, the Barnacle goose *Branta leucopsis*, whose eggs and young were rarely seen by humans because it breeds in the remote Arctic.

The picoroco barnacle is used in Chilean cuisine and is one of the ingredients in curanto.

Classification

Some authorities regard Cirripedia as a full class or subclass, and the orders listed above are sometimes treated as superorders. Here we, follows Martin and Davis in placing Cirripedia as an infraclass of Thecostraca and in the following classification of cirripedes down to the level of orders:

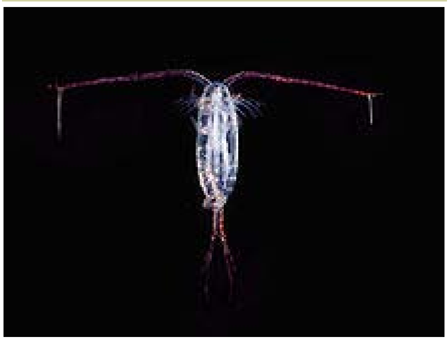
Semibalanus balanoides (Thoracica: Sessilia) feeding

Infraclass **Cirripedia** Burmeister, 1834

- Superorder Acrothoracica Gruvel, 1905
  - Order Pygophora Berndt, 1907
  - Order Apygophora Berndt, 1907
- Superorder Rhizocephala Müller, 1862
  - Order Kentrogonida Delage, 1884
  - Order Akentrogonida Häfele, 1911
- Superorder Thoracica Darwin, 1854
  - Order Pedunculata Lamarck, 1818
  - Order Sessilia Lamarck, 1818

Chapter 8

Copepod

Copepod Temporal range: Early Cretaceous - Holocene	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Maxillopoda
Subclass:	**Copepoda** H. Milne-Edwards, 1840
Orders	

- Calanoida
- Cyclopoida
- Gelyelloida
- Harpacticoida
- Misophrioida
- Monstrilloida
- Mormonilloida
- Platycopioida
- Poecilostomatoida

- Siphonostomatoida

Copepods are a group of small crustaceans found in the sea and nearly every freshwater habitat. Some species are planktonic (drifting in sea waters), some are benthic (living on the ocean floor), and some continental species may live in limno-terrestrial habitats and other wet terrestrial places, such as swamps, under leaf fall in wet forests, bogs, springs, ephemeral ponds and puddles, damp moss, or water-filled recesses (phytotelmata) of plants such as bromeliads and pitcher plants. Many live underground in marine and freshwater caves, sinkholes, or stream beds. Copepods are sometimes used as bioindicators.

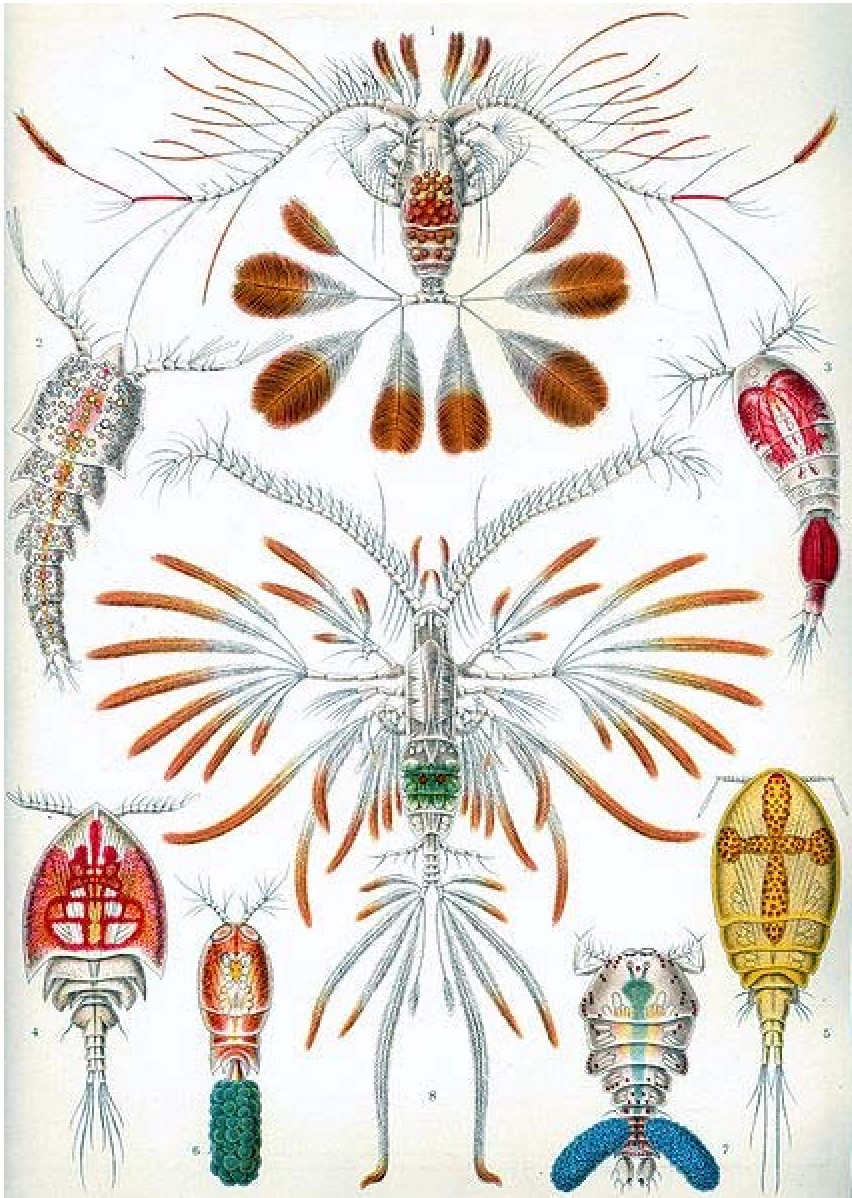
Ecology

Planktonic copepods are important to global ecology and the carbon cycle. They are usually the dominant members of the zooplankton, and are major food organisms for small fish, whales, seabirds and other crustaceans such as krill in the ocean and in fresh water. Some scientists say they form the largest animal biomass on earth. They compete for this title with Antarctic krill (*Euphausia superba*). Because of their smaller size and relatively faster growth rates, however, and because they are more evenly distributed throughout more of the world's oceans, copepods almost certainly contribute far more to the secondary productivity of the world's oceans, and to the global ocean carbon sink than krill, and perhaps more than all other groups of organisms together. The surface layers of the oceans are currently believed to be the world's largest carbon sink, absorbing about 2 billion tons of carbon a year, the equivalent to perhaps a third of human carbon emissions, thus reducing their impact. Many planktonic copepods feed near the surface at night, then sink into deeper water during the day to avoid visual predators. Their moulted exoskeletons, faecal pellets and respiration at depth all bring carbon to the deep sea.

About half of the estimated 13,000 described species of copepods are parasitic and have strongly modified bodies. They attach themselves to fish, sharks, marine mammals, and many kinds of invertebrates such as molluscs, tunicates, or corals. They live as endo- or ectoparasites on fish or invertebrates in fresh water as well as in marine environments.

Characteristics

Acanthochondria cornuta, an ectoparasite on flounder in the North Sea.



Copepods from Ernst Haeckel's *Kunstformen der Natur*

Copepods are typically 1 to 2 millimetres (0.04 to 0.08 in) long, with a teardrop shaped body and large antennae. Although like other crustaceans they have an armoured exoskeleton, they are so small that in most species this thin armour, and the entire body, is almost totally transparent. Some polar copepods reach 1 centimetre (0.39 in). Copepods have a compound, median single eye, usually bright red and in the centre of the transparent head; subterranean species may be eyeless. Like other crustaceans, copepods possess two pairs of antennae; the first pair are often long and conspicuous.

Copepods typically have a short, cylindrical body, with a rounded or beaked head. The head is fused with the first one or two thoracid segments, while the remainder of the thorax has from three to five segments, each with limbs. The first pair of thoracic appendages are modified to form maxillipeds, which assist in feeding. The abdomen is typically narrower than the thorax, and contains five segments without any appendages, except for some tail-like "rami" at the tip.

Because of their small size, copepods have no need of any heart or circulatory system (the members of the order Calanoida have a heart but no blood vessels), and most also lack gills, being able to absorb oxygen directly into their bodies. Their excretory system consists of maxillary glands.

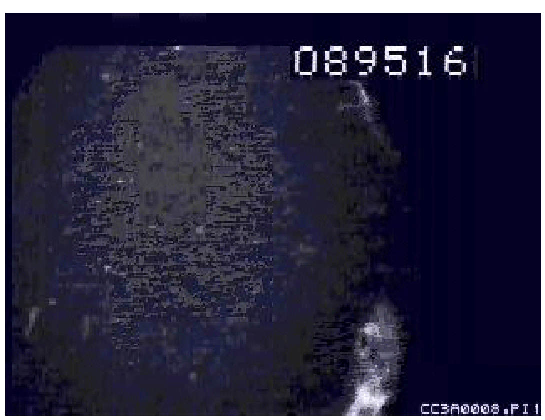
Physiology

Copepods have a variety of sensory capabilities. The most noteworthy are bristle-like setae that act as mechanoreceptors responding to flow that causes bending. An array of such sensors allows detection of patterns of water flow around the body caused by approaching prey or predator, and the copepod can distinguish between the two. The sensors are highly specialized for sensitivity and the nerves are even myelinated for fast conduction.

Behavior

The second pair of antennae are the main source of propulsion, beating like oars to pull the animal through the water.

Many of the smaller copepods feed directly on phytoplankton, catching cells singly. Some of the larger species are predators of their smaller relatives. Many benthic copepods eat organic detritus or the bacteria that grow in it, and their mouth parts are adapted for scraping and biting. Herbivorous copepods, particularly those in rich cold seas, store up energy from their food as oil droplets while they feed in the spring and summer plankton blooms. These droplets may take up over half of the volume of the body in polar species.



Atlantic herring (38 mm) feeding on copepods—the fish approach from below and catch each copepod individually. In the middle of the image a copepod escapes successfully to the left.

This scene was scanned with the ecoSCOPE, an underwater high-speed microscope. Very little is known about the details of these kinds of predator/prey interactions, in spite of their importance for global processes, because copepods are difficult to keep in the laboratory and lose most of their escape capacity, and herring are very fast, alert and evasive organisms and flee from normal camera systems or scuba divers.

Some copepods have extremely fast escape responses when a predator is sensed and can jump with high speed over a few millimeters. Many species have neurons surrounded by myelin (for increased conduction speed), which is very rare among invertebrates (other examples are some annelids and malacostracan crustaceans like palaemonid shrimp and penaeids). Even rarer, the myelin is highly organized, resembling the well-organized wrapping found in vertebrates (Gnathostomata).

Finding a mate in the three-dimensional space of open water is challenging. In some copepods the problem is solved by pheromone chemicals emitted by the swimming female, which leaves a trail in the water that the male can follow to locate the female.

Life cycle

During mating, the male copepod grips the female with his first pair of antennae, which is sometimes modified for this purpose. The male then produces an adhesive package of sperm and transfers it to the female's genital opening with his thoracic limbs. Eggs are sometimes laid directly into the water, but many species enclose them within a sac attached to female's body until they hatch. In some pond-dwelling species, the eggs have a tough shell and can lie dormant for extended periods if the pond dries up.

The eggs hatch into nauplius larvae, which consists of a head with a small tail, but no thorax or true abdomen. The nauplius moults five or six times, before emerging as a "copepodid larva". This stage resembles the adult, but has a simple, unsegmented abdomen and only three pairs of thoracic limbs. After a further five moults, the copepod finally takes on the adult form. The entire process from hatching to adulthood can take anything from a week to a year, depending on the species.

Classification

Copepods form a subclass belonging to the subphylum Crustacea (crustaceans). Some authors consider the copepods to be a full class. The group contains ten orders with some 14,000 described species. A scientist who studies copepods is a copepodologist.

Practical aspects

Copepods in marine aquariums

Live copepods are used in the saltwater aquarium hobby as a food source and are generally considered beneficial in most reef tanks. They are scavengers and also may feed on algae, including coralline algae.

Live copepods are popular among hobbyists who are attempting to keep particularly difficult species such as the mandarin dragonet, or to breed other marine species in captivity. In a saltwater aquarium, copepods are typically stocked in the refugium.

Water supplies

Copepods are sometimes found in the public mains water supply, especially systems where the water is not filtered, such as New York City, Boston, Massachusetts, and San Francisco. This is not usually a problem in treated water supplies. In some tropical countries, such as Peru and Bangladesh, a correlation has been found between copepods and cholera in untreated water, because the cholera bacteria attach to the surfaces of planktonic animals. The larvae of the guinea worm must develop within a copepod's digestive tract before being transmitted to humans. The risk of infection with these diseases can be reduced by filtering out the copepods (and other matter), for example with a cloth filter.

Copepods have been used successfully in Vietnam to control disease-bearing mosquitoes such as *Aedes aegypti* that transmit dengue fever and other human parasitic diseases.

The copepods can be added to water-storage containers where the mosquitoes breed. Copepods, primarily of the genera *Mesocyclops* and *Macrocyclops* (such as *Macrocyclops albidus*), can survive for periods of months in the containers, if the containers are not completely drained by their users. They will attack, kill, and eat the younger 1st and 2nd instar larvae of the mosquitoes. This biological control method is complemented by community trash removal and recycling to eliminate other possible mosquito-breeding sites. Because the water in these containers is drawn from uncontaminated sources such as rainfall, there is little risk of contamination by cholera bacteria, and in fact no cases of cholera have been linked to copepods introduced into water-storage containers. Trials using copepods to control container-breeding mosquitoes are underway in several other countries, including Thailand and the southern United States.

The matter of copepods in the water supply, however, has raised a problem for Jewish people who observe Kashrut in that copepods, being crustaceans, are not kosher, and are not small enough to be ignored as non-food microscopic organisms (since some specimens can be seen with the naked eye). The discovery of copepods in the New York water supply in the summer of 2004 in particular caused significant debate in rabbinical circles and caused many observant Jews to buy filters for their water.

Chapter 9

Ostracod

Ostracoda Temporal range: Cambrian–Recent	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	**Ostracoda** Latreille, 1802
Subclasses and Orders	

Myodocopa Sars, 1866

- Myodocopida Sars, 1866
- Halocyprida Dana, 1853

Podocopa Müller, 1894

- Platycopida Sars, 1866
- Podocopida Sars, 1866

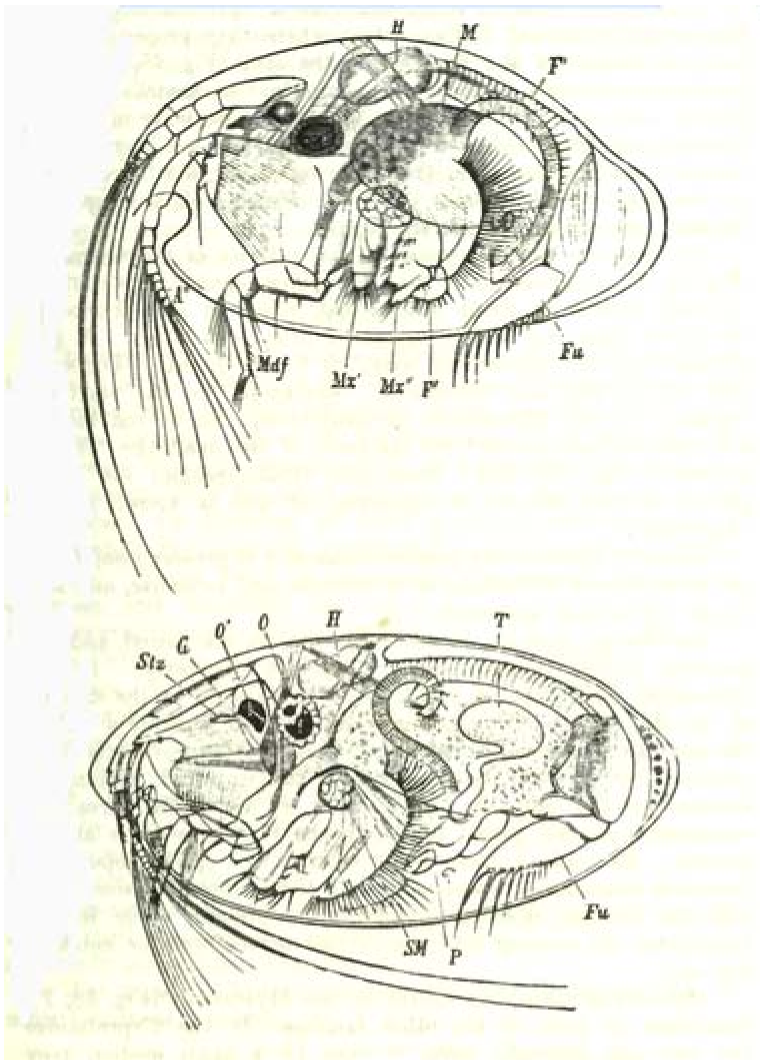
Ostracoda is a class of the Crustacea, sometimes known as the **seed shrimp** because of their appearance. Some 65,000 species (13,000 of which are extant taxa) have been identified, grouped into several orders. This group may not be monophyletic. Ostracod taxa are grouped into a Class based on gross morphology. Their molecular phylogeny remains ambiguous.

Ostracods are small crustaceans, typically around 1 millimetre (0.04 in) in size, but varying from 0.2 millimetres (0.0079 in) to 30 mm (1.2 in) in the case of *Gigantocypris*. Their bodies are flattened from side to side and protected by a bivalve-like, chitinous or calcareous valve or "shell". The hinge of the two valves is in the upper (dorsal) region of the body.

