Malacostraca

(Class of Crustacean)

Cornelius Robert

First Edition, 2012

ISBN 978-81-323-4182-6

Published by:
White Word Publications
4735/22 Prakashdeep Bldg,
Ansari Road, Darya Ganj,
Delhi - 110002
Email: info@wtbooks.com

Table of Contents

Chapter 1

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.

Fossil record

The first malacostracans appeared in the Early Cambrian, when animals belonging to the Phyllocarida appeared.

Chapter 2

Crab

Crabs **Temporal range: Jurassic–Recent**	

Liocarcinus vernalis

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Order:	Decapoda
Suborder:	Pleocyemata
Infraorder:	**Brachyura** Linnaeus, 1758

Sections & subsections

- Dromiacea
- Raninoida
- Cyclodorippoida
- Eubrachyura
    - Heterotremata
    - Thoracotremata

True **crabs** are decapod crustaceans of the infraorder **Brachyura**, which typically have a very short projecting "tail" or where the reduced abdomen is entirely hidden under the thorax. Many other animals with similar names – such as hermit crabs, king crabs, porcelain crabs, horseshoe crabs and crab lice – are not true crabs.

Evolution

Gecarcinus quadratus, a land crab from Central and South America

Crabs are generally covered with a thick exoskeleton, and armed with a single pair of chelae (claws). Crabs are found in all of the world's oceans, while many crabs live in fresh water and on land, particularly in tropical regions. Crabs vary in size from the pea crab, a few millimetres wide, to the Japanese spider crab, with a leg span of up to 4 metres (13 ft).

About 850 species of crab are freshwater, terrestrial or semi-terrestrial species; they are found throughout the world's tropical and semi-tropical regions. They were previously thought to be a monophyletic group, but are now believed to represent at least two distinct lineages, one in the Old World and one in the New World.

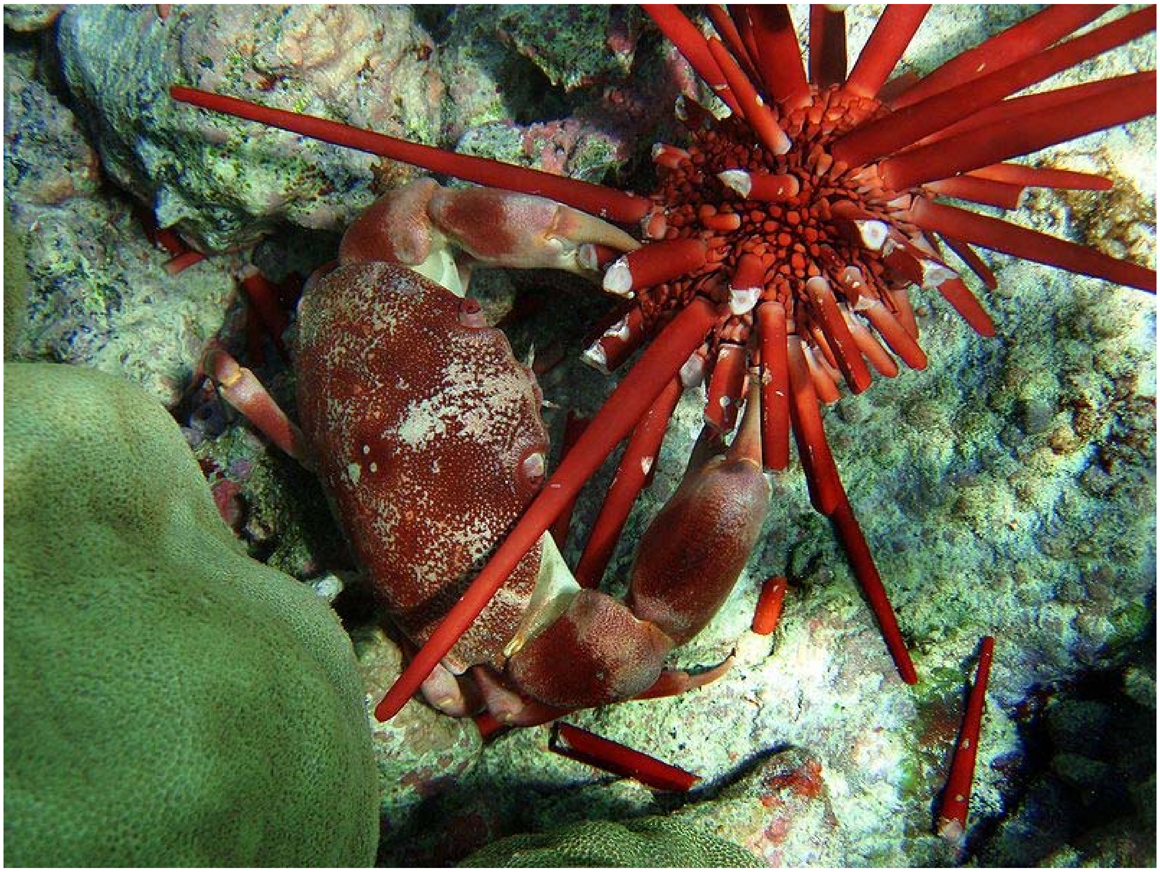
The earliest unambiguous crab fossils date from the Jurassic, although Carboniferous *Imocaris*, known only from its carapace, may be a primitive crab. The radiation of crabs in the Cretaceous and afterward may be linked either to the break-up of Gondwana or to the concurrent radiation of bony fish, crabs' main predators.

Sexual dimorphism

The underside of a male (top) and a female (bottom) individual of *Pachygrapsus marmoratus*, showing the difference in shape of the abdomen

Crabs often show marked sexual dimorphism. Males often have larger claws, a tendency which is particularly pronounced in the fiddler crabs of the genus *Uca* (Ocypodidae). In fiddler crabs, males have one claw which is greatly enlarged and which is used for communication, particularly for attracting a mate. Another conspicuous difference is the form of the pleon (abdomen); in most male crabs, this is narrow and triangular in form, while females have a broader, rounded abdomen. This is due to the fact that female crabs brood fertilised eggs on their pleopods.

Behaviour



Carpilius convexus consuming *Heterocentrotus trigonarius* in Hawaii

Crabs typically walk sideways (a behaviour which gives us the word *crabwise*). This is because of the articulation of the legs which makes a sidelong gait more efficient. However, some crabs prefer to walk forwards or backwards, including raninids, *Libinia emarginata* and *Mictyris platycheles*.. Some crabs, notably the Portunidae and Matutidae, are also capable of swimming.

Crabs are mostly active animals with complex behaviour patterns. They can communicate by drumming or waving their pincers. Crabs tend to be aggressive towards one another and males often fight to gain access to females. On rocky seashores, where nearly all caves and crevices are occupied, crabs may also fight over hiding holes.

Crabs are omnivores, feeding primarily on algae, and taking any other food, including molluscs, worms, other crustaceans, fungi, bacteria and detritus, depending on their availability and the crab species. For many crabs, a mixed diet of plant and animal matter results in the fastest growth and greatest fitness.

Crabs are known to work together to provide food and protection for their family, and during mating season to find a comfortable spot for the female to release her eggs.

Human consumption

Fisheries

Fishermen sorting edible crabs at Fionnphort, Scotland

Crabs make up 20% of all marine crustaceans caught, farmed, and consumed worldwide, amounting to 1½ million tonnes annually. One species accounts for one fifth of that total: *Portunus trituberculatus*. Other commercially important taxa include *Portunus pelagicus*, several species in the genus *Chionoecetes*, the blue crab (*Callinectes sapidus*), *Charybdis spp.*, *Cancer pagurus*, the Dungeness crab (*Metacarcinus magister*) and *Scylla serrata*, each of which yields more than 20,000 tonnes annually.

Pain

Live crabs are often boiled. In 2005, Norwegian scientists concluded that lobsters cannot feel pain. However, later research suggests that crustaceans are indeed able to feel and remember pain.