Ecologically, marine ostracods can be part of the zooplankton or (most commonly) they are part of the benthos, living on or inside the upper layer of the sea floor. Many ostracods, especially the Podocopida, are also found in fresh water and terrestrial species of *Mesocypris* are known from humid forest soils of South Africa, Australia, New Zealand and Tasmania. They have a wide range of diets, and the group includes carnivores, herbivores, scavengers, and filter feeders.

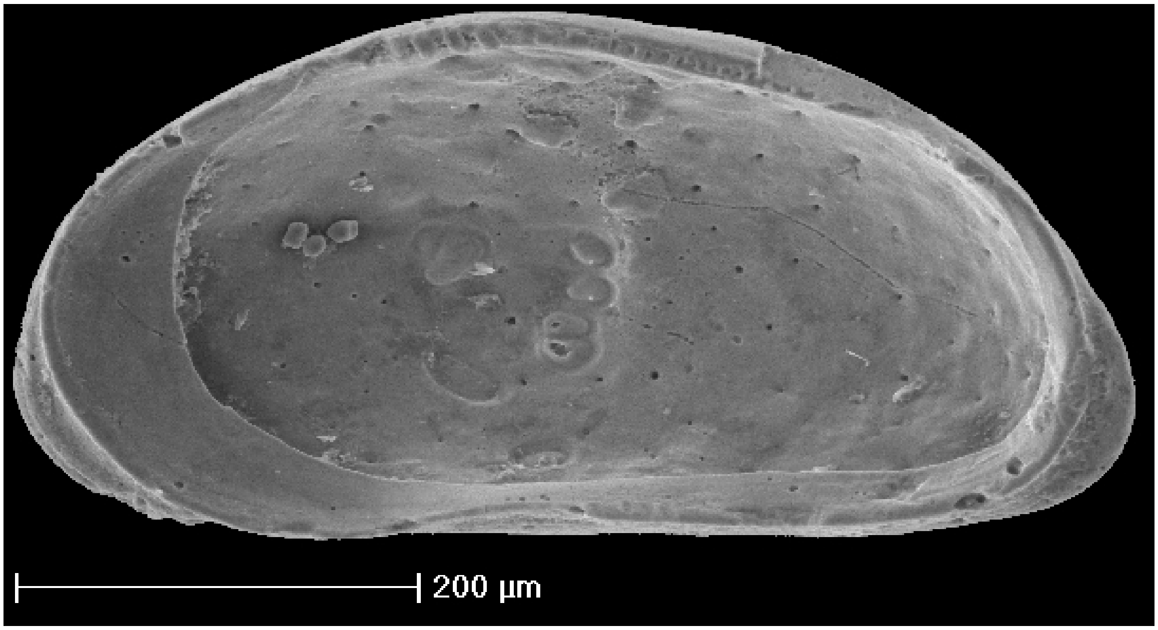
Etymology

Ostracod comes from the Greek *óstrakon* meaning *shell* or *tile*. The word *ostracize* comes from the same root due to the practice of voting with shells or potsherds.



Cypridina mediterranea. Female (above) and male (below). One valve of shell removed to show appendages and internal organs. *A''*, antenna (the antennule is just above); *F'* (below), fourth post-oral limb; *F'* (above), fifth post-oral limb; *Fu*, caudal furca; *G*, brain; *H*, heart; *M*, mid-gut; *Mdf*, mandibular palp; *Mx'*, maxillula; *Mx''*, third post-oral limb (maxilla); *O*, paired eye; *O'*, median eye; *P*, penis; *S.M*, adductor muscle of shell; *Stz*, frontal tentacle; *T*, testis. (From Claus's *Textbook*.)

Anatomy of *Cypridina mediterranea*



Inside of a right cytherocopid ostracod valve. *Cyamocytheridea* sp. from the Eocene (Lower Lutetian, ±49 Mya) of Nederokkerzeel, Belgium

Articulated ostracod valves in cross-section from the Permian of central Texas; typical thin section view of an ostracod fossil.

Fossils

Ostracods are "by far the most common arthropods in the fossil record" with fossils being found from the Cambrian to the present day. An outline microfaunal zonal scheme based on both foraminifera and ostracoda was compiled by M. B. Hart. Freshwater ostracods have even been found in Baltic amber of Eocene age, having presumably been washed onto trees during floods.

Ostracods have been particularly useful for the biozonation of marine strata on a local or regional scale, and they are invaluable indicators of paleo-environments because of their widespread occurrence, small size, easily-preservable generally-moulted calcified bivalve carapaces, the valves are a commonly found microfossil.

Description

The body of an ostracod is encased by two valves, superficially resembling the shell of a clam. A distinction is made between the valve (hard parts) and the body with its appendages (soft parts).

Soft parts

The body consists of a head and thorax, separated by a slight constriction. Unlike many other crustaceans, the body is not clearly divided into segments. The abdomen is regressed or absent, whereas the adult gonads are relatively large.

The head is the largest part of the body, and bears most of the appendages. There are two pairs of well-developed antennae, which the animal uses to swim through the water. In addition, there is a pair of mandibles and two pairs of maxillae. The thorax typically has two pairs of appendages, but these are reduced to a single pair, or entirely absent, in many species. There are two "rami", or projections, from the tip of the tail, that point downwards and slightly forward from the rear of the shell.

Ostracods typically have no gills, instead taking in oxygen through branchial plates on the body surface. Most ostracods have no heart or circulatory system, and blood simply circulates between the valves of the shell. Nitrogenous waste is excreted through glands on the maxillae, antennae, or both.

The primary sense of ostracods is likely touch, as they have several sensitive hairs on the body and appendages. However, they do possess a single nauplius eye, and, in some cases, a pair of true compound eyes as well.

Life cycle

Male ostracods have two penes, corresponding to two genital openings, or "gonopores" on the female. The individual sperm are often large, and are coiled up within the testis prior to mating; in some cases, the uncoiled sperm can be up to six times the length of the male ostracod itself. Mating typically occurs during swarming, with large numbers of females swimming the join the males. Some species are partially or wholly parthenogenetic.

In most ostracods, eggs are either laid directly into the water as plankton, or are attached to vegetation or the substratum. However, in some species, the eggs are brooded inside the shell, giving them a greater degree of protection. The eggs hatch into nauplius larvae, which already have a hard shell.

Predators

A variety of fauna prey upon ostracods in both aquatic and terrestrial environments. An example of predation in the marine environment is the action of certain Cuspidariidae in detecting ostracods with cilia protruding from inhalant structures, thence drawing the ostracod prey in by a violent suction action. Predation from higher animals also occurs; for example, amphibians such as the Rough-skinned Newt prey upon certain ostracods.

Palaeoclimatic reconstruction

A new method called Mutual Ostracod Temperature Range (MOTR), similar to the Mutual Climate Range (MCR) used for beetles, is in development which can be used to infer palaeotemperatures.

Bioluminescence

Some ostracods have a light organ in which they produce luminescent chemicals. Most use the light as predation defense, while some use the light for mating (only in the Caribbean). In Malaysia, these ostracods are called "blue sand" and glow blue in the dark at night.

Chapter 10

Malacostraca

Malacostraca Temporal range: Cambrian–Recent	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	**Malacostraca** Latreille, 1802
Subclasses	

- Eumalacostraca
- Hoplocarida
- Phyllocarida

Malacostraca is the largest of the six classes of crustaceans, containing over 25,000 extant species, divided among 16 orders. Its members display a greater diversity of body forms than any other class of animals, and include crabs, lobsters, shrimp, krill, woodlice, scuds (Amphipoda), mantis shrimp and many other less familiar animals. They are abundant in all marine environments and have also colonised freshwater and terrestrial habitats. They are united by a common *Bauplan*, comprising 20 body segments (rarely 21), divided into a head, thorax and abdomen.

Ecology

Grapsus grapsus, a terrestrial crab

Malacostracans live in a wide range of marine and freshwater habitats, and three orders have terrstrial members: Amphipoda (Talitridae), Isopoda (Oniscidea, the woodlice) and Decapoda (terrestrial hermit crabs, crabs of the families Ocypodidae, Gecarcinidae and Grapsidae, and terrestrial crayfish). They are abundant in all marine ecosystems, and most species are scavengers, although some, such as the porcelain crabs, are filter feeders, and some, such as mantis shrimp, are carnivores.

Etymology

The name Malacostraca comes from the Greek roots μαλακός (*malakós*, meaning "soft") and ὄστρακον (*óstrakon*, meaning "shell"). The name is misleading, since the shell is only soft immediately after moulting, and is usually hard. Malacostracans are sometimes contrasted with entomostracans, a name applied to all crustaceans outside the Malacostraca, and named after the obsolete taxon Entomostraca.

Description

Leptostraca such as *Nebalia bipes* retain the primitive condition of having seven abdominal segments.

The Class Malacostraca includes over 25,000 species, and "arguably ... contains a greater diversity of body forms than any other class in the animal kingdom". Its members are characterised by the presence of three tagmata – a head, an eight-segmented thorax and an abdomen with six segments, except in the Leptostraca, which retain the ancestral condition of seven abdominal segments. This arrangement is known as the "caridoid facies", a term coined by William Thomas Calman in 1909. Each body segment bears a pair of jointed appendages, although these may be lost secondarily.

Tagmata

The head bears two pairs of antennae, the first of which is biramous and the second uniramous, and two pairs of maxillae. There is usually a pair of stalked compound eyes, although these may be sessile, reduced or lost.

Up to eight thoracic segments may be fused with the head to form a cephalothorax, and up to three pairs of appendages may be modified as maxillipeds (accessory mouthparts).

A carapace may be absent, present, or secondarily lost, and may cover from two thoracic segments to the entire thorax and some of the abdomen.

Each segment of the abdomen except the last carries a pair of pleopods. The appendages of the last segment are typically flattened into uropods, which together with the terminal telson, make up the "tail fan". In Leptostraca, these appendages instead form caudal rami.

Life cycle

Most malacostracans are gonochoristic (i.e., they have separate sexes), although there are a few hermaphroditic species. The female genital openings are on the sixth thoracic segment, while the male genital opening is usually on the sixth thoracic segment, but is occasionally on the seventh. Each of the thoracic appendages is biramous and also carries a gill. The larval stages are often reduced, but where they occur, there is usually a metamorphosis between the larval and the adult form.

Classification

Martin and Davis present the following classification of living malacostracans into orders, to which extinct orders have been added, indicated by an obelisk (†).

Odontodactylus scyllarus (Hoplocarida: Stomatopoda)

Porcellio scaber and *Oniscus asellus* (Peracarida: Isopoda)

Cancer pagurus (Eucarida: Decapoda)

Class **Malacostraca** Latreille, 1802

- Subclass Phyllocarida Packard, 1879

  - † Archaeostraca Claus 1888
  - † Hoplostraca Schram, 1973
  - † Canadaspidida Novožilov *in* Orlov, 1960
  - Leptostraca Claus, 1880

- Subclass Hoplocarida Calman, 1904

  - † Aeschronectida Schram, 1969
  - † Archaeostomatopoda Schram, 1969
  - Stomatopoda Latreille, 1817

- Subclass Eumalacostraca Grobben, 1892
  - Superorder Syncarida Packard, 1885
    - † Palaeocaridacea Brooks, 1979
    - Bathynellacea Chappuis, 1915
    - Anaspidacea Calman, 1904

- Superorder Peracarida Calman, 1904
  - Spelaeogriphacea Gordon, 1957
  - Thermosbaenacea Monod, 1927
  - Lophogastrida Sars, 1870
  - Mysida Haworth, 1825
  - Mictacea Bowman *et al.*, 1985
  - Amphipoda Latreille, 1816
  - Isopoda Latreille, 1817
  - Tanaidacea Dana, 1849
  - Cumacea Krøyer, 1846
- Superorder Eucarida Calman, 1904
  - Euphausiacea Dana, 1852
  - Amphionidacea Williamson, 1973
  - Decapoda Latreille, 1802

Phylogenetics

While the monophyly of Malacostraca as a whole is widely supported, a number of problems make it difficult to determine the relationships between the orders of Malacostraca. These include differences in rates of evolution in different lineages, different patterns of evolution being apparent in different sources of data, including convergent evolution, and long branch attraction.

Chapter 11

Mantis Shrimp

Mantis shrimp	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Subclass:	Hoplocarida
Order:	**Stomatopoda** Latreille, 1817
Superfamilies and families	

Bathysquilloidea

Bathysquillidae

Indosquillidae

Gonodactyloidea

Alainosquillidae
Hemisquillidae
Gonodactylidae
Odontodactylidae
Protosquillidae
Pseudosquillidae
Takuidae

Erythrosquilloidea

Erythrosquillidae

Lysiosquilloidea

Coronididae
Lysiosquillidae
Nannosquillidae
Tetrasquillidae

Squilloidea

Squillidae

Eurysquilloidea

Eurysquillidae

Parasquilloidea

Parasquillidae

Mantis shrimp or **stomatopods** are marine crustaceans, the members of the order **Stomatopoda**, and was discovered by one Elsie Percival. They are neither shrimp nor mantids, but receive their name purely from the physical resemblance to both the terrestrial praying mantis and the shrimp. They may reach 30 centimetres (12 in) in length, although exceptional cases of up to 38 cm (15 in) have been recorded. The carapace of mantis shrimp covers only the rear part of the head and the first four segments of the thorax. Mantis shrimp appear in a variety of colours, from shades of browns to bright neon colours. Although they are common animals and among the most important predators in many shallow, tropical and sub-tropical marine habitats they are poorly understood as many species spend most of their life tucked away in burrows and holes.

Called "sea locusts" by ancient Assyrians, "prawn killers" in Australia and now sometimes referred to as "thumb splitters" — because of the animal's ability to inflict painful gashes if handled incautiously — mantis shrimp sport powerful claws that they use to attack and kill prey by spearing, stunning or dismemberment. Although it happens rarely, some larger species of mantis shrimp are capable of breaking through aquarium glass with a single strike from this weapon.

Ecology

These aggressive and typically solitary sea creatures spend most of their time hiding in rock formations or burrowing intricate passageways in the sea-bed. They either wait for prey to chance upon them or, unlike most crustaceans, actually hunt, chase and kill living prey. They rarely exit their homes except to feed and relocate, and can be diurnal, nocturnal or crepuscular, depending on the species. Most species live in tropical and subtropical seas (Indian and Pacific Oceans between eastern Africa and Hawaii), although some live in temperate seas.

Classification and the claw

Around 400 species of mantis shrimp have currently been described worldwide; all living species are in the suborder **Unipeltata**. They are commonly separated into two distinct groups determined by the manner of claws they possess:

Squilla mantis, showing the spearing appendages

- *Spearers* are armed with spiny appendages topped with barbed tips, used to stab and snag prey.
- *Smashers*, on the other hand, possess a much more developed club and a more rudimentary spear (which is nevertheless quite sharp and still used in fights between their own kind); the club is used to bludgeon and smash their meals apart. The inner aspect of the dactyl (the terminal portion of the appendage) can also possess a sharp edge, with which the animal can cut prey while it swims.

Both types strike by rapidly unfolding and swinging their raptorial claws at the prey, and are capable of inflicting serious damage on victims significantly greater in size than themselves. In smashers, these two weapons are employed with blinding quickness, with an acceleration of 10,400 g (102,000 m/s^2 or 335,000 ft/s^2) and speeds of 23 m/s from a standing start, about the acceleration of a .22 calibre bullet. Because they strike so rapidly, they generate cavitation bubbles between the appendage and the striking surface. The collapse of these cavitation bubbles produces measurable forces on their prey in addition to the instantaneous forces of 1,500 newtons that are caused by the impact of the appendage against the striking surface, which means that the prey is hit twice by a single strike; first by the claw and then by the collapsing cavitation bubbles that immediately follow. Even if the initial strike misses the prey, the resulting shock wave can be enough to kill or stun the prey.

The snap can also produce sonoluminescence from the collapsing bubble. This will produce a very small amount of light and high temperatures in the range of several thousand kelvins within the collapsing bubble, although both the light and high temperatures are too weak and short-lived to be detected without advanced scientific equipment. The light emission and temperature increase probably have no biological significance but are rather side-effects of the rapid snapping motion. Pistol shrimp produce this effect in a very similar manner.

Smashers use this ability to attack snails, crabs, molluscs and rock oysters; their blunt clubs enabling them to crack the shells of their prey into pieces. Spearers, on the other hand, prefer the meat of softer animals, like fish, which their barbed claws can more easily slice and snag.

Eyes

The front of *Lysiosquillina maculata*, showing the stalked eyes

The midband region of the mantis shrimp's eye is made up of six rows of specialized ommatidia. Four rows carry 16 differing sorts of photoreceptor pigments, 12 for colour sensitivity, others for colour filtering. The mantis shrimp has such good eyes it can perceive both polarized light, and hyperspectral colour vision. Their eyes (both mounted on mobile stalks and constantly moving about independently of each other) are similarly variably coloured, and are considered to be the most complex eyes in the animal kingdom. They permit both serial and parallel analysis of visual stimuli.

Each compound eye is made up of up to 10,000 separate ommatidia of the apposition type. Each eye consists of two flattened hemispheres separated by six parallel rows of highly specialised ommatidia, collectively called the midband, which divides the eye into three regions. This is a design which makes it possible for mantis shrimp to see objects with three different parts of the same eye. In other words, each individual eye possesses trinocular vision and depth perception. The upper and lower hemispheres are used primarily for recognition of forms and motion, not colour vision, like the eyes of many other crustaceans.