Classification

The infraorder Brachyura contains 6,793 species in 93 families, as many as the remainder of the Decapoda. The evolution of crabs is characterised by an increasingly robust body, and a reduction in the abdomen. Although many other groups have undergone similar processes, carcinisation is most advanced in crabs. The telson is no longer functional in crabs, and the uropods are absent, having probably evolved into small devices for holding the reduced abdomen tight against the sternum.

In most decapods, the gonopores (sexual openings) are found on the legs. However, since crabs use the first two pairs of pleopods (abdominal appendages) for sperm transfer, this arrangement has changed. As the male abdomen evolved into a narrower shape, the gonopores have moved towards the midline, away from the legs, and onto the sternum. A similar change occurred, independently, with the female gonopores. The movement of the female gonopore to the sternum defines the clade Eubrachyura, and the later change in the position of the male gonopore defines the Thoracotremata. It is still a subject of debate whether those crabs where the female, but not male, gonopores are situated on the sternum, form a monophyletic group.

Superfamilies

Dromia personata (Dromiacea: Dromiidae)

Ranina ranina (Raninoida: Raninidae)

Corystes cassivelaunus (Heterotremata: Corystidae)

Ocypode quadrata (Thoracotremata: Ocypodidae)

Numbers of extant and extinct (†) species are given in brackets. The superfamily Eocarcinoidea, containing *Eocarcinus* and *Platykotta*, was formerly thought to contain the oldest crabs; it is now considered part of the Anomura.

- **Section Dromiacea**
  - Dakoticancroidea (6†)
  - Dromioidea (147, 85†)
  - Glaessneropsoidea (45†)
  - Homolodromioidea (24, 107†)
  - Homoloidea (73, 49†)
- **Section Raninoida** (46, 196†)
- **Section Cyclodorippoida** (99, 27†)
- **Section Eubrachyura**
  - **Subsection Heterotremata**
  - Aethroidea (37, 44†)
  - Bellioidea (7)
  - Bythograeoidea (14)
  - Calappoidea (101, 71†)
  - Cancroidea (57, 81†)
  - Carpilioidea (4, 104†)
  - Cheiragonoidea (3, 13†)
  - Corystoidea (10, 5†)

- Componocancroidea (1†)
- Dairoidea (4, 8†)
- Dorippoidea (101, 73†)
- Eriphioidea (67, 14†)
- Gecarcinucoidea (349)
- Goneplacoidea (182, 94†)
- Hexapodoidea (21, 25†)
- Leucosioidea (488, 113†)
- Majoidea (980, 89†)
- Orithyioidea (1)
- Palicoidea (63, 6†)
- Parthenopoidea (144, 36†)
- Pilumnoidea (405, 47†)
- Portunoidea (455, 200†)
- Potamoidea (662, 8†)
- Pseudothelphusoidea (276)
- Pseudozioidea (22, 6†)
- Retroplumoidea (10, 27†)
- Trapezioidea (58, 10†)
- Trichodactyloidea (50)
- Xanthoidea (736, 134†)
- **Subsection Thoracotremata**
- Cryptochiroidea (46)
- Grapsoidea (493, 28†)
- Ocypodoidea (304, 14†)
- Pinnotheroidea (304, 13†)

Cultural influences

Both the constellation Cancer and the astrological sign Cancer are named after the crab, and depicted as a crab. John Bevis first observed the Crab Nebula and its resemblance to the animal in 1731. The Crab pulsar lies at the centre of the nebula.

The Moche people of ancient Peru worshipped nature, especially the sea, and often depicted crabs in their art. In Greek mythology, Karkinos was a crab that came to the aid of the Lernaean Hydra as it battled Heracles.

Chapter 3

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

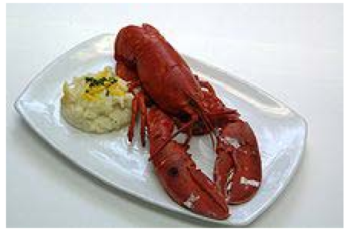
Lobsters are found in all oceans. They live on rocky, sandy, or muddy bottoms from the shoreline to beyond the edge of the continental shelf. They generally live singly in crevices or in burrows under rocks.

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%)



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 4

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

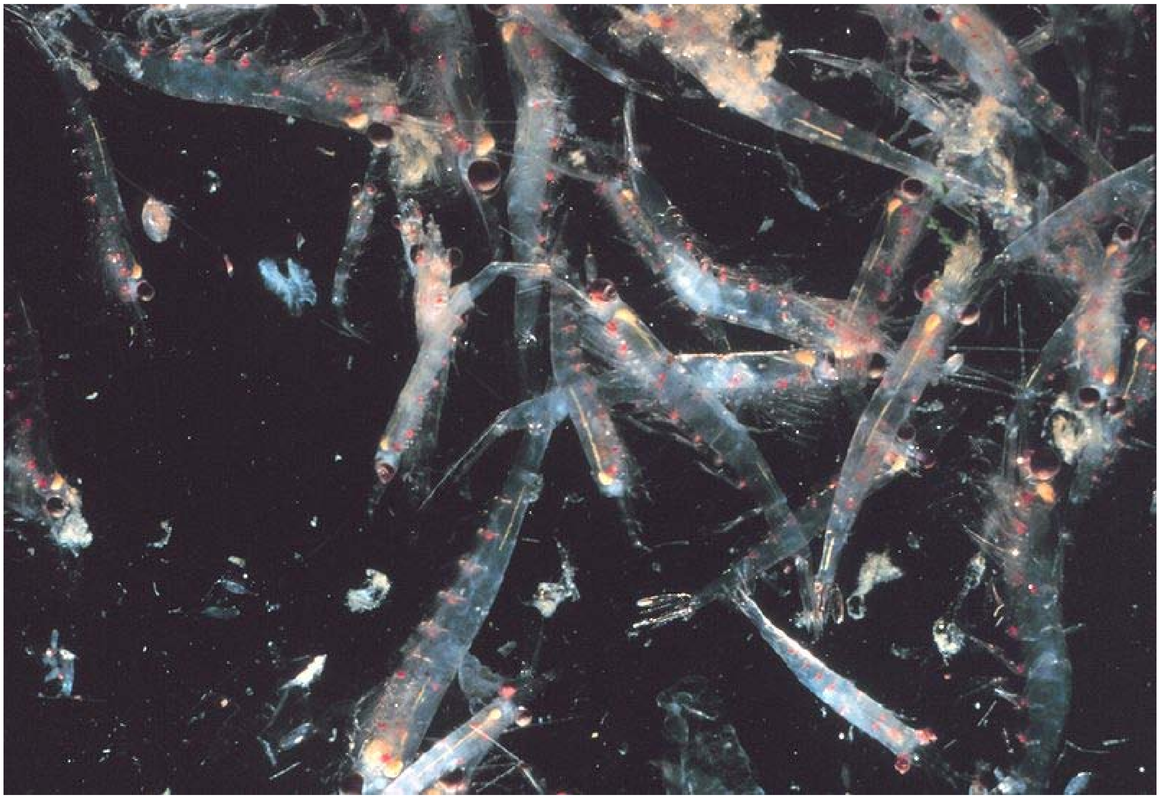
The order Euphausiacea is believed to be monophyletic due to several unique conserved morphological characteristics (autapomorphy) such as the naked filamentous gills or the thin thoracopods. and by molecular studies. There have been many theories of the location of the order Euphausiacea, in fact since 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.