A colourful stomatopod, the peacock mantis shrimp, (*Odontodactylus scyllarus*) seen in the Andaman Sea off Thailand

Rows 1–4 of the midband are specialised for colour vision, from ultra-violet to infra-red. The optical elements in these rows have eight different classes of visual pigments and the rhabdom is divided into three different pigmented layers (tiers), each adapted for different wavelengths. The three tiers in rows 2 and 3 are separated by colour filters (intrarhabdomal filters) that can be divided into four distinct classes, two classes in each row. It is organised like a sandwich; a tier, a colour filter of one class, a tier again, a colour filter of another class, and then a last tier. Rows 5–6 are segregated into different tiers too, but have only one class of visual pigment (a ninth class) and are specialised for polarisation vision. They can detect different planes of polarised light. A tenth class of visual pigment is found in the dorsal and ventral hemispheres of the eye.

The midband only covers a small area of about 5°–10° of the visual field at any given instant, but like in most crustaceans, the eyes are mounted on stalks. In mantis shrimps the movement of the stalked eye is unusually free, and can be driven in all possible axes, up to at least 70°, of movement by eight individual eyecup muscles divided into six functional groups. By using these muscles to scan the surroundings with the midband, they can add information about forms, shapes and landscape which cannot be detected by the upper and lower hemisphere of the eye. They can also track moving objects using large, rapid eye movements where the two eyes move independently. By combining different techniques, including saccadic movements, the midband can cover a very wide range of the visual field.

Some species have at least 16 different photoreceptor types, which are divided into four classes (their spectral sensitivity is further tuned by colour filters in the retinas), 12 of them for colour analysis in the different wavelengths (including four which are sensitive to ultraviolet light) and four of them for analysing polarised light. By comparison, humans have only four visual pigments, three dedicated to see colour. The visual information leaving the retina seems to be processed into numerous parallel data streams leading into the central nervous system, greatly reducing the analytical requirements at higher levels.

At least two species have been reported to be able to detect circular polarized light, and in some cases their biological quarter-wave plates perform more uniformly over the entire visual spectrum than any current man-made polarizing optics, the application of which it is speculated could be applied to a new type of optical media that performs even better than the current generation of Blu-ray disc technology.

The species *Gonodactylus smithii* is the only organism known to simultaneously detect the four linear and two circular polarization components required for Stokes parameters, which yield a full description of polarization. It is thus believed to have optimal polarization vision.

Close-up of the trinocular vision of *Pseudosquilla ciliata*

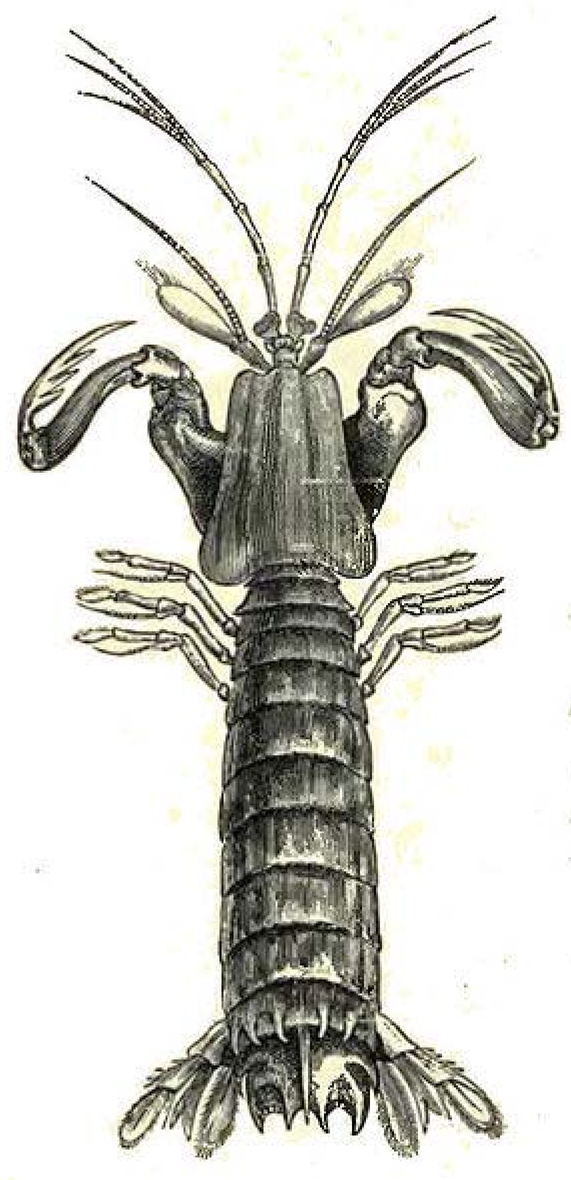
Reasons given for powerful eyesight

The eyes of mantis shrimp may make them able to recognize different types of coral, prey species (which are often transparent or semi-transparent), or predators, such as barracuda, which have shimmering scales. Alternatively, the manner in which mantis shrimp hunt (very rapid movements of the claws) may require very accurate ranging information, which would require accurate depth perception.

The fact that those with the most advanced vision also are the species with the most colourful bodies, suggests the evolution of colour vision has taken the same direction as the peacock's tail.

During mating rituals, mantis shrimp actively fluoresce, and the wavelength of this fluorescence matches the wavelengths detected by their eye pigments. Females are only fertile during certain phases of the tidal cycle; the ability to perceive the phase of the moon may therefore help prevent wasted mating efforts. It may also give mantis shrimp information about the size of the tide, which is important for species living in shallow water near the shore.

Behaviour



An 1896 drawing of a mantis shrimp

Mantis shrimp are long-lived and exhibit complex behaviour, such as ritualised fighting. Some species use fluorescent patterns on their bodies for signalling with their own and maybe even other species, expanding their range of behavioural signals. They can learn and remember well, and are able to recognise individual neighbours with whom they frequently interact. They can recognise them by visual signs and even by individual smell. Many have developed complex social behaviour to defend their space from rivals.

In a lifetime, they can have as many as 20 or 30 breeding episodes. Depending on the species, the eggs can be laid and kept in a burrow, or carried around under the female's tail until they hatch. Also depending on the species, male and female may come together only to mate, or they may bond in monogamous long-term relationships.

In the monogamous species, the mantis shrimp remain with the same partner for up to 20 years. They share the same burrow, and may be able to coordinate their activities. Both sexes often take care of the eggs (biparental care). In *Pullosquilla* and some species in *Nannosquilla*, the female will lay two clutches of eggs, one that the male tends and one that the female tends. In other species, the female will look after the eggs while the male hunts for both of them. Once the eggs hatch the offspring may spend up to three months as plankton.

Although stomatopods typically display the standard locomotion types as seen in true shrimp and lobsters, one species, *Nannosquilla decemspinosa*, has been observed flipping itself into a crude wheel. The species lives in shallow, sandy areas. At low tides, *N. decemspinosa* is often stranded by its short rear legs, which are sufficient for locomotion when the body is supported by water, but not on dry land. The mantis shrimp then performs a forward flip, in an attempt to roll towards the next tide pool. *N. decemspinosa* has been observed to roll repeatedly for 2 metres (6.6 ft), but typically specimens travel less than 1 m (3.3 ft).

Cookery

In Japanese cuisine, the mantis shrimp is eaten boiled as a sushi topping, and occasionally, raw as sashimi; and is called *shako* (蝦蛄).

In Cantonese cuisine, the mantis shrimp is a popular dish known as "pissing shrimp" (瀨尿蝦, Mandarin pinyin: *lài niào xiā*, modern Cantonese: *laaih niuh hā*) because of their tendency to shoot a jet of water when picked up. After cooking, their flesh is closer to that of lobsters than that of shrimp, and like lobsters, their shells are quite hard and require some pressure to crack.

In the Mediterranean countries the mantis shrimp *Squilla mantis* is a common seafood, especially on the Adriatic coasts (canocchia) and the Gulf of Cádiz (galera).

In the Philippines, the mantis shrimp is known as tatampal, hipong-dapa or alupihang-dagat and is cooked and eaten like shrimp.

The usual concerns associated with consuming seafood are an issue with mantis shrimp, as they may dwell in contaminated waters. This is especially true in Hawaii, particularly the Grand Ala Wai Canal in Waikiki, where some have grown unnaturally large.

Aquariums

Many saltwater aquarists keep stomatopods in captivity. These aquarists may play a role in understanding the mysteries of the mantis shrimp. However, mantis shrimp are considered pests by other aquarium hobbyists because many smasher species create burrows in the exoskeletons of dead corals. These coral remains are useful in the marine aquarium trade and are often collected. It is not uncommon for a piece of coral skeleton, also known as live rock, to also ferry a live mantis shrimp into the aquarium that this live rock is placed into. Once inside the tank, they may feed on fish, corals and smaller crustaceans. They are notoriously difficult to catch when established in a well-stocked tank, and although there are accounts of them breaking and destroying glass tanks, such incidents are very rare.

Chapter 12

Amphipoda

Amphipoda Temporal range: Eocene–Recent	
	
Gammarus roeseli	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Superorder:	Peracarida
Order:	**Amphipoda** Latreille, 1816
Suborders	

- Gammaridea
- Caprellidea *or* Corophiidea
- Hyperiidea
- (Ingolfiellidea)

Amphipoda is an order of malacostracan crustaceans with no carapace and generally with laterally compressed bodies. The name *amphipoda* means "different-footed", and refers to the different forms of appendages, unlike isopods, where all the legs are alike.

Of the 7,000 species, 5,500 are classified into one suborder, Gammaridea. The remainder are divided into two or three further suborders. Amphipods range in size from 1 to 340 millimetres (0.039 to 13 in) and are mostly detritivores or scavengers. They live in almost all aquatic environments; 750 species live in caves and the order also includes terrestrial animals and sandhoppers such as *Talitrus saltator*.

Description

Although they are very abundant, widespread and diverse, amphipods do not feature strongly in the public imagination. Thomas Roscoe Rede Stebbing wrote in 1899:

No panegyrist of the Amphipoda has yet been able to evoke anything like popular enthusiasm in their favour. To the generality of observers they are only not repelled because the glance which falls upon them is unarrested, ignores them, is unconscious of their presence.

Anatomy

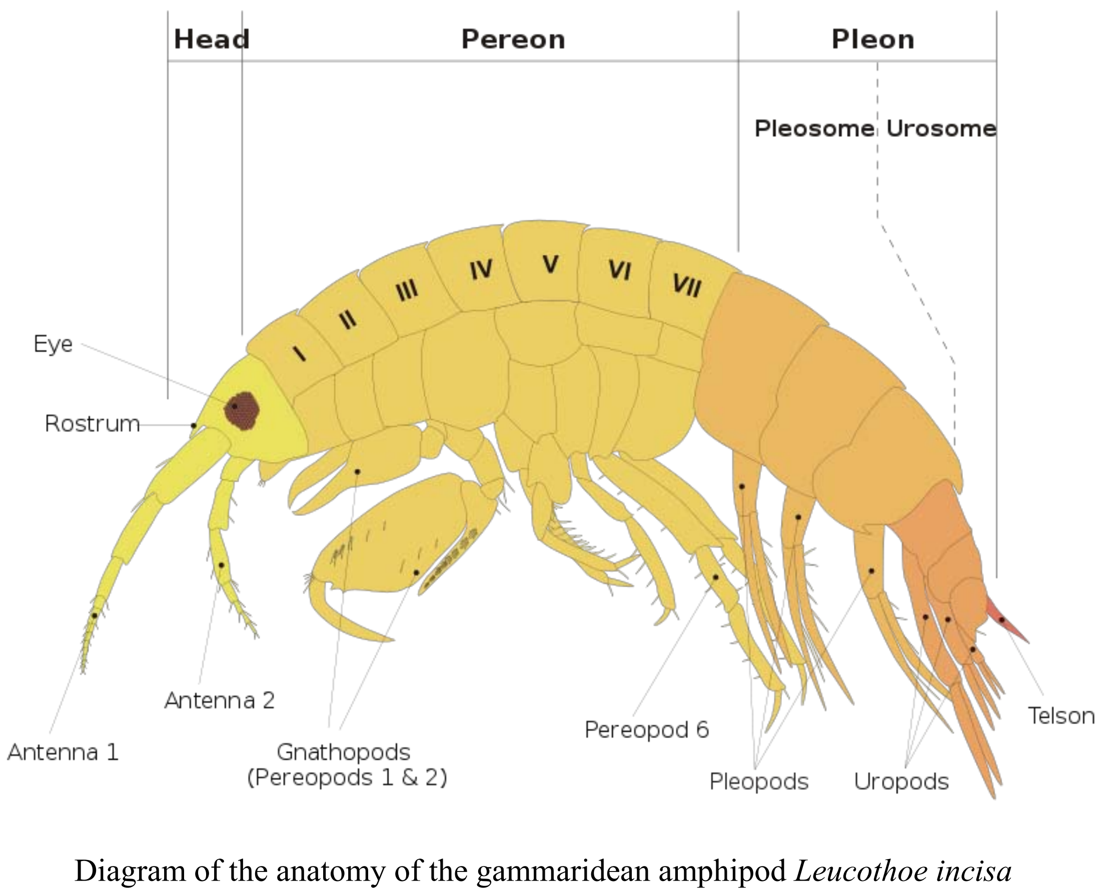


Diagram of the anatomy of the gammaridean amphipod *Leucothoe incisa*

The body of an amphipod is divided into 13 segments, which can be grouped into a head, a thorax and an abdomen.

The head is fused to the thorax, and bears two pairs of antennae and one pair of sessile compound eyes. It also carries the mouthparts, but these are mostly concealed.

The thorax and abdomen are usually quite distinct and bear different kinds of legs; they are typically laterally compressed, and there is no carapace. The thorax bears eight pairs of uniramous appendages, the first of which are used as accessory mouthparts; the next four pairs are directed forwards, and the last three pairs are directed backwards. Gills are present on the thoracic segments, and there is an open circulatory system with a heart, using haemocyanin to carry oxygen in the haemolymph to the tissues. The uptake and excretion of salts is controlled by special glands on the antennae.

The abdomen is divided into two parts: the pleosome which bears swimming legs; and the urosome, which comprises a telson and three pairs of uropods which do not form a tail fan as they do in animals such as true shrimp.

Size

Amphipods are typically less than 10 millimetres (0.39 in) long, but the largest recorded living amphipods were 28 centimetres (11 in) long, and were photographed at a depth of 5,300 metres (17,400 ft) in the Pacific Ocean. Samples from the Atlantic Ocean with a reconstructed length of 34 centimetres (13 in) have been assigned to the same species, *Alicella gigantea*. The smallest known amphipods are less than 1 millimetre (0.04 in) long. The size of amphipods is limited by the availability of dissolved oxygen, such that the amphipods in Lake Titicaca at an altitude of 3,800 metres (12,500 ft) can only grow up to 22 millimetres (0.87 in), compared to lengths of 90 millimetres (3.5 in) in Lake Baikal at 455 metres (1,500 ft).

Reproduction and life cycle

Mature females bear a *marsupium*, or brood pouch, which holds her eggs while they are fertilised, and until the young are ready to hatch. As a female ages, she produces more eggs in each brood. Mortality is around 25%–50% for the eggs. There are no larval stages; the eggs hatch directly into a juvenile form, and sexual maturity is generally reached after 6 moults. Some species have been known to eat their own exuviae after moulting.

Diversity and classification

Amphipods are difficult to identify, due to their small size, and the fact that they must be dissected. As a result, ecological studies and environmental surveys often lump all amphipods together. Carolus Linnaeus described two species of amphipods in the tenth edition of his *Systema Naturae*, which is defined as the starting point for zoological nomenclature. His descriptions (such as that for *Gammarus pulex*: "Cancer macrourus articularis, manibus adactylis, cauda attenuata spinis bifidis") were, however, "very poor", and could apply to "nearly every species of amphipod".

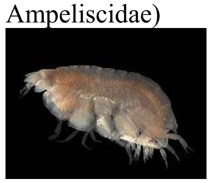
Around 7,000 species of amphipods have so far been described, and placed in three or four suborders. One suborder, Gammaridea, contains more than 5,500 species, including all the freshwater and terrestrial species. Suborder Ingolfiellidea contains around 40 species in 2 families, and the group is sometimes treated among the Gammaridea, rather than as a suborder in their own right.

The classification of the Amphipoda is not yet settled, with the relationships within the suborder Gammaridea suffering the most confusion. The classification given here, from the rank of suborder down to superfamily, follows that of Martin & Davis, except that superfamilies are recognised here within the Gammaridea. An alternative classification proposed by Myers & Lowry in 2003 moved some families from Gammaridea and united them with the Caprellidea to form a larger Corophiidea.

Gammaridea

- Ampeliscoidea
- Crangonyctoidea
- Dexaminoidea
- Eusiroidea
- Gammaroidea
- Hadzioidea
- Iphimedioidea
- Kurioidea
- Leucothoidea
- Liljborgioidea
- Lysianassoidea
- Melphidippoidea
- Oedicerotoidea
- Pardaliscoidea
- Phoxocephaloidea
- Stegocephaloidea
- Stenothoidea
- Synopioidea
- Talitroidea
- Thurstonelloidea

Ampelisca brevicornis (Gammaridea: Ampeliscidae)



Lepidepecreum longicorne (Gammaridea: Lysianassidae)

Caprellidea

- Caprellida
  - Caprelloidea
  - Phtisicoidea
- Cyamida
  - Cyamidae

Hyperiidea

- Physosomata
  - Scinoidea
  - Lanceoloidea
- Physocephalata
  - Vibilioidea
  - Phronimoidea
  - Lycaeopsoidea
  - Platysceloidea

Ingolfiellidea

- Ingolfiellidae
- Metaingolfiellidae

Pariambus typicus (Caprellidea: Caprellidae)

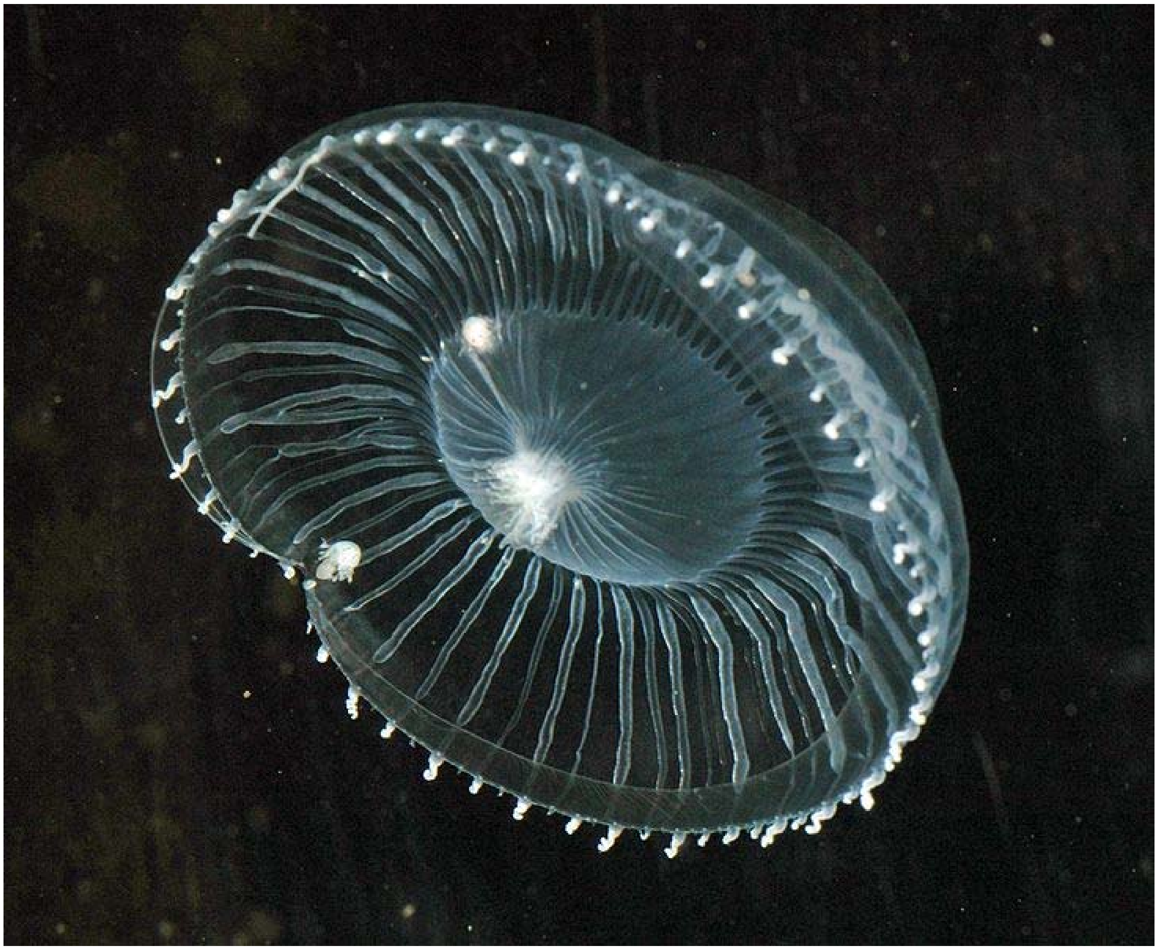
Hyperia sp. (Hyperiidea: Hyperiidae)

Fossil record

Amphipods are thought to have originated in the Lower Carboniferous. Despite the group's age, however, the fossil record of the order Amphipoda is meagre, comprising specimens of 11 species dating back only as far as the Upper Eocene, where they have been found in Baltic amber.

Ecology

Talitrus saltator is an abundant animal of sandy beaches around Europe.



The jellyfish *Aequorea victoria*, with a commensal hyperiid amphipod

Amphipods are found in almost all aquatic environments, from fresh water to water with twice the salinity of sea water. They are almost always an important component of aquatic ecosystems. Most species in the suborder Gammaridea are epibenthic, although they are often collected in plankton samples. Members of the Hyperiidea are all planktonic and marine. Many are symbionts of gelatinous animals, including salps, medusae, siphonophores, colonial radiolarians and ctenophores, and most hyperiids are associated with gelatinous animals during some part of their life cycle.

The landhoppers of the family Talitridae (which also includes semi-terrestrial and marine animals) are terrestrial, living in damp environments such as leaf litter. Landhoppers have a wide distribution in areas that were formerly part of Gondwanaland, but have colonised parts of Europe and North America in recent times.

Around 750 species in 160 genera and 30 families are troglobitic, and are found in almost all suitable habitats, but with their centres of diversity in the Mediterranean Basin, southeastern North America and the Caribbean.

Compared to other crustacean groups, such as the Isopoda, Rhizocephala or Copepoda, relatively few amphipods are parasitic on other animals. The most notable example of parasitic amphipods are the whale lice (family Cyamidae); unlike other amphipods, these are dorso-ventrally flattened, and have large, strong claws, with which they attach themselves to baleen whales. They are the only parasitic crustaceans which cannot swim during any part of their life cycle.

Most amphipods are detritivores or scavengers, with some being grazers of algae, omnivores or predators on small insects and crustaceans. Food is grasped with the front two pairs of legs which are armed with large claws.

Names and etymology

The name *Amphipoda* comes, via the New Latin *amphipoda*, from the Greek roots ἀμφί ("different") and πούς ("foot"), in reference to the two kinds of legs that amphipods possess. This contrasts with the related Isopoda, which have a single kind of leg. Particularly among anglers, amphipods are known as *freshwater shrimp*, *scuds* or *sideswimmers*.

Chapter 13

Woodlouse

Woodlouse	
	
Porcellio scaber (left) and *Oniscus asellus* (centre) living on fallen wood	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Order:	Isopoda
Suborder:	**Oniscidea** Latreille, 1802
Infraorders and sections	

- Diplocheta
- Holoverticata
  - Tylida
  - Microcheta
  - Synocheta

- Crinocheta

A **woodlouse** (known by many common names: see below; plural woodlice) is a crustacean with a rigid, segmented, long exoskeleton and fourteen jointed limbs. Woodlice form the suborder **Oniscidea** within the order Isopoda, with over 3,000 known species.

Woodlice in the genus *Armadillidium* can roll up into an almost perfect sphere as a defensive mechanism, hence some of the common names such as pill bug or roly-poly. Most woodlice, however, cannot do this.

Common names

Common names for woodlice vary throughout the English-speaking world. A number of common names make reference to the fact that some species of woodlice can roll up into a ball. Other names compare the woodlouse to a pig.

Names include: "armadillo bug", "carpenter" (Newfoundland), "cheeselog" (Reading, Berkshire), "cheesy bug" (North-West Kent), "doodlebug" (also used for the larva of an antlion), "pill bug" (usually applied only to the genus *Armadillidium*), "potato bug", "roly-poly", "sow bug", "roll up bug", "chuggypig" or "chucky pig", "slater", "gramersow" (Cornwall), "butcher boy" or "butchy boy" (Australia), and "wood bug" (British Columbia, Canada).

Description and life cycle

The woodlouse has a shell-like exoskeleton, which it must progressively shed as it grows. The moult takes place in two stages; the back half is lost first, followed two or three days later by the front. This method of moulting is different from that of most arthropods, which shed their cuticle in a single process. Metabolic rate is temperature-dependent in woodlice. In contrast to mammals and birds, invertebrates are not "self heating": the external environmental temperature relates directly to their rate of respiration.

A female woodlouse will keep fertilised eggs in a marsupium on the underside of her body until they hatch into small, white offspring. The mother then appears to "give birth" to her offspring.

Woodlice are not generally regarded as a serious household pest as they do not spread disease and do not damage wood or structures; however, their presence can indicate dampness problems.

Pillbugs and pill millipedes

Comparison of the pill bug *Armadillidium vulgare* and the pill millipede *Glomeris marginata*

Pillbugs (woodlice of the family Armadillidiidae) can be confused with pill millipedes. Both of these groups of terrestrial segmented arthropods are about the same size. They live in very similar habitats, and they can both roll up into a ball. Pill millipedes and pillbugs appear superficially similar to the naked eye. This is an example of convergent evolution.

Pill millipedes can be distinguished from woodlice on the basis of having two pairs of legs per body segment instead of one pair like all isopods. Pill millipedes also have thirteen body segments, whereas the woodlouse has eleven. In addition, pill millipedes are smoother, and resemble normal millipedes in overall colouring and the shape of the segments.

Ecology

Environmental extremes

Hemilepistus reaumuri lives in "the driest habitat conquered by any species of crustacean".

Ligia oceanica is aquatic.

Living in a terrestrial environment, woodlice breathe through trachea-like lungs in their paddle-shaped hind legs (pleopods), called pleopodal lungs. Woodlice need moisture because they rapidly lose water by excretion and through their cuticle, and so are usually found in damp, dark places, such as under rocks and logs, although one species, *Hemilepistus reaumuri*, inhabits "the driest habitat conquered by any species of crustacean". They are usually nocturnal and are detritivores, feeding mostly on dead plant matter, although they have been known to feed on cultivated plants, such as ripening strawberries and tender seedlings. Woodlice then recycle the nutrients back into the soil. In artificial environments such as greenhouses where it can be very moist, woodlice may become abundant and damage young plants.

Few woodlice have returned to water. Evolutionary ancient species are amphibious, such as the marine-intertidal sea slater (*Ligia oceanica*), which belongs to family Ligiidae.

Other examples include some *Haloniscus* species from Australia (family Scyphacidae), and in the northern hemisphere several species of Trichoniscidae and *Thailandoniscus annae* (family Styloniscidae). Species for which aquatic life is assumed include *Typhlotricholigoides aquaticus* (Mexico) and *Cantabroniscus primitivus* (Spain).

The specialist predator *Dysdera crocata* feeds exclusively on woodlice.

Woodlice are eaten by a wide range of insectivores, but the only animals known to prey exclusively on woodlice are spiders of the genus *Dysdera*, such as the woodlouse spider *Dysdera crocata*.

British Isles

There are over 40 native or naturalised species of woodlouse in the British Isles, ranging in colour and in size (3–30 millimetres or 0.1–1.2 inches) of which only five are common: *Oniscus asellus* (the common shiny woodlouse), *Porcellio scaber* (the common rough woodlouse), *Philoscia muscorum* (the common striped woodlouse), *Trichoniscus pusillus* (the common pygmy woodlouse), and *Armadillidium vulgare* (the common pill bug).

Classification

Infraorder/Section Diplocheta

- Ligiidae

Infraorder Holoverticata

- Section: Tylida

    - Tylidae

- Section: Microcheta

    - Mesoniscidae

- Section: Synocheta

    - Buddelundiellidae
    - Schoebliidae
    - Styloniscidae
    - Titaniidae
    - Trichoniscidae
    - Tunanoniscidae

- Section: Crinocheta

    - Agnaridae
    - Alloniscidae
    - Armadillidae
    - Armadillidiidae
    - Balloniscidae
    - Bathytropidae
    - Berytoniscidae
    - Cylisticidae
    - Delatorreidae
    - Detonidae
    - Eubelidae
    - Halophilosciidae
    - Olibrinidae
    - Oniscidae
    - Philosciidae
    - Platyarthridae
    - Porcellionidae
    - Pudeoniscidae
    - Rhyscotidae
    - Scleropactidae
    - Scyphacidae
    - Spelaeoniscidae
    - Stenoniscidae
    - Tendosphaeridae
    - Trachelipodidae

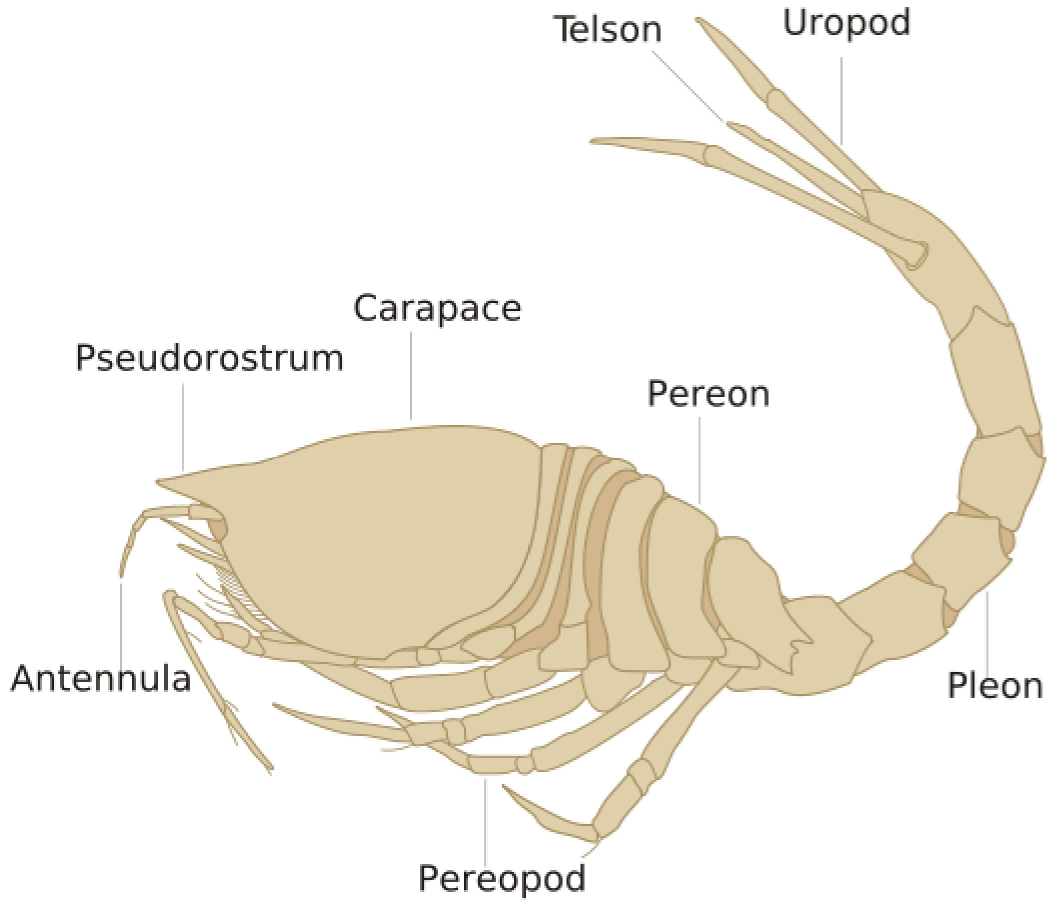
Chapter 14

Cumacea

Cumacea **Temporal range: Mississippian–Recent**	
	
Iphinoe trispinosa	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Superorder:	Peracarida
Order:	**Cumacea** Krøyer, 1846

Cumacea is an order of small marine crustaceans, occasionally called **hooded shrimp**. Their unique appearance and uniform body plan makes them easy to distinguish from other crustaceans.

Anatomy



General body plan of a cumacean

Cumaceans have a strongly enlarged carapace (head shield) and pereon (breast shield), a slim abdomen and a forked tail. The length of most species varies from 1 to 10 millimetres (0.04 to 0.39 in).

The carapace of a typical cumacean is composed of several fused dorsal head parts and the first three somites of the thorax. This carapace encloses the appendages that serve for respiration and feeding. In most species, there are two eyes at the front side of the head shield, often merged into a single eye lobe. The five posterior somites of the thorax form the pereon. The pleon (abdomen) consists of six cylindrical somites.

The first antenna (antennule) has two flagella, the outer flagellum usually being longer than the inner one. The second antenna is strongly reduced in females, and consists of numerous segments in males.

Cumaceans have six pairs of mouthparts: one pair of mandibles, one pair of maxillules, one pair of maxillae and three pairs of maxillipeds.

Ecology

Bodotria scorpioides

Cumaceans are mainly marine crustaceans. However, some species can survive in water with a lower salinity, like brackish water (e.g. estuaries). In the Caspian Sea they even reach some rivers that flow into it. Few species live in the intertidal zone.

Most species live only one year or less, and reproduce twice in their lifetime. Deepsea species have a slower metabolism and presumably live much longer.

Cumaceans feed mainly on microorganisms and organic material from the sediment. Species that live in the mud filter their food, while species that live in sand browse individual grains of sand. In the genus *Campylaspis* and a few related genera, the mandibles are transformed into piercing organs, which can be used for predation on forams and small crustaceans.

Many shallow water species show a diurnal cycle, with males emerging from the sediment at night and swarming to the surface.

Importance

Like Amphipoda, cumaceans are an important food source for many fishes. Therefore, they are an important part of the marine food chain. They can be found on all continents.