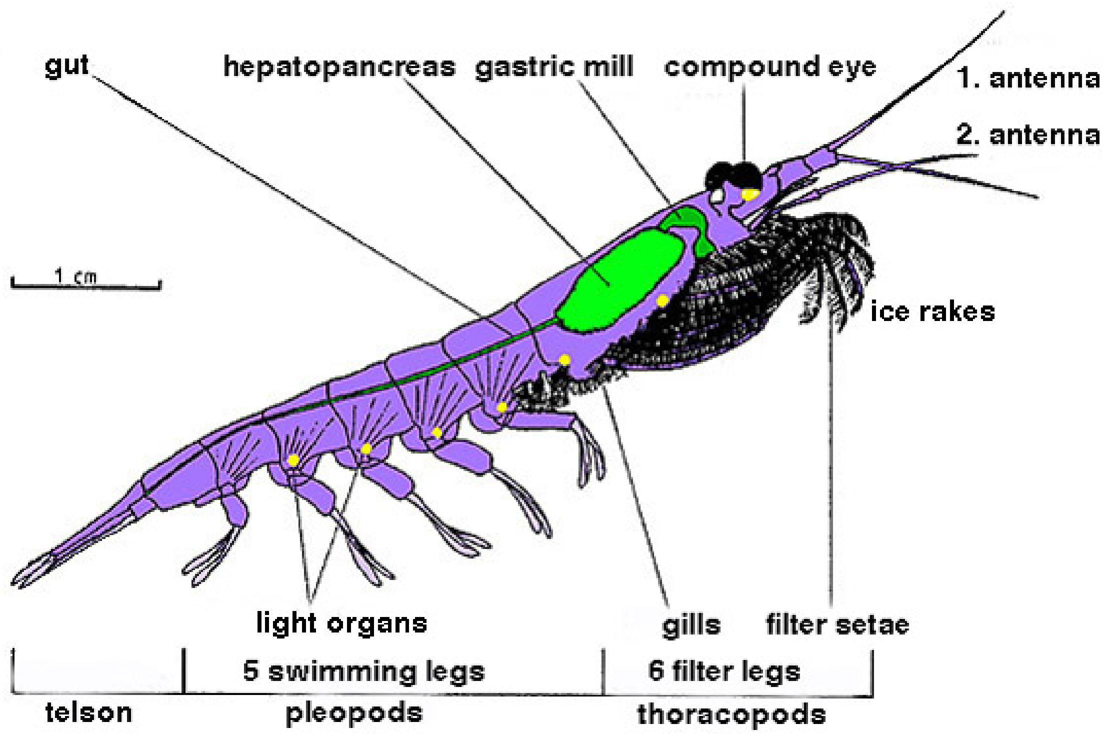
Species of the genus *Thysanoessa* occur in both the Atlantic and Pacific oceans. The Pacific is home to *Euphausia pacifica*. Northern krill occur across the Atlantic from the Mediterranean Sea northward.

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.

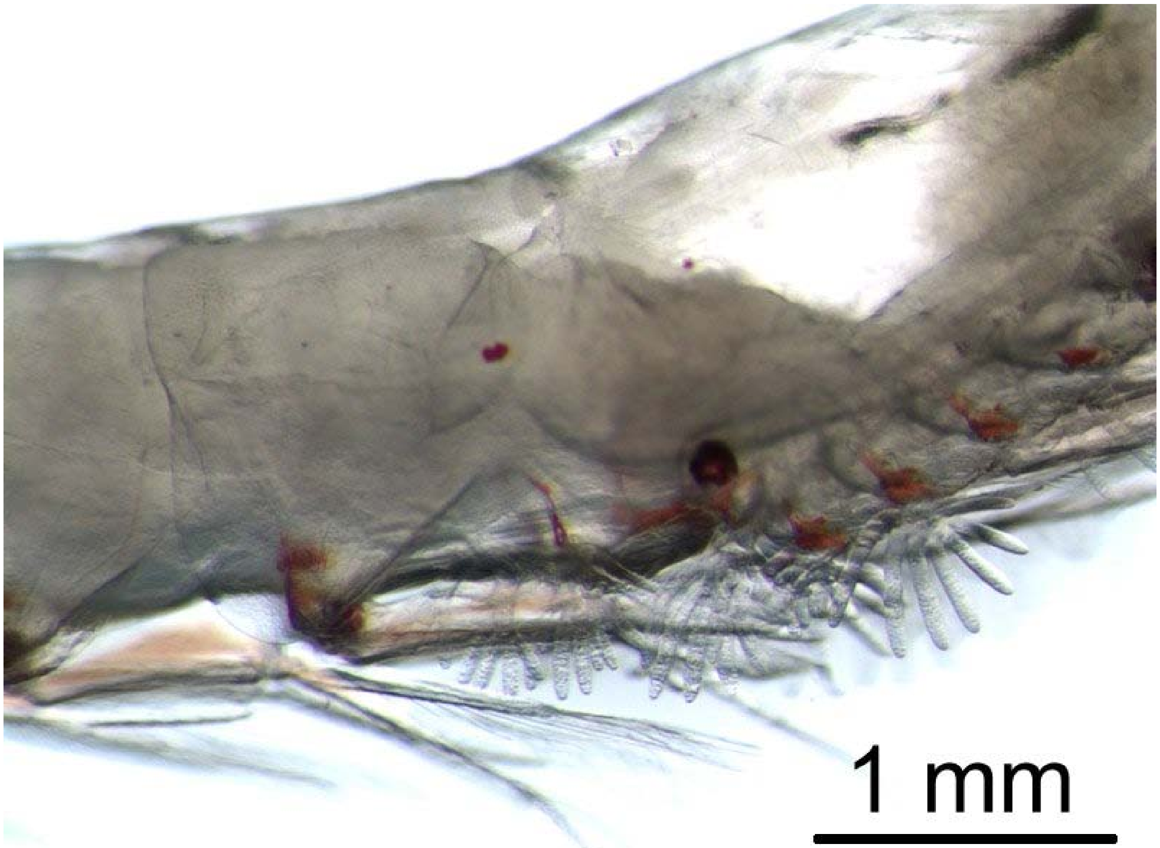
In the Antarctic, seven species are known, one species of the genus *Thysanoessa* (*T. macrura*) and six of the genus *Euphausia*. The Antarctic krill (*Euphausia superba*) commonly lives at depths of as much as 100 m (330 ft), whereas ice krill (*Euphausia* *crystallorophias*) have been recorded at 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

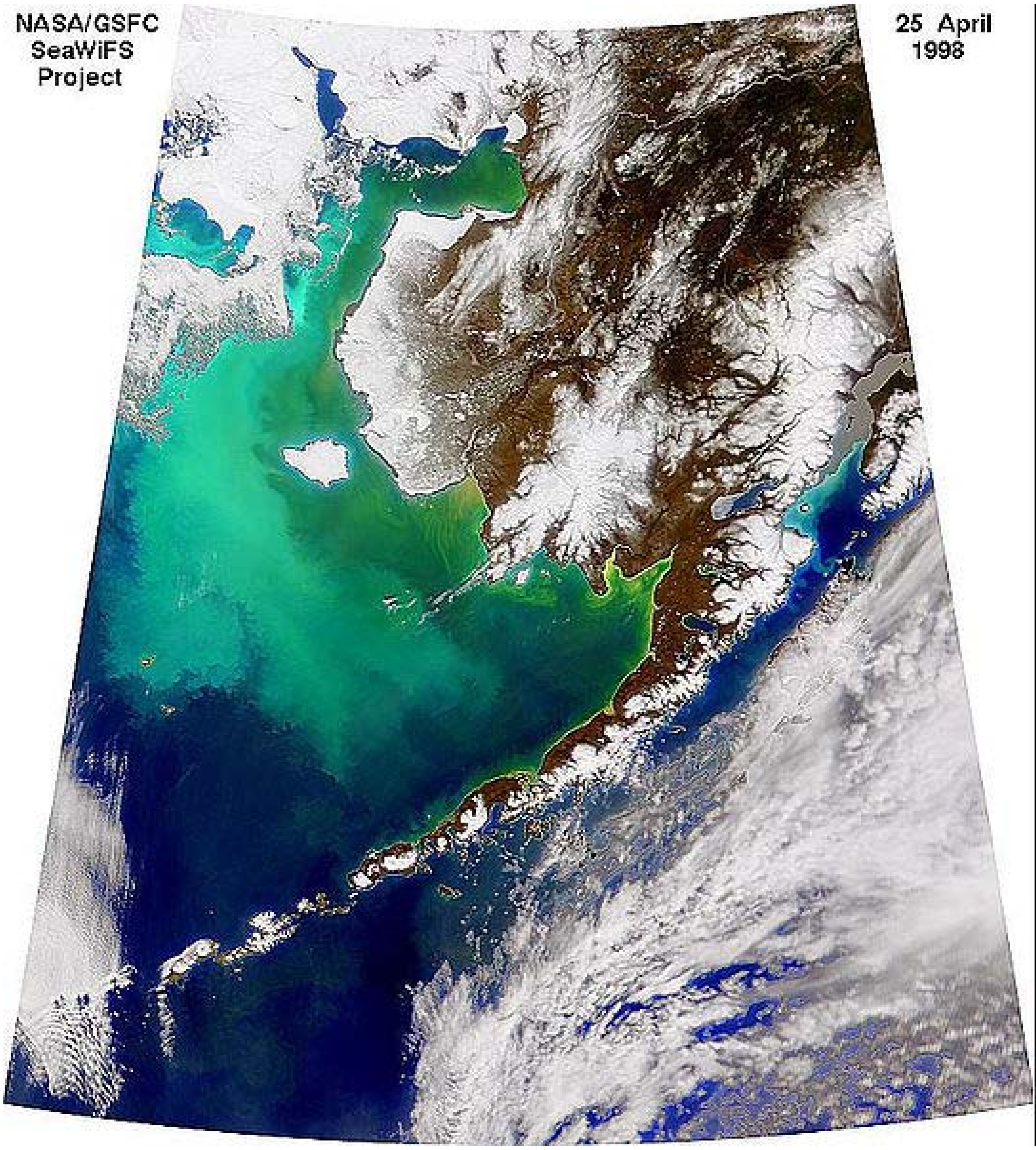
Most krill are swarming animals; the sizes and densities of such swarms vary greatly depending on the species and the region. For *Euphausia superba*, there have been reports of swarms of up to 10,000 to 60,000 individuals per cubic metre. Swarming is a defensive mechanism, confusing smaller predators 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