Reproduction and development

Pseudocuma longicorne

Cumaceans are a clear example of sexual dimorphism: males and females differ significantly in their appearance. Both sexes have different ornaments (setation, knobs, and ridges) on their carapace. Other differences are the length of the second antenna, the existence of pleopods in males, and the development of a marsupium in females. There are generally more females than males, and females are also larger than their male counterparts.

Cumaceans are *epimorphic*, which means that the number of body segments doesn't change during the different developmental stages. This is a form of incomplete metamorphosis. Females carry the embryos in their marsupium for some time. The larvae leave the marsupium during the so-called *manca* stage, in which they are almost fully grown and only miss their last pair of pereopods.

History of research

The order of Cumacea was already known since 1780, when Ivan Ivanovich Lepekhin described the species *Oniscus scorpioides* (later renamed to *Diastylis scorpioides*).

During that time, many scientists thought that the cumaceans were some kind of larval stage of decapods. In 1846, they were recognized as a separate order by Henrik Nikolaj Krøyer. Twenty-five years later about fifty different species had been described, and currently there are more that 1,400 described species. The German zoologist Carl Wilhelm Erich Zimmer studied the order Cumacea very intensively.

Fossil record

The fossil record of cumaceans is very sparse, but extends back into the Mississippian age.

Taxonomy

Diastylis laevis

Cumaceans belong to the superorder Peracarida, within the class Malacostraca. The order Cumacea is subdivided into 8 to 11 families, about 139 genera, and 1593 species. The families most marine zoologists recognize are:

- Bodotriidae Scott, 1901 (360 species)
- Ceratocumatidae Calman, 1905 (8 species)
- Diastylidae Bate, 1856 (281 species)

- Gynodiastylidae Stebbing, 1912 (103 species)
- Lampropidae Sars, 1878 (90 species)
- Leuconidae Sars, 1878 (121 species)
- Nannastacidae Bate, 1866 (350 species)
- Pseudocumatidae Sars, 1878 (29 species)

Chapter 15

Krill

Euphausiacea	
	
A northern krill (*Meganyctiphanes norvegica*)	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Superorder:	Eucarida
Order:	**Euphausiacea** Dana, 1852
Families and genera	

Euphausiidae

- *Euphausia* Dana, 1852
- *Meganyctiphanes* Holt and W. M. Tattersall, 1905
- *Nematobrachion* Calman, 1905
- *Nematoscelis* G. O. Sars, 1883
- *Nyctiphanes* G. O. Sars, 1883
- *Pseudeuphausia* Hansen, 1910
- *Stylocheiron* G. O. Sars, 1883

- *Tessarabrachion* Hansen, 1911
- *Thysanoessa* Brandt, 1851
- *Thysanopoda* Latreille, 1831

Bentheuphausiidae

- *Bentheuphausia amblyops* G. O. Sars, 1883

Krill is the common name given to the order **Euphausiacea** of shrimp-like marine crustaceans. Also known as **euphausiids**, these small invertebrates are found in all oceans of the world. The common name *krill* comes from the Norwegian word *krill* meaning "young fry of fish", which is also often attributed to other species of fish.

Krill are considered an important trophic connection—near the bottom of the food chain—because they feed on phytoplankton and to a lesser extent zooplankton, converting these into a form suitable for many larger animals for whom krill makes up the largest part of their diet. In the Southern Ocean, one species, the Antarctic krill, *Euphausia superba*, makes up an estimated biomass of over 500,000,000 tonnes (490,000,000 LT; 550,000,000 ST), roughly twice that of humans. Of this, over half is eaten by whales, seals, penguins, squid and fish each year, and is replaced by growth and reproduction. Most krill species display large daily vertical migrations, thus providing food for predators near the surface at night and in deeper waters during the day.

Commercial fishing of krill is done in the Southern Ocean and in the waters around Japan. The total global harvest amounts to 150,000–200,000 tonnes (150,000–200,000 LT; 170,000–220,000 ST) annually, most of this from the Scotia Sea. Most of the krill catch is used for aquaculture and aquarium feeds, as bait in sport fishing, or in the pharmaceutical industry. In Japan and Russia, krill is also used for human consumption and is known as *okiami* (オキアミ?) in Japan.

Taxonomy

Krill belong to the large arthropod subphylum, the Crustacea. The most familiar and largest group of crustaceans, the class Malacostraca, includes the superorder Eucarida comprising the three orders, Euphausiacea or krill, Decapoda (shrimp, lobsters, crabs), and the minuscule Amphionides.

The order Euphasiacea comprises two families. The more abundant Euphausiidae contains ten different genera with a total of 85 species. Of these, the genus *Euphausia* is the largest, with 31 species. The lesser known family, the Bentheuphausiidae, has only one species, *Bentheuphausia amblyops*, a bathypelagic krill living in deep waters below 1,000 metres (3,300 ft). It is considered the most primitive living species of all krill.

Well-known species of the Euphausiidae of commercial krill fisheries include Antarctic krill (*Euphausia superba*), Pacific krill (*Euphausia pacifica*) and Northern krill (*Meganyctiphanes norvegica*).

Phylogeny

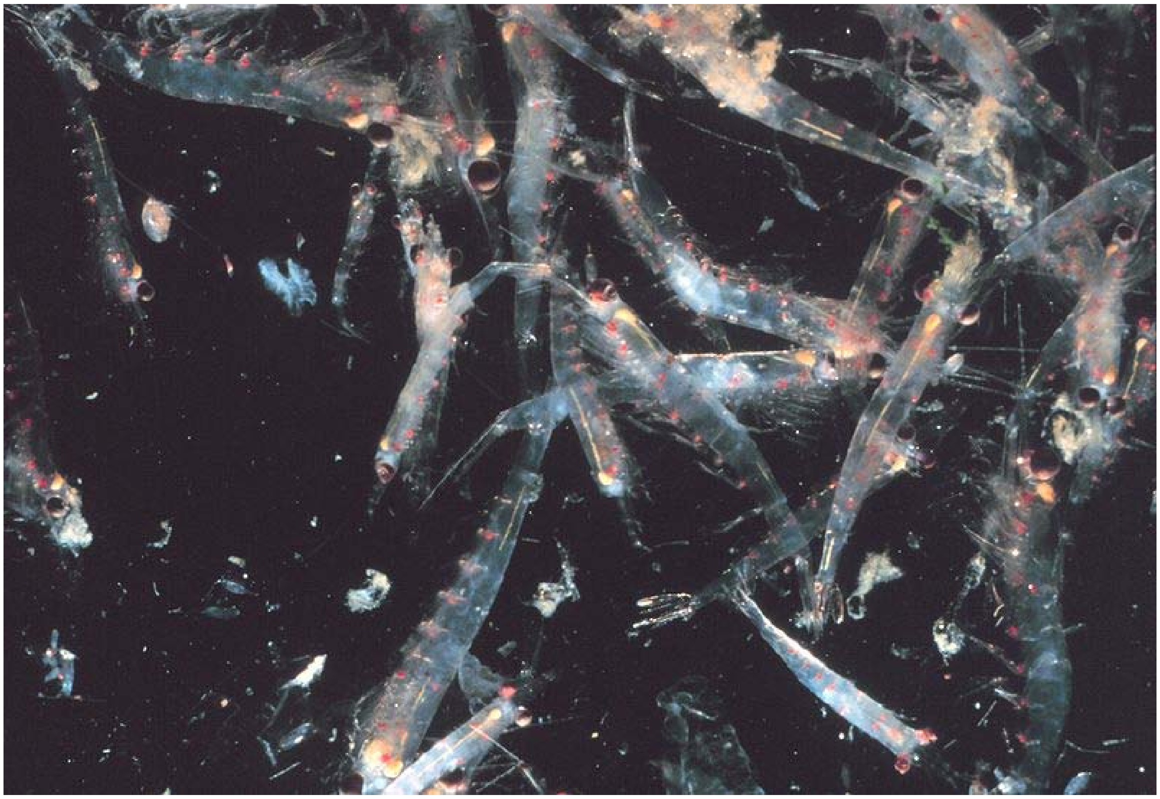
The order Euphausiacea is believed to be monophyletic due to several unique conserved morphological characteristics (autapomorphy) such as the naked filamentous gills or the thin thoracopods. and by molecular studies. There have been many theories of the location of the order Euphausiacea, in fact since the first description of *Thysanopode tricuspide* by Henri Milne-Edwards in 1830, the similarity of their biramous thoracopods had led zoologists to group euphausiids and Mysidacea in the order of Schizopoda, which was split by Johan Erik Vesti Boas in 1883 into two separate orders. Later, William Thomas Calman (1904) ranked the Mysidacea in the Peracarida super-order and euphausiids in Eucarida super-order, although even up to the 1930s the order Schizopoda was advocated. It was later also proposed that order Euphausiacea should be grouped with the Penaeidae (family of prawns) in the Decapoda based on developmental similarities, as noted by Robert Gurney and Isabella Gordon. The reason for this debate is that krill share some morphological features of decapods and others of mysids.

Molecular studies have also no been able to unambiguously group them, possibly due to the lack of many key rare species such as *Bentheuphausia amblyops* in krill and *Amphionides reynaudii* in Eucarida. One study supports Eucarida monophyly (with basal Mysida), another groups Euphausiacea with Mysida (the Schizopoda), while yet another groups Euphausiacea with Hoplocarida.

Timeline

Unusual for crustaceans, no fossil has been found that can be unequivocally assigned to the order Euphausiacea. Some extinct eumalacostracan taxa have been thought to be euphausiaceans such as *Anthracophausia*, *Crangopsis* —now assigned to the Aeschronectida (Hoplocarida)—and *Palaeomysis*. Consequently the dating of the speciation events have been estimated by means of molecular clock methods, which place the last common ancestor of the krill family Euphausiidae (order Euphausiacea minus *Bentheuphausia amblyops*) to have lived in the Lower Cretaceous about 130 million years ago.

Distribution



A krill swarm

Krill occur worldwide in all oceans, although many individual species have endemic or neritic (*i.e.,* coastal) restricted distributions. *Bentheuphausia amblyops*, a bathypelagic species, has a cosmopolitan distribution within its deep-sea habitat.

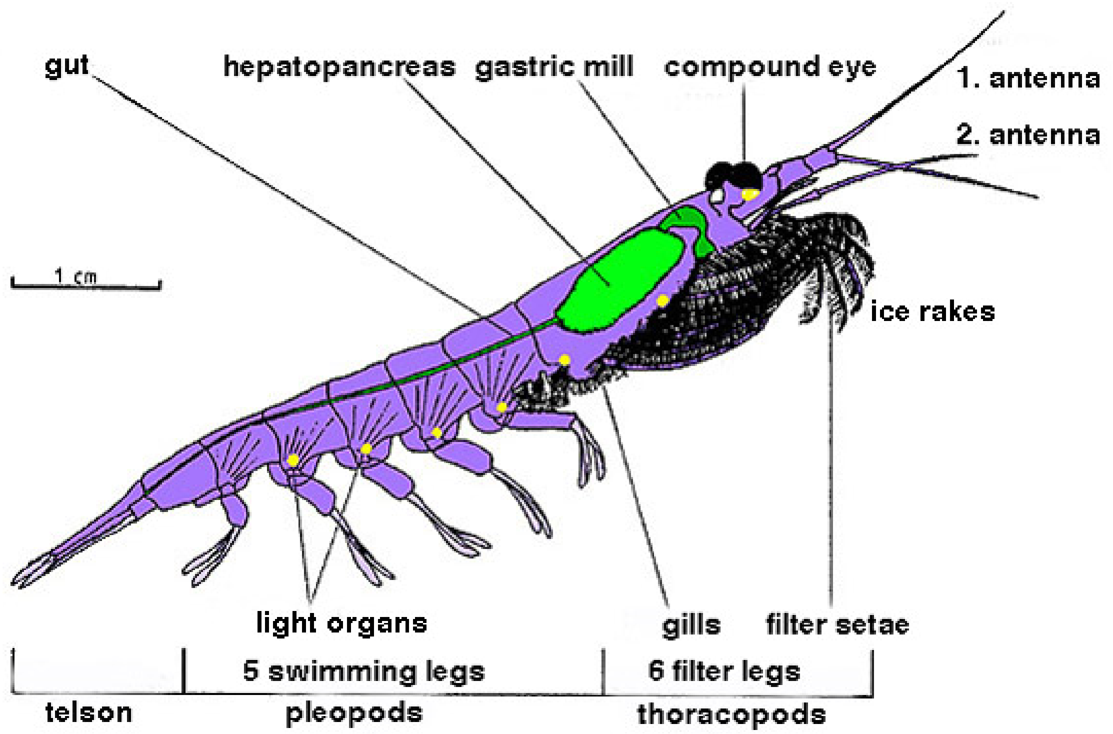
Species of the genus *Thysanoessa* occur in both the Atlantic and Pacific oceans. The Pacific is home to *Euphausia pacifica*. Northern krill occur across the Atlantic from the Mediterranean Sea northward.

Species with neritic distributions include the four species of the genus *Nyctiphanes*. They are highly abundant along the upwelling regions of the California, Humboldt, Benguela, and Canarias current systems. Another species having only neritic distribution is *E. crystallorophias*, which occurs only along the Antarctic coastline (and thus also is endemic to that region).

Species with endemic distributions include *Nyctiphanes capensis*, which occurs only in the Benguela current, *E. mucronata* in the Humboldt current, and the six *Euphausia* species native to the Southern Ocean.

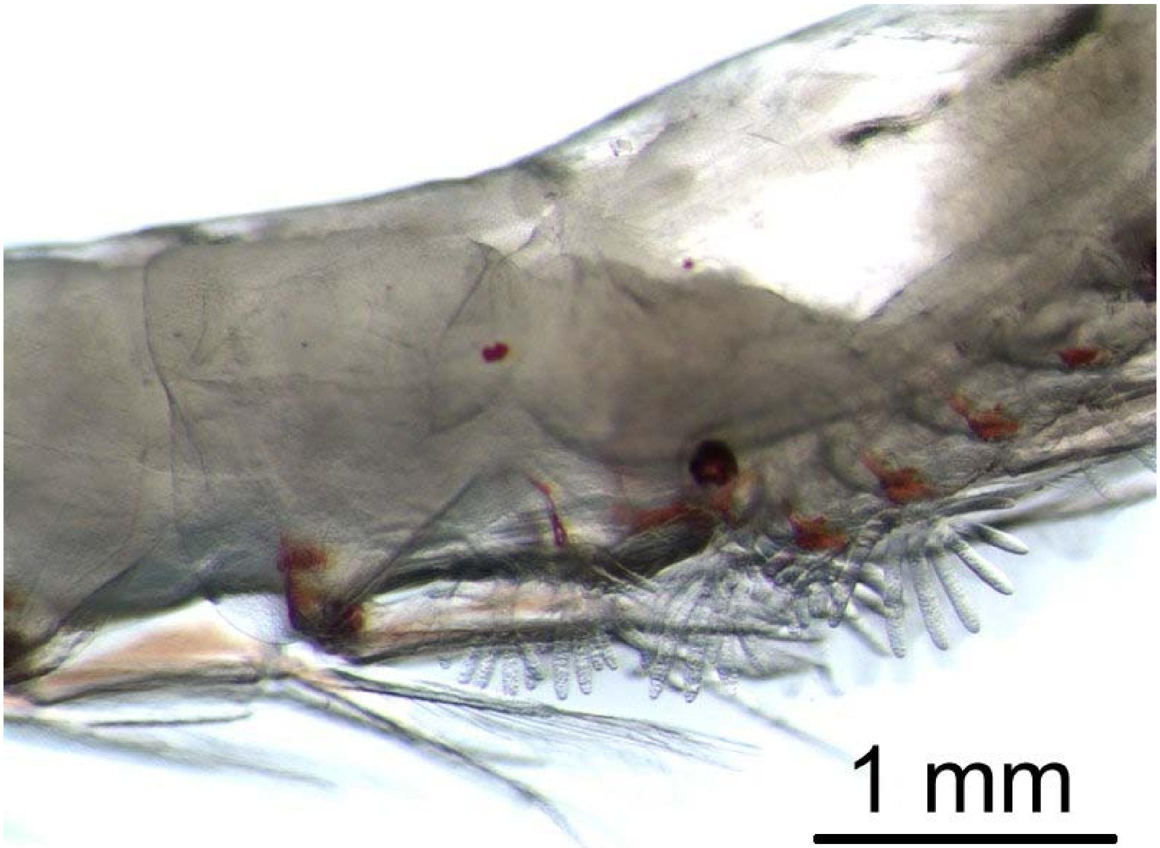
In the Antarctic, seven species are known, one species of the genus *Thysanoessa* (*T. macrura*) and six of the genus *Euphausia*. The Antarctic krill (*Euphausia superba*) commonly lives at depths of as much as 100 m (330 ft), whereas ice krill (*Euphausia* *crystallorophias*) have been recorded at a depth of 4,000 m (13,100 ft), though they commonly live at depths of at most 300–600 m (1,000–2,000 ft). Both are found at latitudes south of 55° S, with *E. crystallorophias* dominating south of 74° S and in regions of pack ice. Other species known in the Southern Ocean are *E. frigida*, *E. longirostris*, *E. triacantha* and *E. vallentini*.