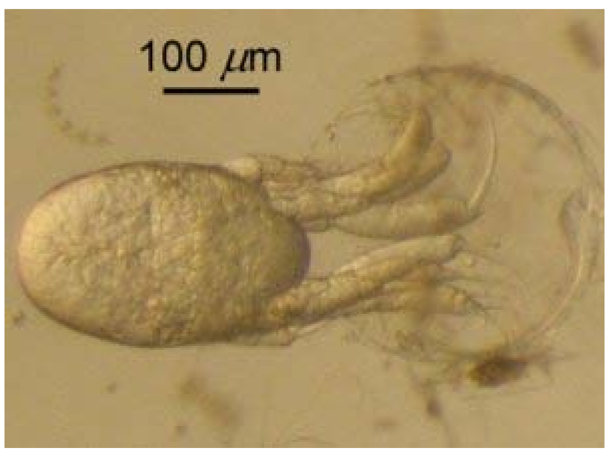
NASA SeaWiFS satellite image of the large phytoplankton bloom in the Bering Sea in 1998

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.

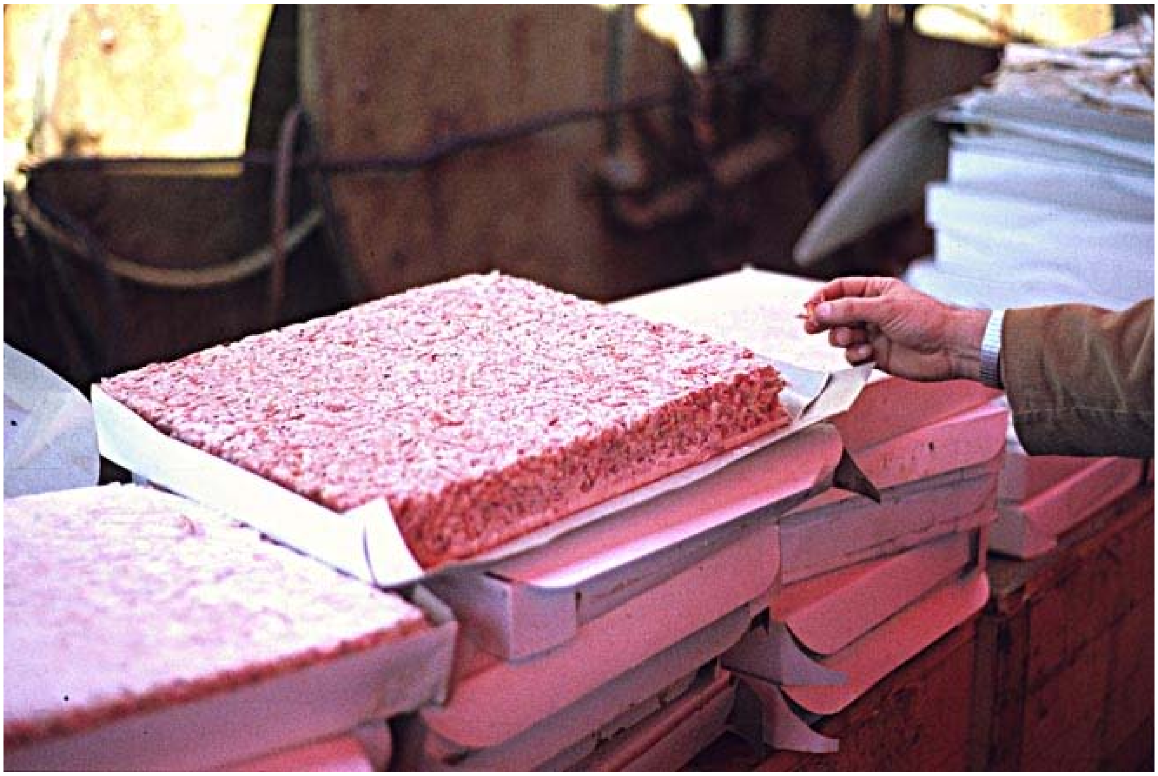
The head of a female krill of the sac-spawning species *Nematoscelis difficilis* with her brood sac. The eggs have a diameter of 0.3–0.4 millimetre (0.012–0.016 in).

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.

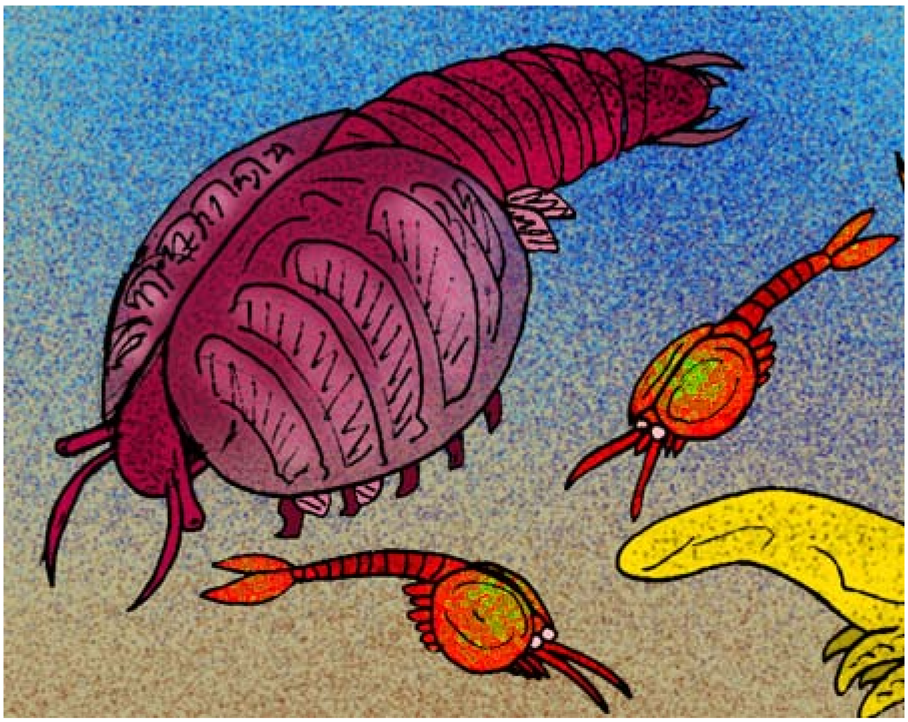
Chapter 5

Canadaspis and Leptostraca

Canadaspis

Canadaspis **Temporal range: Mid Cambrian**	
	
	
Specimens of *Canadaspis perfecta* from the Burgess Shale	
Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca (?)

Order:	†Canadaspidida
Family:	**†Canadaspididae**
Genus:	***†Canadaspis*** Briggs, 1978
Species	
C. perfecta Briggs, 1978 (type)	
C. laevigata Hou and Bergström, 1991	



Canadaspis perfecta & *Waptia fieldensis*

Canadaspis ("Shield of Canada") was a Cambrian genus of crustacean or euarthropod, a benthic feeder that moved mainly by walking and possibly used its biramous appendages to stir mud in search of food. The genus has been placed within subclass Phyllocarida in class Malacostraca that includes shrimps and lobsters.

The organism

Canadaspis had claws on the end of its frontal appendages which may have been used to stir up sediment, or to scrape off the top layer, which may have been a nutritious layer of microbes. Large particles it stirred up would have been captured by spines on the inside of its legs; these spines would have directed the food particles to the organism's mouth, where it used its mandibles to grind larger particles.

Its antennae served a sensory function. Spines on its head probably served to protect its vulnerable eyes from predators. Its limbs probably moved in sequence to produce a rippling motion. Although *Canadaspis* probably did not swim, this could have helped propel the organism from under soft sediments. The appendages also produced currents which would have helped with feeding and respiration.

Canadaspis is very closely related to the similar organism *Perspicaris*, differing only in morphological detail.

Classification of Canadaspis

Three alternatives exist for *Canadaspis'*s classification. They concern its relationship to the crustacea; it was originally thought that it falls within that clade, but this no longer appears to be the case. The alternatives are that it is a stem group crustacean, but others believe it is more basal still, falling in the base of the euarthropoda.

Fossil occurrences

4525 specimens of *Canadaspis* are known from the Greater Phyllopod bed, where they comprise 8.6% of the community. *Canadapsis perfecta*, the type species, comes from the Cambrian-age Burgess Shale in British Columbia, Canada. *Canadaspis* are also found in different formations of the House Range of western Utah as well as the Pioche Shale of Nevada. *Canadaspis laevigata*, coming from the Chengjiang biota and thus some 10 million years older than *Canadapsis perfecta*, is an equivocal member of the genus. Some scientists believe *Canadaspis laevigata* to be a more primitive Crustaceomorpha antecedent of *Canadaspis*, and others consider it a bi-valved arthropod of uncertain affinity.

Leptostraca

Leptostraca Temporal range: Cambrian–Recent	
 *Nebalia bipes*	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Subclass:	**Phyllocarida** Packard, 1879
Order:	**Leptostraca** Claus, 1880
Families	

- Nebaliidae
- Nebaliopsididae
- Paranebaliidae

Leptostraca (from the Greek words for *thin* and *shell*) is an order of small, marine crustaceans. Its members, including the well-studied *Nebalia*, occur throughout the world's oceans and are usually considered to be filter-feeders. It is the only extant order in the subclass **Phyllocarida**. They are believed to represent the most primitive members of their class, the Malacostraca, and first appear in the fossil record during the Cambrian period.

Description

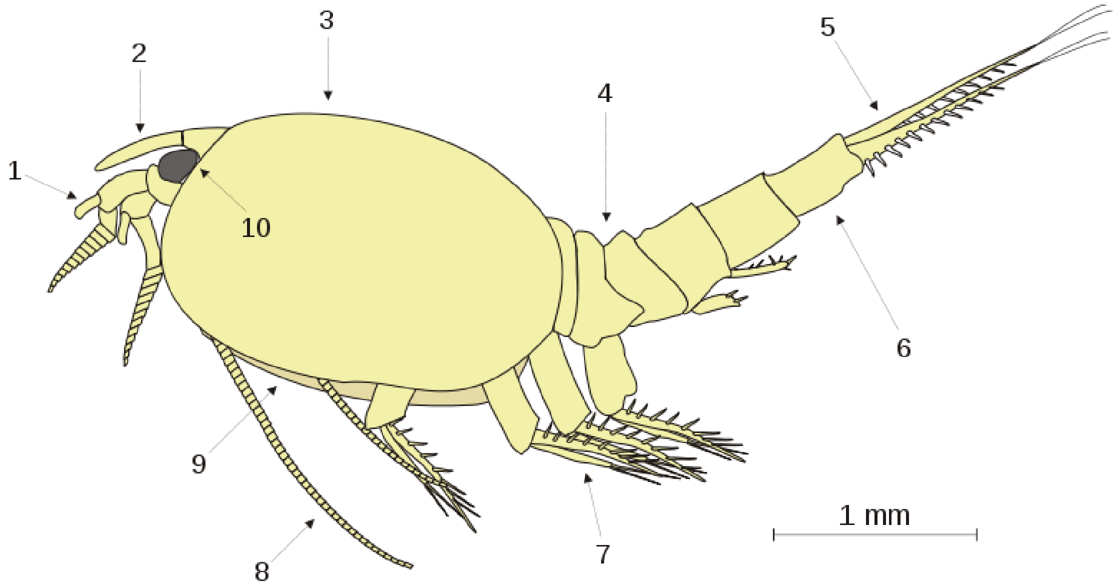


Diagram of *Nebalia bipes* showing the major features of the external anatomy: **1**: antennule; **2**: rostrum; **3**: carapace; **4**: abdomen / pleon; **5**: furca; **6**: telson; **7**: pleopods; **8**: antenna; **9**: thoracopods; **10**: eye

Leptostracans are usually small, typically 5 to 15 millimetres (0.2 to 0.6 in) long, crustaceans distinguished from all other members of their class in having seven abdominal segments, instead of six. Their head has stalked compound eyes, two pairs of antennae (one biramous, one uniramous), and a pair of mandibles but no maxillipeds. The carapace is large and comprises two valves which cover the head and the thorax, including most of the thoracic appendages, and serves as a brood pouch for the developing embryos. The first six abdominal segments bear pleopods, while the seventh bears a pair of caudal furcae, which may be homologous to uropods of other crustaceans.

Leptostracans have gills on their thoracic limbs, but also breathe through a respiratory membrane on the inside of the carapace. The eggs hatch as a postlarval, or "manca" stage, which lacks a fully developed carapace, but otherwise resembles the adult.

Classification

It is now accepted that leptostracans belong to the Malacostraca, and the sister group to Leptostraca is Eumalacostraca.

The Order Leptostraca is divided into three families, with ten genera containing a total of around 40 valid described species:

Species	Authority	Date	Family	Distribution
Nebaliopsis typica	Sars	1887	Nebaliopsididae	Southern Hemisphere
Pseudonebaliopsis atlantica	Petryachov	1996	Nebaliopsididae	North Atlantic
Nebalia antarctica	Dahl	1990	Nebaliidae	Antarctica
Nebalia bipes	Fabricius	1780	Nebaliidae	Arctic and sub-Arctic
Nebalia borealis	Dahl	1985	Nebaliidae	north-east Atlantic Ocean
Nebalia brucei	Olesen	1999	Nebaliidae	Tanzania
Nebalia cannoni	Dahl	1990	Nebaliidae	South Georgia
Nebalia capensis	Barnard	1914	Nebaliidae	South Africa
Nebalia clausi	Dahl	1985	Nebaliidae	Italy
Nebalia dahli	Kazmi & Tirmizi	1989	Nebaliidae	Pakistan
Nebalia daytoni	Vetter	1996	Nebaliidae	California
Nebalia falklandensis	Dahl	1990	Nebaliidae	Falkland Islands
Nebalia geoffroyi	Milne-Edwards	1828	Nebaliidae	north-east Atlantic Ocean
Nebalia gerkenae	Haney & Martin	2000	Nebaliidae	California
Nebalia herbstii	Leach	1814	Nebaliidae	north-east Atlantic Ocean
Nebalia hessleri	Martin *et al.*	1996	Nebaliidae	California
Nebalia ilheoensis	Kensley	1976	Nebaliidae	south-western Africa
Nebalia kensleyi	Haney & Martin	2005	Nebaliidae	California
Nebalia kocatasi	Kocak, Moreira & Katagan	2007	Nebaliidae	Mediterranean Sea
Nebalia lagartensis	Escobar & Villalobos-Hiriart	1995	Nebaliidae	Mexico
Nebalia longicornis	Thomson	1879	Nebaliidae	South Pacific, South Africa, Caribbean Sea
Nebalia marerubi	Wägele	1983	Nebaliidae	Red Sea
Nebalia patagonica	Dahl	1990	Nebaliidae	Magellan region
Nebalia schizophthalma	Haney, Hessler & Martin	2001	Nebaliidae	western Atlantic Ocean
Nebalia strausi	Risso	1826	Nebaliidae	north-east Atlantic Ocean, Mediterranean Sea
Nebalia troncosoi	Moreira, Cacabelos	2003	Nebaliidae	Spain

	& Dominguez			
Nebaliella antarctica	Thiele	1904	Nebaliidae	Kerguelen, New Zealand
Nebaliella brevicarinata	Kikuchi & Gamô	1992	Nebaliidae	Antarctica
Nebaliella caboti	Clark	1932	Nebaliidae	Cabot Strait, New Jersey
Nebaliella declivatas	Walker-Smith	1998	Nebaliidae	Australia
Nebaliella extrema	Thiele	1905	Nebaliidae	Antarctica
Dahlella caldariensis	Hessler	1984	Nebaliidae	East Pacific Rise
Sarsinebalia cristobi	Moreira, Gestoso & Troncoso	2003	Nebaliidae	north-east Atlantic Ocean
Sarsinebalia typhlops	(Sars)	1870	Nebaliidae	North Atlantic, Australia
Sarsinebalia urgorrii	Moreira, Gestoso & Troncoso	2003	Nebaliidae	north-east Atlantic Ocean
Speonebalia cannoni	Bowman, Yager & Iliffe	1985	Nebaliidae	Turks and Caicos Islands
Levinebalia fortunata	(Wakabara)	1976	Paranebaliidae	New Zealand
Levinebalia maria	Walker-Smith	2000	Paranebaliidae	Australia
Paranebalia belizensis	Modlin	1991	Paranebaliidae	Belize
Paranebalia longipes	(Willemöes-Suhm)	1875	Paranebaliidae	Atlantic, Pacific and Indian Oceans
Saronebalia guanensis	Haney & Martin	2004	Paranebaliidae	British Virgin Islands

Chapter 6

Eumalacostraca and Anaspidacea

Eumalacostraca

Eumalacostraca

Atlantic blue crabs, *Callinectes sapidus*

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Subclass:	**Eumalacostraca** Grobben, 1892

Superorders

Syncarida
Peracarida
Eucarida

The **Eumalacostraca** (Greek: "true soft shell") are a subclass of crustaceans, containing almost all living malacostracans, about 22,000 described species. (The outgroups are the Phyllocarida and possibly the Hoplocarida or mantis shrimps.)

Eumalacostracans have 19 segments (5 cephalic, 8 thoracic, 6 abdominal). The thoracic limbs are jointed and used for swimming or walking. The common ancestor is thought to have had a carapace, and most living species possess one, but it has been lost in some subgroups.

Classification

Martin and Davis present the following classification of living eumalacostracans into orders, to which extinct orders have been added, indicated by †.

The group as originally described by Karl Grobben included the Stomatopoda (mantis shrimp), and some modern experts continue to use this definition.

Subclass ***Eumalacostraca*** Grobben, 1892

- Superorder Syncarida Packard, 1885
  - †Order Palaeocaridacea
  - Order Bathynellacea Chappuis, 1915
  - Order Anaspidacea Calman, 1904 (including Stygocaridacea)
- Superorder Peracarida Calman, 1904
  - Order Spelaeogriphacea Gordon, 1957
  - Order Thermosbaenacea Monod, 1927
  - Order Lophogastrida Sars, 1870
  - Order Mysida Haworth, 1825
  - Order Mictacea Bowman, Garner, Hessler, Iliffe & Sanders, 1985
  - Order Amphipoda Latreille, 1816
  - Order Isopoda Latreille, 1817 (pillbugs, sowbugs, woodlice)
  - Order Tanaidacea Dana, 1849
  - Order Cumacea Krøyer, 1846
- Superorder Eucarida Calman, 1904
  - Order Euphausiacea Dana, 1852
  - Order Amphionidacea Williamson, 1973
  - Order Decapoda Latreille, 1802 (crabs, lobsters, shrimp)

Anaspidacea

Anaspidacea	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Superorder:	Syncarida
Order:	**Anaspidacea** Calman, 1904

Anaspidacea is an order of crustaceans, comprising eleven genera in four families. Species in the family Anaspididae vary from being strict stygobionts (only living underground) to species living in lakes, streams and moorland pools, and are found only in Tasmania. Koonungidae is found in Tasmania and the south-eastern part of the Australian mainland, where they live in the burrows made by crayfish and in caves. The families Psammaspididae and Stygocarididae are both restricted to caves, but Stygocarididae has a much wider distribution than the other families, with *Parastygocaris* having species in New Zealand and South America as well as Australia; two other genera in the family are endemic to South America, and one, *Stygocarella*, is endemic to New Zealand .

Genera

- Anaspididae Thomson, 1893
  - *Allanaspides* Swain, Wilson, Hickman & Ong, 1970 — Tasmania
  - *Anaspides* Thomson, 1894 — Tasmania
  - *Paranaspides* Smith, 1908 — Tasmania
- Koonungidae Sayce, 1908
  - *Koonunga* Sayce, 1907 — south-eastern Australia and Tasmania
  - *Micraspides* Nicholls, 1931 — south-eastern Australia and Tasmania
- Psammaspididae Schminke, 1974
  - *Eucrenonaspides* Knott & Lake, 1980 — Tasmania
  - *Psammaspides* Schminke, 1974 — south-eastern Australia
- Stygocarididae Noodt, 1963
  - *Oncostygocaris* Schminke, 1980 — southern South America
  - *Parastygocaris* Noodt, 1963 — southern South America
  - *Stygocarella* Schminke, 1980 — New Zealand
  - *Stygocaris* Noodt, 1963 — southern South America, south-eastern Australia and New Zealand