Anatomy and morphology



Krill anatomy explained, using *Euphausia superba* as a model

Krill are crustaceans and have a chitinous exoskeleton made up of three segments: the cephalon (head), the thorax, and the abdomen. The first two segments are fused into one segment, the cephalothorax. This outer shell of krill is transparent in most species. Krill feature intricate compound eyes; some species can adapt to different lighting conditions through the use of screening pigments. They have two antennae and several pairs of thoracic legs called pereiopods or thoracopods, so named because they are attached to the thorax; their number varies among genera and species. These thoracic legs include the feeding legs and the grooming legs. Additionally all species have five swimming legs called pleopods or "swimmerets", very similar to those of a lobster or freshwater crayfish. Most krill are about 1–2 centimetres (0.4–0.8 in) long as adults; a few species grow to sizes on the order of 6–15 centimetres (2.4–5.9 in). The largest krill species is the bathypelagic *Thysanopoda spinicauda*. Krill can be easily distinguished from other crustaceans such as true shrimp by their externally visible gills.



The gills of krill are externally visible.

Many krill are filter feeders: their frontmost appendages, the thoracopods, form very fine combs with which they can filter out their food from the water. These filters can be very fine indeed in those species (such as *Euphausia spp.*) that feed primarily on phytoplankton, in particular on diatoms, which are unicellular algae. However, it is believed that krill are mostly omnivorous. A few species are carnivorous, preying on small zooplankton and fish larvae.

Except for *Bentheuphausia amblyops*, krill are bioluminescent animals having organs called photophores that can emit light. The light is generated by an enzyme-catalysed chemiluminescence reaction, wherein a luciferin (a kind of pigment) is activated by a luciferase enzyme. Studies indicate that the luciferin of many krill species is a fluorescent tetrapyrrole similar but not identical to dinoflagellate luciferin and that the krill probably do not produce this substance themselves but acquire it as part of their diet, which contains dinoflagellates. Krill photophores are complex organs with lenses and focusing abilities, and they can be rotated by muscles. The precise function of these organs is as yet unknown; they might have a purpose in mating, social interaction or orientation. Some researchers (e.g., Lindsay & Latz and Johnsen) have proposed that krill use the light as a form of counter-illumination camouflage to compensate their shadow against the ambient light from above to make themselves less visible to predators from below.

Behaviour

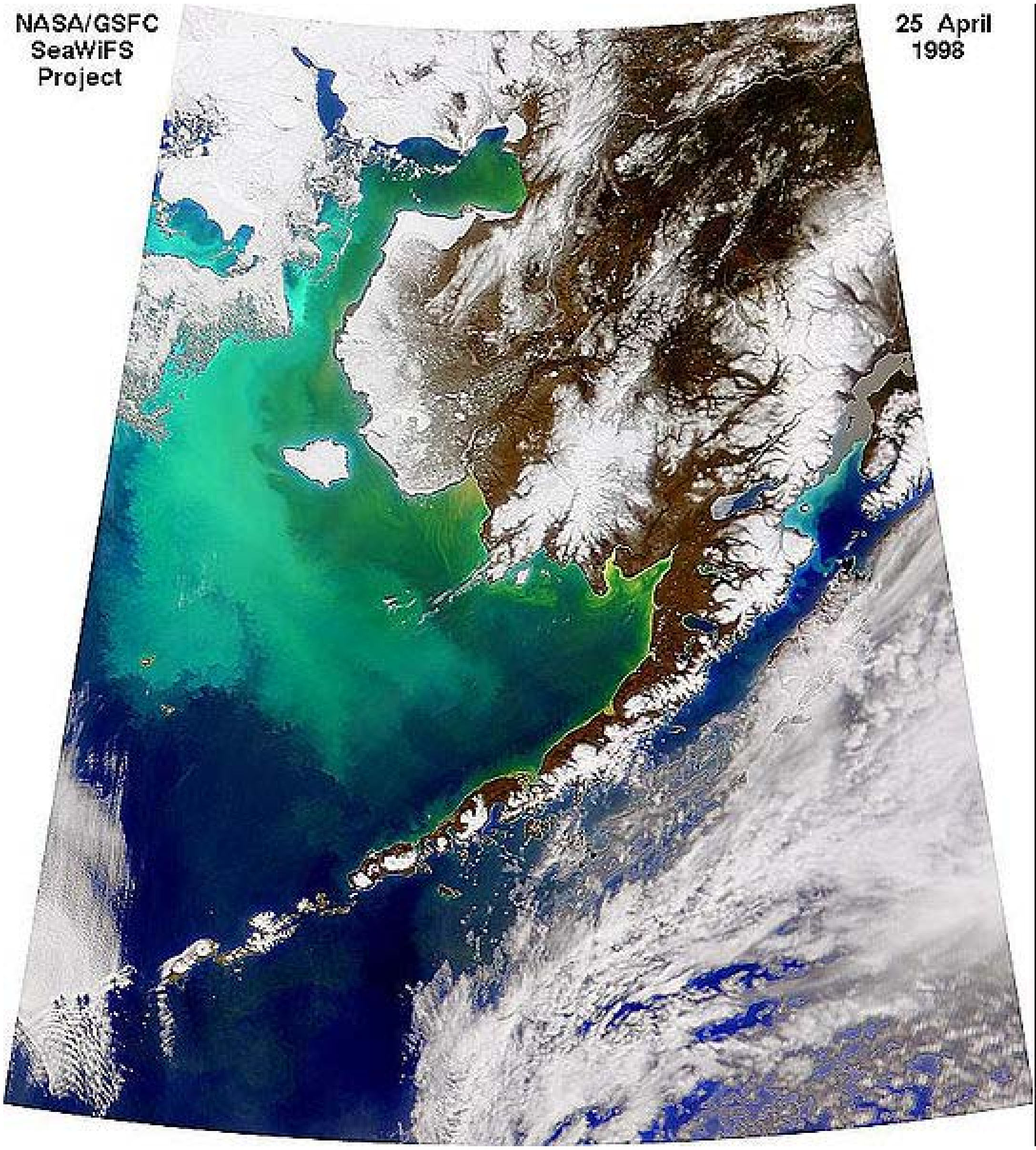
Most krill are swarming animals; the sizes and densities of such swarms vary greatly depending on the species and the region. For *Euphausia superba*, there have been reports of swarms of up to 10,000 to 60,000 individuals per cubic metre. Swarming is a defensive mechanism, confusing smaller predators that would like to pick out single individuals. Krill typically follow a diurnal vertical migration. Until recently it has been assumed that they spend the day at greater depths and rise during the night toward the surface. It has been found that the deeper they go, the more they reduce their activity, apparently to reduce encounters with predators and to conserve energy. Later work suggested that swimming activity in krill varied with stomach fullness. Satiated animals that had been feeding at the surface swim less actively and therefor sink below the mixed layer. As they sink they produce faeces which may mean that they have an important role to play in the Antarctic carbon cycle. Krill with empty stomachs were found to swim more actively and thus head towards the surface. This implies that vertical migration may be a bi or tri daily occurrence. Some species (e.g., *Euphausia superba*, *E. pacifica*, *E. hanseni*, *Pseudeuphausia latifrons*, and *Thysanoessa spinifera*) also form surface swarms during the day for feeding and reproductive purposes even though such behaviour is dangerous because it makes them extremely vulnerable to predators.

Beating pleopods of a swimming Antarctic krill

Dense swarms may elicit a feeding frenzy among fish, birds and mammal predators, especially near the surface. When disturbed, a swarm scatters, and some individuals have even been observed to moult instantaneously, leaving the exuvia behind as a decoy.

Krill normally swim at pace of 5–10 cm/s (2–3 body lengths per second), using their swimmerets for propulsion. Their larger migrations are subject to the currents in the ocean. When in danger, they show an escape reaction called lobstering—flicking their caudal structures, the telson and the uropods, they move backwards through the water relatively quickly, achieving speeds in the range of 10 to 27 body lengths per second, which for large krill such as *E. superba* means around 0.8 m/s (3 ft/s). Their swimming performance has led many researchers to classify adult krill as micro-nektonic life-forms, i.e., small animals capable of individual motion against (weak) currents. Larval forms of krill are generally considered zooplankton.

Ecology and life history



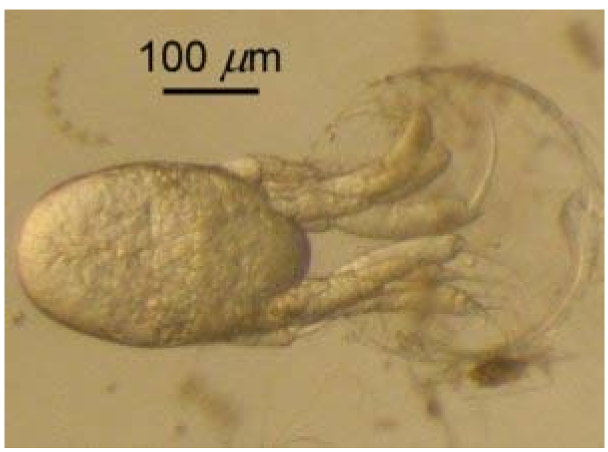
NASA SeaWiFS satellite image of the large phytoplankton bloom in the Bering Sea in 1998

Krill are an important element of the food chain. Antarctic krill feed directly on phytoplankton, converting the primary production energy into a form suitable for consumption by larger animals that cannot feed directly on the minuscule algae. Some species like the Northern krill have a relatively small filtering basket and actively hunt for copepods and larger zooplankton. Many animals feed on krill, ranging from smaller animals like fish or penguins to larger ones like seals and even baleen whales.

Disturbances of an ecosystem resulting in a decline in the krill population can have far-reaching effects. During a coccolithophore bloom in the Bering Sea in 1998, for instance, the diatom concentration dropped in the affected area. Krill cannot feed on the smaller coccolithophores, and consequently the krill population (mainly *E. pacifica*) in that region declined sharply. This in turn affected other species: the shearwater population dropped, and the incident was even thought to have been a reason for salmon not returning to the rivers of western Alaska that season.

Other factors besides predation and food availability can influence the mortality rate in krill populations. As temperatures have risen over the past couple decades, Antarctic sea ice has melted. In this way, climate change poses a threat to krill populations as they feed on algae beneath the ice. There are several single-celled endoparasitoidic ciliates of the genus *Collinia* that can infect different species of krill and cause massive decline in affected populations. Such diseases have been reported for *Thysanoessa inermis* in the Bering Sea and also for *E. pacifica*, *Thysanoessa spinifera*, and *T. gregaria* off the North American Pacific coast. There are also some ectoparasites of the family Dajidae (epicaridean isopods) that afflict krill (and also shrimp and mysids); one such parasite is *Oculophryxus bicaulis*, which has been found on the krill *Stylocheiron affine* and *S. longicorne*. It attaches itself to the eyestalk of the animal and sucks blood from its head; it is believed that it inhibits the reproduction of its host, as none of the afflicted animals found reached maturity.

Life history



A nauplius of *Euphausia pacifica* hatching, emerging backwards from the egg

The general life cycle of krill has been the subject of several studies (e.g., Gurney, 1942 and Mauchline & Fisher, 1969) performed on a variety of species and is thus relatively well understood, although there are minor variations in detail from species to species. After krill hatch from the egg, they go through several larval stages called the *nauplius*, *pseudometanauplius*, *metanauplius*, *calyptopsis*, and *furcilia* stages, each of which is sub-divided into several sub-stages. The pseudometanauplius stage is exclusive to species that lay their eggs within an ovigerous sac: so-called "sac-spawners". The larvae grow and moult multiple times as they develop, shedding their rigid exoskeleton whenever it becomes too small and growing a new one. Smaller animals moult more frequently than larger ones. Up through the metanauplius stage, the larvae are nourished by yolk reserves within their body. Only by the calyptopsis stages has differentiation progressed far enough for them to develop a mouth and a digestive tract, and they begin to feed upon phytoplankton. By that time, the larvae must have reached the photic zone, the upper layers of the ocean where algae flourish, for their yolk reserves are exhausted by then and they would starve otherwise. During the furcilia stages, segments with pairs of swimmerets are added, beginning at the frontmost segments. Each new pair becomes functional only at the next moult. The number of segments added during any one of the furcilia stages may vary even within one species depending on environmental conditions. After the final furcilia stage, the krill emerges in a shape similar to an adult, but it is still an immature juvenile, that only subsequently develops gonads and matures.

During the mating season, which varies depending on the species and the climate, the male deposits a sperm sack at the genital opening (named *thelycum*) of the female. The females can carry several thousand eggs in their ovary, which may then account for as much as one third of the animal's body mass. Krill can have multiple broods in one season, with interbrood periods in the order of days.

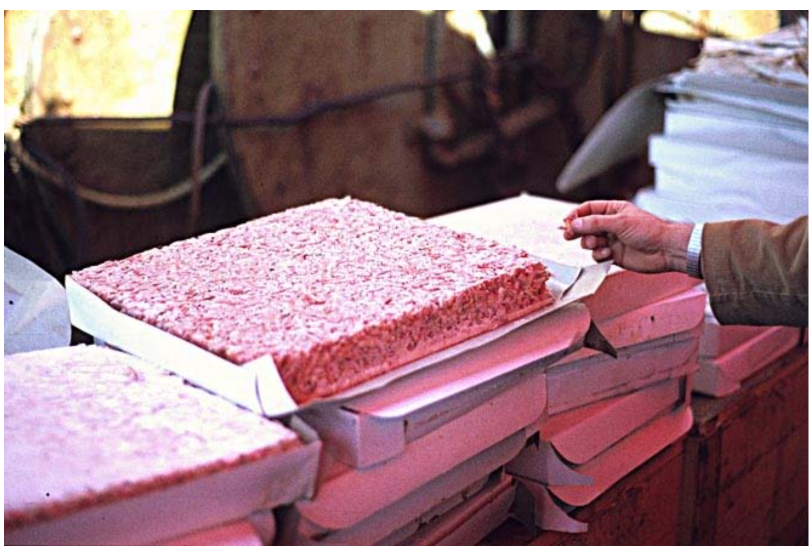
The head of a female krill of the sac-spawning species *Nematoscelis difficilis* with her brood sac. The eggs have a diameter of 0.3–0.4 millimetre (0.012–0.016 in).

There are two types of spawning mechanism. The 57 species of the genera *Bentheuphausia*, *Euphausia*, *Meganyctiphanes*, *Thysanoessa*, and *Thysanopoda* are "broadcast spawners": the female releases the fertilised eggs into the water, where they usually sink into deeper waters, disperse, and are on their own. These species generally hatch in the nauplius 1 stage, but have recently been discovered to hatch sometimes as metanauplius or even as calyptopis stages. The remaining 29 species of the other genera are "sac spawners", where the female carries the eggs with her, attached to the rearmost pairs of thoracopods until they hatch as metanauplii, although some species like *Nematoscelis difficilis* may hatch as nauplius or pseudometanauplius.

Some high-latitude species of krill can live for more than six years (e.g., *Euphausia superba*); others, such as the mid-latitude species *Euphausia pacifica*, live for only two years. Subtropical or tropical species' longevity is still shorter, e.g., *Nyctiphanes simplex*, which usually lives for only six to eight months.

Moulting occurs whenever the animal outgrows its rigid exoskeleton. Young animals, growing faster, moult more often than older and larger ones. The frequency of moulting varies widely from species to species and is, even within one species, subject to many external factors such as the latitude, the water temperature, and the availability of food. The subtropical species *Nyctiphanes simplex*, for instance, has an overall inter-moult period in the range of two to seven days: larvae moult on the average every four days, while juveniles and adults do so on average every six days. For *E. superba* in the Antarctic sea, inter-moult periods ranging between 9 and 28 days depending on the temperature between −1 and 4 °C (30 and 39 °F) have been observed, and for *Meganyctiphanes norvegica* in the North Sea the inter-moult periods range also from 9 and 28 days but at temperatures between 2.5 and 15 °C (37 and 59 °F). *E. superba* is able to reduce its body size when there is not enough food available, moulting also when its exoskeleton becomes too large. Similar shrinkage has also been observed for *E. pacifica*, a species occurring in the Pacific Ocean from polar to temperate zones, as an adaptation to abnormally high water temperatures. Shrinkage has been postulated for other temperate-zone species of krill as well.

Economy



Deep frozen plates of Antarctic krill for use as animal feed and raw material for cooking

Krill has been harvested as a food source for humans (*okiami*) and domesticated animals since the 19th century, in Japan maybe even earlier. Large-scale fishing developed only in the late 1960s and early 1970s, and now occurs only in Antarctic waters and in the seas around Japan. Historically, the largest krill fishery nations were Japan and the Soviet Union, or, after the latter's dissolution, Russia and Ukraine. A peak in krill harvest had been reached in 1983 with more than 528,000 tonnes in the Southern Ocean alone (of which the Soviet Union produced 93%). In 1993, two events led to a drastic decline in krill production: first, Russia abandoned its operations, and second, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) defined maximum catch quotas for a sustainable exploitation of Antarctic krill. The annual catch in Antarctic waters seems to have stabilised around 100,000 tonnes of krill, which is roughly one fiftieth of the CCAMLR catch quota. The main limiting factor is probably the high cost associated with Antarctic operations, although there are some political and legal issues as well. The fishery around Japan appears to have saturated at some 70,000 tonnes.

Experimental small-scale harvesting is being carried out in other areas, for example, fishing for *Euphausia pacifica* off British Columbia and harvesting *Meganyctiphanes norvegica*, *Thysanoessa raschii* and *Thysanoessa inermis* in the Gulf of St. Lawrence. These experimental operations produce only a few hundred tonnes of krill per year. Nicol & Foster consider it unlikely that any large-scale harvesting operations in these areas will be started due to opposition from local fishing industries and conservation groups.

Krill tastes salty and somewhat stronger than shrimp. For mass-consumption and commercially prepared products they must be peeled, because their exoskeleton contains fluorides, which are toxic in high concentrations. There is a small but growing market for krill oil as a dietary supplement ingredient. Two clinical trials have been published; tests included lipid lowering, arthritis pain and function, and C-reactive protein.

Chapter 16

Shrimp

Shrimp Temporal range: Lower Jurassic–Recent	

Heterocarpus ensifer

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Order:	Decapoda
Suborder:	Pleocyemata
Infraorder:	**Caridea** Dana, 1852

Superfamilies

- Alpheoidea
- Atyoidea
- Bresilioidea
- Campylonotoidea
- Crangonoidea
- Galatheacaridoidea
- Nematocarcinoidea
- Oplophoroidea
- Palaemonoidea
- Pandaloidea

- Pasiphaeoidea
- Physetocaridoidea
- Procaridoidea
- Processoidea
- Psalidopodoidea
- Stylodactyloidea

Shrimp are swimming, decapod crustaceans classified in the infraorder Caridea, found widely around the world in both fresh and salt water. Adult shrimp are filter feeding benthic animals living close to the bottom. They can live in schools and can swim rapidly backwards. Shrimp are an important food source for larger animals from fish to whales. They have a high tolerance to toxins in polluted areas, and may contribute to high toxin levels in their predators. Together with prawns, shrimp are widely caught and farmed for human consumption.

Taxonomy

A number of more or less unrelated crustaceans share the word "shrimp" in their common name. Examples are the mantis shrimp and the opossum or mysid shrimp, both of which belong to the same class (Malacostraca) as decapods including shrimp, but constitute two different orders within it, the Stomatopoda and the Mysidacea. *Triops longicaudatus* and *Triops cancriformis* are also popular animals in freshwater aquaria, and are often called shrimp, although they belong instead to the Notostraca, a quite unrelated group.

Biological definition

Shrimp (Caridea), such as *Pandalus borealis*, typically have two pairs of claws, and the second segment of the abdomen overlaps the segments on either side. The abdomen shows a pronounced *caridean bend*.

Prawns (Dendrobanchiata), such as *Penaeus monodon*, typically have three pairs of claws, and even-sized segments on the abdomen. There is no pronounced bend in the abdomen.

The class Malacostraca contains about half of the crustaceans. The members of this class have a primitive body plan that can be described as shrimp-like, consisting of a 5-8-7 body plan. They have a small carapace that encloses the head and the thorax, and have a muscular abdomen for swimming. They also have a thin exoskeleton to maintain a light weight. These general characters are common in all members of the class.

The class can be further divided into the decapods, which are even still divided into the dendrobranchiates (prawns) and the carideans (shrimp and snapping shrimp).

The prawns have sequentially overlapping body segments (segment one covers the segment two, segment two covers segment three, etc), chelate (claw like) first three leg pairs, and have a very basic larval body type.

The shrimps also have overlapping segments, however, in a different pattern (segment two overlaps segments one and three), only the first two leg pairs are chelate, and they have a more complex larval form.

Biologists distinguish the true shrimp from the true prawn because of the differences in their gill structures. The gill structure is lamellar in shrimp but branching in prawns. The easiest practical way to separate true shrimps from true prawns is to examine the second abdominal segment. The second segment of a shrimp overlaps both the first and the third segment, while the second segment of a prawn overlaps only the third segment.

The infraorder Caridea is divided into 16 superfamilies:

- Alpheoidea Rafinesque, 1815
- Atyoidea De Haan, 1849
- Bresilioidea Calman, 1896
- Campylonotoidea Sollaud, 1913
- Crangonoidea Haworth, 1825
- Galatheacaridoidea Vereshchaka, 1997
- Nematocarcinoidea Smith, 1884
- Oplophoroidea Dana, 1852
- Palaemonoidea Rafinesque, 1815
- Pandaloidea Haworth, 1825
- Pasiphaeoidea Dana, 1852
- Physetocaridoidea Chace, 1940a
- Procaridoidea Chace & Manning, 1972
- Processoidea Ortmann, 1896
- Psalidopodoidea Wood-Mason, 1892
- Stylodactyloidea Bate, 1888

A number of extinct genera cannot be placed in any superfamily:

- *Acanthinopus* Pinna, 1974
- *Alcmonacaris* Polz, 2009
- *Bannikovia* Garassino & Teruzzi, 1996
- *Blaculla* Münster, 1839
- *Buergerocaris* Schweigert & Garassino, 2004
- *Gampsurus* von der Marck, 1863
- *Hefriga* Münster, 1839
- *Leiothorax* Pinna, 1974
- *Parvocaris* Bravi & Garassino, 1998
- *Pinnacaris* Garassino & Teruzzi, 1993

Commercial and culinary definition

While in biological terms shrimps and prawns belong to different suborders of Decapoda, they are very similar in appearance. In commercial farming and fisheries, the terms "shrimp" and "prawn" are often used interchangeably. However, recent aquaculture literature increasingly uses the term "prawn" only for the freshwater forms of palaemonids and "shrimp" for the marine penaeids.

In the United Kingdom, the word “prawn” is more common on menus than “shrimp”; while the opposite is the case in North America. The term “prawn” is also loosely used to describe any large shrimp, especially those that come 15 (or fewer) to the pound (such as “king prawns”, yet sometimes known as “jumbo shrimp”). Australia and some other Commonwealth nations follow this British usage to an even greater extent, using the word “prawn” almost exclusively. When Australian comedian Paul Hogan used the phrase, “I'll slip an extra shrimp on the barbie for you” in an American television advertisement, it was intended to make what he was saying easier for his American audience to understand, and was thus a deliberate distortion of what an Australian would typically say.

In Britain very small crustaceans with a brownish shell are called shrimp, and are used to make potted shrimp. They are also used in dishes where they are not the primary ingredient.

Consumption

A fresh catch of brown shrimp, *Crangon crangon*

As with other seafood, shrimp is high in calcium, iodine and protein but low in food energy. A shrimp-based meal is also a significant source of cholesterol, from 122 mg to 251 mg per 100 g of shrimp, depending on the method of preparation. Shrimp consumption, however, is considered healthy for the circulatory system because the lack of significant levels of saturated fat in shrimp means that the high cholesterol content in shrimp actually improves the ratio of LDL to HDL cholesterol and lowers triglycerides.

Shrimp and other shellfish are among the most common food allergens. They are not kosher and thus are forbidden in Jewish cuisine. Shrimp, on the other hand are halal according to some Madh'hab, and therefore are permissible in Islamic cuisine.

Commercial fishing

Double-rigged shrimp trawler hauling in the nets

Common commercial methods for catching shrimp and prawns include otter trawls, cast nets, seines, shrimp baiting and dip netting. Trawling involves the use of a system of nets. In some parts of the Pacific Northwest, fishing with baited traps is also common.

The following table shows the yearly weight of shrimp and prawns captured globally in millions of tonnes:

Production	1999	2000	2001	2002	2003	2004	2005
Million tonnes	3.03	3.09	2.96	2.97	3.55	3.54	3.42

The highest rates of incidental catch of non-target species is associated with shrimp trawling. In 1997, the FAO documented the estimated bycatch and discard levels from shrimp fisheries around the world. They found discard rates as high as 20 pounds for every pound of shrimp, with a world average of 5.7 pounds for every pound of shrimp.

Trawl nets in general, and shrimp trawls in particular, have been identified as sources of mortality for species of finfish and cetaceans. Bycatch is often discarded dead or dying by the time it is returned to the sea, and may alter the ecological balance in discarded regions. Worldwide, shrimp trawl fisheries generate about 2% of the world's catch of fish in weight, but result in more than one third of the global bycatch total.

Farming

Tanks in a shrimp hatchery

A shrimp farm is an aquaculture business for the cultivation of marine shrimp or prawns for human consumption. Commercial shrimp farming began in the 1970s, and production grew steeply, particularly to match the market demands of the United States, Japan and Western Europe. The total global production of farmed shrimp reached more than 1.6 million tonnes in 2003, representing a value of nearly 9 billion U.S. dollars. About 75% of farmed shrimp are produced in Asia, in particular in China, Thailand and in the Philippines (normally shrimp or prawns are caught in lake, river and sea and are not farmed in tanks). The other 25% are produced mainly in Latin America, where Brazil is the largest producer. The largest exporting nation is Thailand.

Marketing

Shrimp are marketed and commercialized with several issues in mind. Most shrimp are sold frozen and marketed based on their categorization of presentation, grading, colour, and uniformity.

Preparation

A steamed tail-on shrimp

Traditional preparation of tiger shrimp curry in Bengali cusine

Preparing shrimp for consumption usually involves removing the head, shell, tail, and "sand vein".

To de-shell a shrimp, the tail is held while gently removing the shell around the body. The tail can be detached completely at this point, or left attached for presentation purposes.

Removing the "vein" (a euphemism for the digestive tract) can be referred to as "deveining", though in fact shrimp do not have any real veins; they have an open circulatory system. The "vein" can be removed by making a shallow cut lengthwise down the outer curve of the shrimp's body, allowing the dark ribbon-like digestive tract to be removed with a pointed utensil. Alternatively, if the tail has been detached, the vein can be pinched at the tail end and pulled out completely with the fingers. The shrimp is then rinsed under cold running water.

Shrimp and prawns are versatile ingredients, and are often used as an accompaniment to fried rice. Common methods of preparation include baking, boiling, frying, and grilling.

Recipes using shrimp form part of the cuisine of many cultures. Strictly speaking, dishes containing scampi should be made from the Norway lobster, a shrimp-like crustacean more closely related to the lobster than shrimp, but in some places it is quite common for large shrimp to be used instead.

Wet shrimp is commonly used as a flavouring and as a soup base in Asian cuisines (such as Thai tom yum goong) while fried shrimp is popular in North America. In Europe, shrimp is very popular, forming a necessary ingredient in Spanish *paella de marisco*, Italian *cacciucco*, Portuguese *caldeirada* and many other seafood dishes. Shrimp curry is very popular in South Asia and Southeast Asia. Shrimp are also found in Latin and Caribbean dishes such as enchiladas and coconut shrimp. Other recipes include jambalaya, okonomiyaki, poon choi and bagoong. Shrimp are also consumed as salad, by frying, with rice, and as shrimp guvec (a dish baked in a clay pot) in the Western and Southern coasts of Turkey.

Life cycle

Most shrimp mature and breed only in a marine habitat, although there are a small number of freshwater species. The females lay 50,000 to 1 million eggs, which hatch after some 24 hours into tiny nauplii. These nauplii feed on yolk reserves within their body and then undergo a metamorphosis into zoeae. This second larval stage feeds in the wild on algae and after a few days metamorphoses again into the third stage to become myses. At this stage the myses already begin to appear like tiny versions of fully developed adults and feed on algae and zooplankton. After another three to four days they metamorphose a final time into postlarvae: young shrimp having all the characteristics of adults. The whole process takes about 12 days from hatching. In the wild, the marine postlarvae then migrate into estuaries, which are rich in nutrients and low in salinity. There they grow and eventually migrate back into open waters when they mature. Most adult shrimp are benthic animals living primarily on the sea floor.

Common shrimp species include pink, brown and snapping shrimp. Depending on the species and location, they grow from about 1.2 to 30 centimetres (0.47 to 12 in) long, and live between one and 6.5 years.

Fossil record

The fossil record of shrimp is sparse, with only 57 exclusively fossil species known. The earliest of these cannot be assigned to any family, but date from the Lower Jurassic and Cretaceous.

Home aquaria

Lysmata debelius, a popular aquarium shrimp

Several types of shrimp are kept in home aquaria. Some are purely ornamental, while others are useful in controlling algae and removing debris. Freshwater shrimp commonly available for aquaria include the Bamboo shrimp, Japanese marsh shrimp (*Caridina multidentata,* also called "Amano shrimp," as their use in aquaria was pioneered by Takashi Amano), cherry shrimp (*Neocaridina heteropoda*), and ghost or glass shrimp (*Palaemonetes* spp.). Popular saltwater shrimp include the cleaner shrimp *Lysmata amboinensis*, the fire shrimp (*Lysmata debelius*) and the harlequin shrimp (*Hymenocera picta*).

Etymology

The term *shrimp* originated around the 14th century with the Middle English *shrimpe*, akin to the Middle Low German *schrempen*, and meaning to contract or wrinkle; and the Old Norse *skorpna*, meaning to shrivel up.

Chapter 17

Lobster

Lobster Temporal range: Valanginian–Recent	

American lobster, *Homarus americanus*

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Order:	Decapoda
Infraorder:	Astacidea
Family:	**Nephropidae**

Dana, 1852

Genera

- *Acanthacaris* Bate, 1888
- *Eunephrops* Smith, 1885
- *Homarinus* Kornfield, Williams & Steneck, 1995
- *Homarus* Weber, 1795
- *Hoploparia* † M'Coy, 1849
- *Jagtia* † Tshudy & Sorhannus, 2000
- *Metanephrops* Jenkins, 1972
- *Nephropides* Manning, 1969
- *Nephrops* Leach, 1814
- *Nephropsis* Wood-Mason, 1873
- *Oncopareia* † Bosquet, 1854
- *Palaeonephrops* † Mertin, 1941
- *Paraclythia* † Fritsch & Kafka, 1887
- *Pseudohomarus* † van Hoepen, 1962
- *Thaumastocheles* Wood-Mason, 1874
- *Thaumastochelopsis* Bruce, 1988
- *Thymopides* Burukovsky & Averin, 1977
- *Thymops* Holthuis, 1974
- *Thymopsis* Holthuis, 1974

Clawed **lobsters** comprise a family (**Nephropidae**, sometimes also **Homaridae**) of large marine crustaceans. Lobsters are economically important as seafood, forming the basis of a global industry that nets more than US$1 billion annually.

Though several groups of crustaceans are known as "lobsters," the clawed lobsters are most often associated with the name. They are also revered for their flavor and texture. Clawed lobsters are not closely related to spiny lobsters or slipper lobsters, which have no claws (*chelae*), or squat lobsters. The closest relatives of clawed lobsters are the reef lobsters and the three families of freshwater crayfish.

The fossil record of clawed lobsters extends back at least to the Valanginian Age of the Cretaceous.

Evolution

Lobsters were more diverse in the Cretaceous period (53 species) than in the Tertiary (16 or 18 species), which has been postulated to have been caused by mass extinction at the K–T boundary. However, diversity rebounded in the Eocene, and it may be that the lower Tertiary diversity was mainly due to lobsters abandoning shelf depths in the late Eocene/early Oligocene, as fossils of deep-dwelling lobsters are rare. It is nevertheless clear that shelf-dwelling lobsters were more diverse during the Cretaceous.

Description

A 3 kg (6.6 lb) European lobster

Lobsters are invertebrates, with a hard protective exoskeleton. Like most arthropods, lobsters must molt in order to grow, which leaves them vulnerable. During the molting process, several species change color. Lobsters have 10 walking legs; the front three pairs bear claws, the first of which are larger than the others. Although, like most other arthropods, lobsters are largely bilaterally symmetrical, they often possess unequal, specialized claws, like the king crab.

Lobster anatomy includes the cephalothorax which fuses the head and the thorax, both of which are covered by the chitinous carapace and the abdomen. The lobster's head bears antennae, antennules, mandibles, the first and second maxillae, and the first, second, and third maxillipeds. Because lobsters live in a murky environment at the bottom of the ocean, they mostly use their antennae as sensors. The lobster eye has a reflective structure above a convex retina. In contrast, most complex eyes use refractive ray concentrators (lenses) and a concave retina. The abdomen includes swimmerets and its tail is composed of uropods and the telson.

Lobsters, like snails and spiders, have blue blood due to the presence of haemocyanin, which contains copper. (In contrast, mammals and many other animals have red blood from iron-rich haemoglobin.) Lobsters possess a green hepatopancreas, called the tomalley by chefs, which functions as the animal's liver and pancreas.

In general, lobsters are 25–50 centimetres (10–20 in) long and move by slowly walking on the sea floor. However, when they flee, they swim backwards quickly by curling and uncurling their abdomen. A speed of 5 metres per second (11 mph) has been recorded. This is known as the caridoid escape reaction.

Longevity

Recent research suggests that lobsters may not slow down, weaken, or lose fertility with age. In fact, older lobsters are more fertile than younger lobsters. This longevity may be due to telomerase, an enzyme that repairs DNA sequences of the form "TTAGGG". This sequence is often referred to as the telomeres of the DNA. It has been argued that lobsters may exhibit negligible senescence and some scientists have claimed that they could effectively live indefinitely, barring injury, disease, capture, etc.; however, this claim is highly speculative. Their undoubted longevity allows them to reach impressive sizes. According to the Guinness World Records, the largest lobster was caught in Nova Scotia, Canada, and weighed 20.15 kilograms (44.4 lb).

Symbion

Animals of the genus *Symbion*, the only member of the animal phylum Cycliophora, live exclusively on lobster gills and mouthparts.

Ecology

Lobsters are found in all oceans. They live on rocky, sandy, or muddy bottoms from the shoreline to beyond the edge of the continental shelf. They generally live singly in crevices or in burrows under rocks.

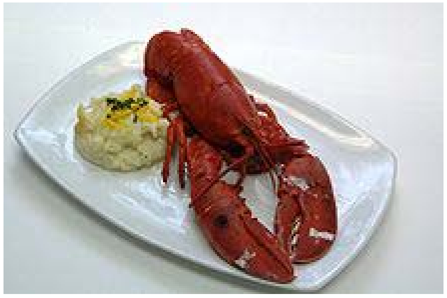
Lobsters are omnivores, and typically eat live prey such as fish, mollusks, other crustaceans, worms, and some plant life. They scavenge if necessary, and may resort to cannibalism in captivity; however, this has not been observed in the wild. Although lobster skin has been found in lobster stomachs, this is because lobsters eat their shed skin after molting.