Chapter 7

Peracarida, Lophogastrida and Mysida

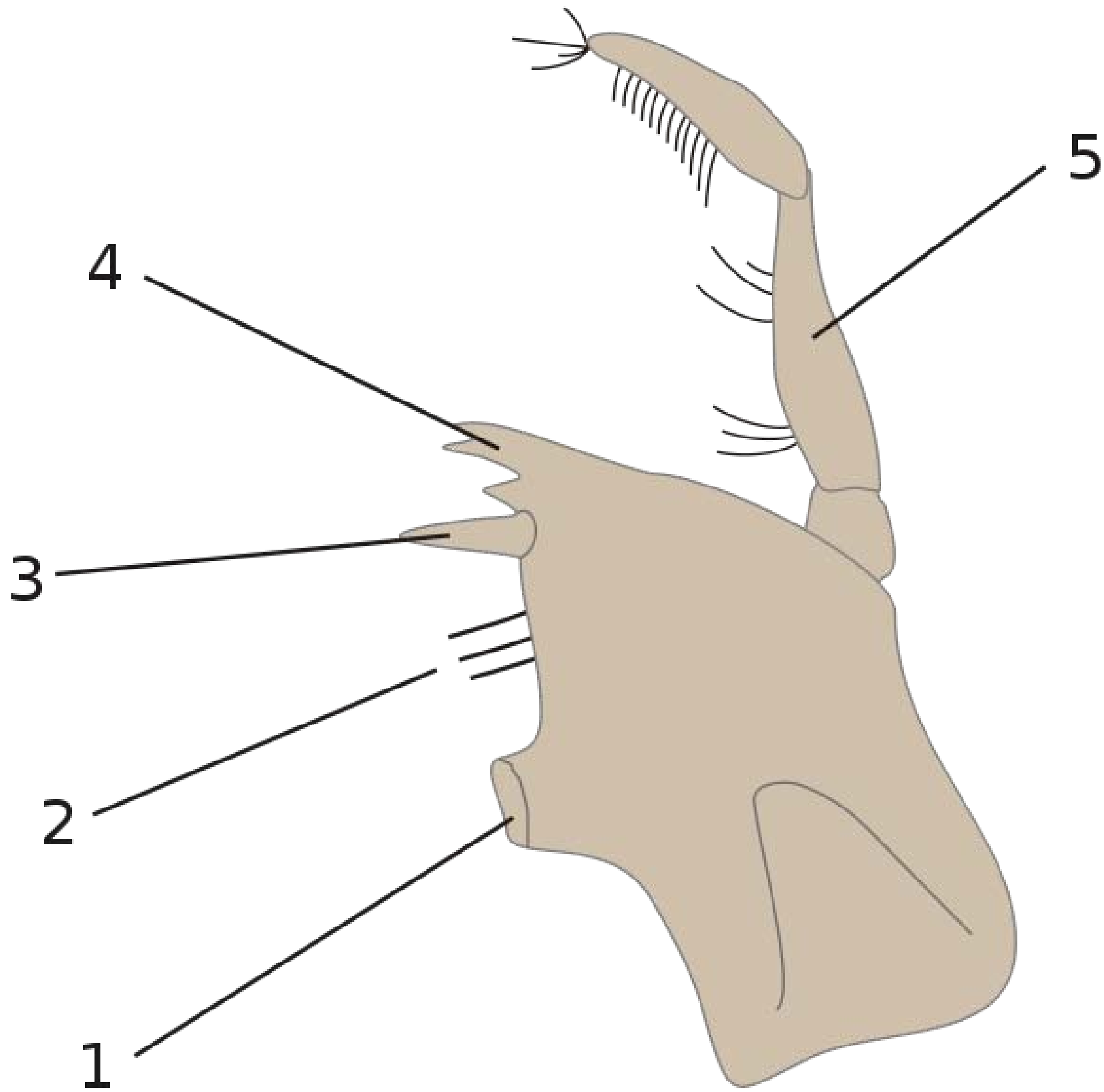
Peracarida

Peracarida	
	
The amphipod *Bathyporeia elegans* with an egg in its marsupium	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Subclass:	Eumalacostraca
Superorder:	**Peracarida** Calman, 1904
Orders	

- Amphipoda
- Cumacea
- Isopoda
- Lophogastrida
- Mictacea
- Mysida

- Pygocephalomorpha
- Spelaeogriphacea
- Stygiomysida
- Tanaidacea
- Thermosbaenacea

The superorder **Peracarida** is a large group of malacostracan crustaceans, having members in marine, freshwater, and terrestrial habitats. They are defined by the possession of a single pair of maxillipeds (rarely 2–3), of mandibles with an articulated accessory process between the molar and incisor teeth in the adults (called the *lacinia mobilis*), and of a carapace which is often reduced in size and is not fused with the posterior thoracic somites. In all orders except the Thermosbaenacea, where the carapace is used to brood eggs, the basalmost segments of the legs bear thin flattened plates (oostegites) which enclose a ventral brood pouch, known as a *marsupium*. The young hatch at a post-larval, prejuvenile stage called a *manca* which lacks the last pair of legs.



General bauplan of a peracarid mandibula: 1. Molar process; 2. Spine row; 3. Lacinia mobilis; 4. Incisor process; 5. Palp

Lophogastrida

Lophogastrida	
	
Gnathophausia zoea (Gnathophausiidae)	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Subclass:	Eumalacostraca
Superorder:	Peracarida
Order:	**Lophogastrida** G. O. Sars, 1870
Families	

- Eucopiidae
- Gnathophausiidae
- Lophogastridae

The **Lophogastrida** is an order of malacostracan crustaceans in the superorder Peracarida. The Lophogastrida are shrimp-like animals that mostly inhabit the relatively deep pelagic waters of the oceans throughout the world.

Most lophogastridan species are 1–8 centimetres (0.4–3.1 in) long, but *Gnathophausia ingens* can be up to 35 cm, probably the largest pelagic crustacean in the world. Some 56 extant species in total are currently known. They are classified into three families and nine genera.

The external features of the Lophogastrida include stalked compound eyes, a carapace that covers the head and thoracic segments, and a muscular cylindrical abdomen. The carapace often extends beyond the head to form an elongated rostrum. As with other Peracarida, the Lophogastrida are separated from true shrimps in that they carry their developing embryos and young in a brood pouch, or *marsupium*, and they thus lack a separate planktonic larval stage.

Previously, the Lophogastrida were classified as a suborder of a broader peracaridan order Mysidacea, together with the Mysida (and Stygiomysida), but that taxon is currently generally abandoned. Features distinguishing the Lophogastrida from the Mysida include the absence of statocysts in their uropods, and the presence of well-developed biramous pleopods on the abdomen, as well as molecular characters.

Mysida

Mysida	
	
Hemimysis anomala (Mysidae)	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Subclass:	Eumalacostraca
Superorder:	Peracarida
Order:	**Mysida** A. H. Haworth, 1825
Families	

- Mysidae
- Petalophthalmidae
- Lepidomysidae
- Stygiomysidae

Mysida is a group of small, shrimp-like crustaceans, an order in the malacostracan superorder Peracarida. Their common name **opossum shrimps** stems from the presence of a brood pouch, or *marsupium*, in females. Mysids are mostly found in marine waters throughout the world, but are also important in some fresh- and brackish-water ecosystems of the Northern hemisphere. Some mysids are cultured for experimental purposes and as food source for orther cultured marine organisms.

Description

The majority of species are 5–25 millimetres (0.2–1.0 in) long, and vary in colour from pale, almost transparent, through to bright orange or brown. Unlike true shrimps, but as with other orders of Peracarida, embryos are carried in a brood pouch, or marsupium, which is located in the thoracic segments between the legs. They differ from other species within the superorder Peracarida by featuring statocysts in their uropods (located at the last abdominal segment). These are clearly seen as circular vesicles and together with the pouch are often used as a diagnostic feature of the group. Other features include stalked compound eyes, and a carapace that covers the head and thoracic segments.

Systematics

The Mysida belong to the superorder Peracarida, which means “near to shrimps”. Although in many respects mysids appear similar to some shrimps, the main characteristic separating them from the superorder Eucarida is their lack of free-swimming larvae. The order Mysida is extensive and currently includes approximately 160 genera, containing more than 1000 species.

Traditionally, Mysida were united with another, externally similar group of pelagic crustaceans, the Lophogastrida, into a broader order Mysidacea, but that classification is currently generally abandoned. While the previous grouping had good morphological support, molecular studies do not corroborate the monophyly of this group.. Moreover the unity of Mysida itself has been challenged, with a suggestion to remove two of the four families, Lepidomysidae and Stygiomysidae, to form the order Stygiomysida.

Ecology

Mysids have a cosmopolitan distribution and are found in both marine and freshwater environments, benthic and pelagic areas. Most mysids are free-living but a few species, mostly in the tribe Heteromysini, are commensal and are associated with sea anemones and hermit crabs. Several taxa have also been described from different groundwater habitats and caves.

The majority of Mysida are omnivores, feeding on algae, detritus, and zooplankton. Scavenging and cannibalism are also common, with the adults preying on their young once they emerge from the marsupium. Pelagic species are filter feeders while benthic species, common for the tribe Erythropini, have been observed feeding on small particles which they collect by grooming their body surface and legs. The first pair of legs in the thorax can also function as accessory feeding limbs.