Lobster

Nutritional value per 100 g (3.5 oz)

Energy	410 kJ (98 kcal)
Carbohydrates	0 g
Sugars	0 g
Dietary fibre	0 g
Fat	0.59 g
saturated	0.107 g
monounsaturated	0.091 g
polyunsaturated	0.16 g
Protein	20.5 g
Thiamine (Vit. B_1)	0 mg (0%)
Riboflavin (Vit. B_2)	4 mg (267%)
Niacin (Vit. B_3)	4 mg (27%)
Pantothenic acid (B_5)	2 mg (40%)
Vitamin B_6	4 mg (308%)
Folate (Vit. B_9)	2 μg (1%)
Vitamin C	0 mg (0%)
Calcium	6 mg (1%)
Iron	2 mg (16%)
Magnesium	8 mg (2%)
Phosphorus	15 mg (2%)
Potassium	0 mg (0%)
Zinc	15 mg (150%)

Percentages are relative to US recommendations for adults.



Steamed whole lobster, with claws cracked and tail split

A dish including a European lobster, Dubrovnik

Japanese lobster served in butter sauce

Lobster recipes include Lobster Newberg and Lobster Thermidor. Lobster is used variously, for example in soup, bisque, lobster rolls, and cappon magro. Lobster meat may be dipped in clarified butter, resulting in a sweetened flavour.

Cooks boil live lobsters in water or steam. The lobster simmers for seven minutes for the first pound and three minutes for each additional pound.

According to the United States Food and Drug Administration (FDA), the mean level of mercury in American lobster is 0.31 ppm.

History

In North America, the American lobster did not achieve popularity until the mid-19th century, when New Yorkers and Bostonians developed a taste; not until the invention of a special vessel, the lobster smack, did a commercial fishery flourish. Prior to this time, lobster was considered a mark of poverty or as a food for indentured servants or lower members of society in Maine, Massachusetts and the Canadian Maritimes, and servants specified in employment agreements that they would not eat lobster more than twice per week. American lobster was initially deemed worthy of being used as fertilizer or fish bait, and it was not until well into the twentieth century that it was viewed as more than a low-priced canned staple food.

Caught lobsters are graded as new-shell, hard-shell and old-shell and, because lobsters that have recently shed their shells are the most delicate, there is an inverse relationship between the price of American lobster and its flavor. New-shell lobsters have paper-thin shells and a worse meat-to-shell ratio, but what meat exists is very sweet. However, the lobsters are so delicate that even transport to Boston almost kills them, making the market for new-shell lobsters strictly local to the fishing towns where they are offloaded. Hard-shell lobsters with firm shells but with less sweet meat can survive shipping to Boston, New York and even Los Angeles so command a higher price than new-shell lobsters. Meanwhile, old-shell lobsters, which have not shed since the previous season and have a coarser flavor, can be air-shipped anywhere in the world and arrive alive, making them the most expensive. One seafood guide notes that an eight dollar lobster dinner at a restaurant overlooking fishing piers in Maine is consistently delicious, while "the eighty-dollar lobster in a three-star Paris restaurant is apt to be as much about presentation as flavor."

Animal welfare issues

The most common way of killing a lobster is by placing it, live, in boiling water, or by splitting: severing the body in half, lengthwise. Lobsters may also be killed or rendered insensate immediately before boiling through a stab into the brain, in the belief that this will stop suffering. However, a lobster's brain operates from not one but several ganglia and disabling only the frontal ganglion does not usually result in death or unconsciousness. The boiling method is illegal in some places, such as in Reggio Emilia, Italy, where offenders face fines of up to €495.

Fishery and aquaculture

Fishing boats in Yarmouth, Nova Scotia

Lobsters are caught using baited, one-way traps with a color-coded marker buoy to mark cages. Lobster is fished in water between 1 and 500 fathoms (2 and 900 m), although some lobsters live at 2,000 fathoms (3,700 m). Cages are of plastic-coated galvanized steel or wood. A lobster fisher may tend as many as 2,000 traps. Around the year 2000, due to overfishing and high demand, lobster farming expanded. As of 2008, no lobster farming operation had achieved commercial success.

Species

Metanephrops japonicus

Nephropsis rosea

This list contains all extant species in the family Nephropidae:

- *Acanthacaris caeca*
- *Acanthacaris tenuimana*
- *Eunephrops bairdii*
- *Eunephrops cadenasi*
- *Eunephrops luckhursti*
- *Eunephrops manningi*
- *Homarinus capensis* — Cape lobster
- *Homarus americanus* — American lobster
- *Homarus gammarus* — European lobster
- *Metanephrops andamanicus* — Andaman lobster
- *Metanephrops arafurensis*
- *Metanephrops armatus*
- *Metanephrops australiensis* — Australian scampi
- *Metanephrops binghami* — Caribbean lobster
- *Metanephrops boschmai* — bight lobster
- *Metanephrops challengeri* — New Zealand scampi
- *Metanephrops formosanus*
- *Metanephrops japonicus* — Japanese lobster
- *Metanephrops mozambicus*
- *Metanephrops neptunus*
- *Metanephrops rubellus*
- *Metanephrops sagamiensis*

- *Metanephrops sibogae*
- *Metanephrops sinensis* — China lobster
- *Metanephrops thomsoni*
- *Metanephrops velutinus*
- *Nephropides caribaeus*
- *Nephrops norvegicus* — Norway lobster
- *Nephropsis acanthura*
- *Nephropsis aculeata* — Florida lobsterette
- *Nephropsis agassizii*
- *Nephropsis atlantica*
- *Nephropsis carpenteri*
- *Nephropsis ensirostris*
- *Nephropsis hamadai*
- *Nephropsis holthuisii*
- *Nephropsis macphersoni*
- *Nephropsis malhaensis*
- *Nephropsis neglecta*
- *Nephropsis occidentalis*
- *Nephropsis rosea*
- *Nephropsis serrata*
- *Nephropsis stewarti*
- *Nephropsis suhmi*
- *Nephropsis sulcata*
- *Thymopides grobovi*
- *Thymops birsteini*
- *Thymopsis nilenta*

Chapter 18

Crayfish

Crayfish Temporal range: Mesozoic–Recent	
	
Northern koura, *Paranephrops planifrons* (Parastacidae)	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Order:	Decapoda
Suborder:	Pleocyemata
Infraorder:	Astacidea
Superfamily:	**Astacoidea** Latreille, 1802 **Parastacoidea** Huxley, 1879
Families	

Astacoidea

- Astacidae

- Cambaridae

Parastacoidea

- Parastacidae

Crayfish, **crawfish**, or **crawdads** – members of the superfamilies **Astacoidea** and **Parastacoidea** – are freshwater crustaceans resembling small lobsters, to which they are related. They breathe through feather-like gills and are found in bodies of water that do not freeze to the bottom; they are also mostly found in brooks and streams where there is fresh water running, and which have shelter against predators. Most crayfish cannot tolerate polluted water, although some species such as the invasive *Procambarus clarkii* are more hardy. Crayfish feed on living and dead animals and plants.

In Australia, New Zealand and South Africa, the term *crayfish* or *cray* generally refers to a saltwater spiny lobster, of the genus *Jasus* that is indigenous to much of southern Oceania, while the freshwater species are usually called *yabby* or *koura*, from the indigenous Australian and Māori names for the animal respectively. An exception is the Murray crayfish found on the Murray River.

The study of crayfish is called **astacology**.

Names

The name "crayfish" comes from the Old French word *escrevisse* (Modern French *écrevisse*) from Old Frankish **krebitja* (cf. crab), from the same root as *crawl*. The word has been modified to "crayfish" by association with "fish" (folk etymology). The largely American variant "crawfish" is similarly derived.

Some kinds of crayfish are known locally as lobsters, **crawdads**, **mudbugs**, and yabbies. In the Eastern United States, "crayfish" is more common in the north, while "crawdad" is heard more in central and western regions, and "crawfish" further south, although there are considerable overlaps.

Anatomy

A crayfish in its burrow

The body of a decapod crustacean, such as a crab, lobster, or prawn, is made up of nineteen body segments grouped into two main body parts, the cephalothorax and the abdomen. Each segment may possess one pair of appendages, although in various groups these may be reduced or missing. On average, crayfish grow to 17.5 centimetres (6.9 in) in length, but some grow larger.

Geographical distribution and classification

Austropotamobius pallipes, Astacidae

Procambarus clarkii, Cambaridae

Cherax sp., Parastacidae

There are three families of crayfish, two in the northern hemisphere and one in the southern hemisphere. The southern-hemisphere (Gondwana-distributed) family Parastacidae lives in South America, Madagascar and Australasia, and is distinguished by the lack of the first pair of pleopods. Of the other two families, members of the Astacidae live in western Eurasia and western North America and members of the family Cambaridae live in eastern Asia and eastern North America.

Australasia has over 100 species in a dozen genera. Many of the better-known Australian crayfish are of the genus *Cherax*, and include the marron (*Cherax tenuimanus*), red-claw crayfish (*Cherax quadricarinatus*), yabby (*Cherax destructor*) and western yabby (*Cherax preissii*). The world's largest freshwater crayfish, *Astacopsis gouldi*, which can achieve a mass of up to 5 kilograms (11 lb), is found in the rivers of northern Tasmania.

Madagascar has an endemic genus, *Astacoides*, containing seven species.

Europe is home to seven species of crayfish in the genera *Astacus* and *Austropotamobius*.

Cambaroides is native to Japan and eastern mainland Asia.

North America

The greatest diversity of crayfish species is found in south-eastern North America, with over 330 species in nine genera, all in the family Cambaridae. A further genus of astacid crayfish is found in the Pacific Northwest and the headwaters of some rivers east of the Continental Divide. Many crayfish are also found in lowland areas where the water is abundant in calcium and oxygen rises from underground springs.

Crayfish were introduced purposely into a few Arizona reservoirs and other bodies of water decades ago, primarily as a food source for sport fish. They have since dispersed beyond those original sites.

Fossil record

Fossil records of crayfish older than 30 million years are rare, but fossilised burrows have been found from strata as old as the late Palaeozoic or early Mesozoic. The oldest records of the Parastacidae are in Australia, and are 115 million years old.

Crayfish plague

Some crayfish suffer from a disease called crayfish plague. This is caused by the water mould *Aphanomyces astaci*. Species of the genus *Astacus* are particularly susceptible to infection, allowing the more resistant signal crayfish to invade parts of Europe. Crayfish plague is not indigenous to Europe, rather it was brought there when North American species of crayfish were introduced.

Uses

Bait

Crayfish are commonly sold and used as bait, either live or with only the tail meat, and are good at attracting channel catfish, largemouth bass, pike and muskellunge. Sometimes the claws are removed so that the crayfish don't stop fish from biting the hook. Crayfish also easily fall off the hook, so casting should be slow.

The result of using crayfish as bait has led to various ecological problems at times. According to a report prepared by Illinois State University, on the Fox River and Des Plaines River watershed, "The rusty crayfish (used as bait) has been dumped into the water and its survivors outcompete the native clearwater crayfish". This situation has been repeated elsewhere, as the crayfish bait eliminates native species.

As zebra mussels have also been known to attach themselves to the crayfish bait, this is one of the ways it has spread to different waterways.

Food

Boiled crawfish, in Louisiana

Crayfish are eaten all over the world. Like other edible crustaceans, only a small portion of the body of a crayfish is edible. In most prepared dishes, such as soups, bisques and étouffées, only the tail portion is served. At crawfish boils or other meals where the entire body of the crayfish is presented, other portions may be eaten.

Claws of larger boiled specimens are often pulled apart to access the meat inside. Another favourite is to suck the head of the crayfish, as seasoning and flavour can collect in the fat of the boiled interior. A popular double entendre laden phrase heard around crawfish season in Louisiana derives from this practice: "suck the head; pinch the tail".

A common myth is that a crawfish with a straight tail died before it was boiled and is not safe to eat. In reality, crawfish that died before boiling can have curled tails as well as straight, as can those that were alive, and may very well be fine to eat. Boiled crawfish which died before boiling are safe to eat if they were kept chilled before boiling and were not dead for a long time. (This does not mean that a sack of crawfish that are all dead should be boiled.) A much better test than the straight tail as to the edibility of any crawfish is the tail meat itself; if it is mushy, it is usually an indication that it should be avoided.

Like all crustaceans, crayfish are not kosher because they are aquatic animals that do not have both fins and scales. They are therefore not eaten by observant Jews.

Scandinavia

Crayfish is a popular dish in Sweden and Finland, and is by tradition primarily consumed during the fishing season in August. The boil is typically flavored with salt, sugar, ale, and large quantities of the flowers of the dill plant. While most Americans eat them warm, the Swedish and Finnish normally eat them cold. The catch of domestic freshwater crayfish, *Astacus astacus*, and even of a transplanted American species, *Pacifastacus leniusculus*, is very limited, and to satisfy demand, the majority of what is consumed has to be imported. Sales depended on imports from Turkey for several decades, but after a decline in supply, China and the United States are today the biggest sources of import.

France

In France, dishes with a base or garnish of crayfish (*écrevisse*) are frequently given the suffix *à la Nantua*.

Spain

In Spain, crayfish is called *cangrejo de río* (lit. "river crab"). They used to be widely consumed, especially in Castile and León and Aragon, but over-fishing and the introduction of non-native crayfish species (e.g. *Procambarus clarkii*, commonly called *cangrejo americano*) lead to a dramatic decline in crayfish population. Nowadays they remain as a seasonal delicacy, usually stewed in tomato sauce, although fishing the native crayfish is strictly forbidden since the species is nearly extinct. Instead of the native crayfish, it is common to fish *Procambarus clarkii* or *Pacifastacus leniusculus*, also present in most of the Spanish rivers.

United States

Louisiana supplies 98% of the crayfish (referred to locally as crawfish) harvested in the United States. In 1987, Louisiana produced 90% of the crayfish in the world, 70% of which were consumed locally. About 70%–80% of crayfish produced in Louisiana are *Procambarus clarkii* (red swamp crawfish), with the remaining 20%–30% being *Procambarus zonangulus* (white river crawfish).

Louisiana crawfish are usually boiled live in a large pot with heavy seasoning (salt, cayenne pepper, lemon, garlic, bay leaves, etc.) and other items such as potatoes, corn on the cob, onions, garlic, mushrooms and sausage. There are many differing methods used to season a crawfish boil, and an equal number of opinions on which one is correct. They are generally served at a gathering known as a crawfish boil. Other popular dishes in the Cajun and Creole cuisines of Louisiana include crawfish étouffée, fried crawfish, crawfish pie, crawfish dressing, crawfish bread and crawfish beignets.

Mexico

The Mexican crayfish is named locally as acocil and was a very important nutrition source of the ancient Mexican Aztec culture; now this kind of crayfish is consumed (mainly boiled) and prepared with typically Mexican sauces or condiments in central and southern Mexico.

Nigeria

Crayfish are usually smoked, and occasionally sun-dried, and they form an indispensable food item in the diet of the people of the entire southern states in particular and Nigeria as a whole. It is the core of Nigerian cooking.

China

The culinary popularity of crayfish swept across mainland China in the late 1990s. Crayfish is generally served with Mala flavour (a combined flavour of Sichuan pepper and hot chili) or otherwise plainly steamed whole, to be eaten with a preferred sauce. In Beijing, the *ma la* flavoured crayfish (麻辣小龙虾) is shortened to "ma xiao" (麻小) and is often enjoyed with beer in a hot mid-summer evening.

Pets

Procambarus clarkii in a freshwater aquarium

Crayfish are kept as pets in freshwater aquariums. They prefer foods like shrimp pellets or various vegetables, but will also eat tropical fish food, regular fish food, algae wafers, and even small fish that can be captured by their claws, such as goldfish or minnows. Their disposition towards eating almost anything will also cause them to consume most aquarium plants in a fish tank.

When keeping a crayfish as a pet, it is suggested they are provided with a hiding space. At night, some fish become less energetic and settle to the bottom. The crayfish might see this as a chance for an easy meal, or a threat, and injure or kill the fish with its claws. Crayfish are effective scavengers and will consume fish carcasses. They sometimes will consume their old exoskeleton after it has molted.

Since crayfish are accustomed to being in ponds or rivers, they will have a tendency to shift gravel around on the bottom of the tank, creating mounds or trenches to emulate a burrow. Crayfish will often try to climb out of the tank, especially if an opening exists at the top that they can fit through. Crayfish kept as pets in the United States from local waters are usually kept with bluegill or bass, rather than goldfish or other tropical or subtropical fish.

However, most species of dwarf crayfish, such as *Cambarellus patzcuarensis*, will not destructively dig or eat live aquarium plants. They are also relatively non-aggressive and can even be kept safely with dwarf shrimp. Because of their very small size of 1.5 inches (38 mm) or less, some fish are often a threat to the crayfish rather than the other way around.

In some nations, such as the United Kingdom, United States, Australia, and New Zealand, imported alien crayfish are a danger to local rivers. The three species commonly imported to Europe from the Americas are *Orconectes limosus*, *Pacifastacus leniusculus* and *Procambarus clarkii*. Crayfish may spread into different bodies of water because specimens captured for pets in one river are often released into a different catchment. There is a potential for ecological damage when crayfish are introduced into non-native bodies of water (e.g., crayfish plague in Europe).