The size of a mysid brood generally correlates to body length and environmental factors such as density and food availability. Mating usually takes place at night and lasts only a few minutes. The length of time until mysids reach sexual maturity depends on water temperature and food availability. For the species *Mysidopsis bahia*, this is normally 12 to 20 days. The young are released soon after, and although their numbers are usually low, the short reproductive cycle of mysid adults means a new brood can be produced every 4 to 7 days.

Mysid culture

Mysids are good candidates for large scale culture as they are highly adaptive, and can occur in a wide range of habitats, and despite their low fecundity, having a short reproductive cycle means they can quickly reproduce in vast numbers. They can be cultured in static or flow-through systems, the latter shown to be able to carry a higher stocking density than a static system. In flow-through systems, juvenile mysids are continuously separated from the adult brood stock, to reduce mortality due to cannibalism.

Artemia (brine shrimp) juveniles (incubated for 24 hours) are the most common food in mysid cultures, sometimes enriched with highly unsaturated fatty acids (HUFA) to increase the nutritional value.

Culturing mysids are thought to provide an ideal food source for many marine organisms. They are often fed to cephalopods, fish larvae and in commercial shrimp farms due to their small size and low costs. Their high protein and fat content also makes them a good alternative to live enriched *Artemia* when feeding juveniles (especially those that are difficult to maintain such as seahorses) and other small fauna.

Their sensitivity to water quality also makes them suitable for bioassays. *Mysidopsis bahia* and *Mysidopsis almyra* are used frequently to test for pesticides and other toxicants, with *M. bahia* found to be more sensitive during moulting periods.

Chapter 8

Isopoda and Tanaidacea

Isopoda

Isopoda
Temporal range: 300–0 Ma

Eurydice pulchra (Cirolanidae)

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Subclass:	Eumalacostraca
Superorder:	Peracarida
Order:	**Isopoda** Latreille, 1817

Suborders

- Asellota
- Calabozoida
- Cymothoida
- Limnoriidea
- Microcerberidea
- Oniscidea
- Phoratopidea
- Phreatoicidea

- Sphaeromatidea
- Tainisopidea
- Valvifera

Isopods are an order of peracarid crustaceans, including familiar animals such as woodlice and pill bugs. The name *Isopoda* derives from the Greek roots ἴσος (*iso-*, meaning "same") and ποδός (*podos*, meaning "foot"). The fossil record of isopods dates back to the Carboniferous period (in the US Pennsylvanian epoch), at least 300 million years ago.

Description

The woodlouse *Oniscus asellus* from the side

Isopods are relatively small crustaceans with seven pairs of legs of similar size and form, ranging in size from 300 micrometres (0.012 in) to nearly 50 centimetres (20 in) in the case of *Bathynomus giganteus*. They are typically flattened dorso-ventrally, although many species deviate from this plan, particularly those from the deep sea or from ground water. Isopods lack an obvious carapace, which is reduced to a "cephalic shield" covering only the head. Gas exchange is carried out by specialised gill-like pleopods towards the rear of the animal's body. In terrestrial isopods, these are often adapted into structures which resemble lungs, and these "lungs" are readily visible on the underside of a woodlouse. Eyes, when present, are always sessile, never on stalks. They share with the Tanaidacea the fusion of the last abdominal body segment with the telson, forming a "pleotelson", and the first body segment of the thorax is fused to the head. The pereiopods are uniramous, but the pleopods are biramous.

Ecology

Anilocra (Cymothoidae) parasitising *Spicara maena*, Italy

Around 4,500 species of isopods are found in marine environments, mostly on the sea floor. Some 500 species are found in fresh water; and another 5,000 species are the woodlice in the suborder Oniscidea, which are thus by far the most successful group of terrestrial crustaceans. In the deep sea, members of the suborder Asellota predominate, to the near exclusion of all other isopods, having undergone a large adaptive radiation in that environment.

A number of isopod groups have evolved a parasitic lifestyle. The suborder Cymothoida is exclusively parasitic, while the polyphyletic suborder Flabellifera is partly parasitic. *Cymothoa exigua*, for example, is a parasite of the spotted rose snapper fish *Lutjanus guttatus* in the Gulf of California; it eats the tongue of the fish, and takes its place, in the only known instance of a parasite functionally replacing a host structure.

In marine and reef aquariums, parasitic isopods can become a pest, endangering both the fish and the aquarium keepers.

Diversity and classification

Isopods belong to the larger group Peracarida, which are united by the presence of a special brood pouch for brooding eggs. There are around 10,215 described species of isopod, classified into ten suborders.

Development

Isopod larvae hatch as mancae, which resemble adults except for the lack of the last pair of pereiopods (thoracic legs). The lack of a swimming phase in the life cycle is a limiting factor in isopod dispersal, and may be responsible for the high levels of endemism in the order. As adults, isopods differ from other crustaceans in that they replace their exoskeleton (in the process called ecdysis) in two phases; this is known as "biphasic moulting".

Tanaidacea

Tanaidacea

Tanaissus lilljeborgi
(a tanaid from the North Sea)

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Superorder:	Peracarida
Order:	**Tanaidacea** Dana, 1849

Suborders

- Tanaidomorpha
- Neotanaidomorpha
- Apseudomorpha

The crustacean order **Tanaidacea** (known as **tanaids**) make up a minor group within the class Malacostraca. There are about 940 species in this order.

Description

Tanaids are small, shrimp-like creatures ranging from 0.5 to 120 millimetres (0.020 to 4.7 in) in adult size, with most species being from 2 to 5 millimetres (0.08 to 0.2 in). Their carapace covers the first two segments of the thorax. There are three pairs of limbs on the thorax; a small pair of maxillipeds, a pair of large clawed gnathopods, and a pair of pereiopods adapted for burrowing into the mud. Unusually among crustaceans, the remaining six thoracic segments have no limbs at all, but each of the first five abdominal segments normally carry pleopods. The final segment is fused with the telson and carries a pair of uropods.

The gills lie on the inner surface of the carapace. The thoracic limbs wash water towards the mouth, filtering out small particles of food with the mouthparts or maxillipeds. Some species actively hunt prey, either as their only food source, or in combination with filter feeding.

Habitat

Most are marine, but some are also found in freshwater coastal habitat or estuaries. The majority of species are bottom-dwellers in shallow water environments, but a few live in very deep water, exceeding for some species 9,000 metres (30,000 ft). In some deep sea environment, they represent the most abundant and diverse fauna to be found.

Life cycle

Tanaids do not undergo a true planktonic stage. The early developmental period is spent while young are within the marsupium of the mother. Subsequently, post-larvae, called mancas, emerge as epibenthic forms. Some species are hermaphroditic.

Taxonomy

The order Tanaidacea is divided into the following sub-orders, superfamilies and families:

Tanaidomorpha Sieg, 1980

- Tanaoidea Dana, 1849
    - Tanaidae Dana, 1849
- Paratanaoidea Lang, 1949
    - Anarthruridae Lang, 1971
    - Leptochelidae Lang, 1973
    - Nototanaidae Sieg, 1976
    - Paratanaidae Lang, 1949

- Pseudotanaidae Sieg, 1976
- Pseudozeuxidae Sieg, 1982
- Typhlotanaidae Sieg, 1986

Neotanaidomorpha Sieg, 1980

- Neotanaidae Lang, 1956

Apseudomorpha Sieg, 1980

- Apseudoidea Leach, 1814
    - Anuropodidae Bačescu, 1980
    - Apseudellidae Gutu, 1972
    - Apseudidae Leach, 1814
    - Gigantapseudidae Kudinova-Pasternak, 1978
    - Kalliapseudidae Lang, 1956
    - Metapseudidae Lang, 1970
    - Pagurapseudidae Lang, 1970
    - Parapseudidae Gutu, 1981
    - Sphyrapidae Gutu, 1980
    - Tanapseudidae Bačescu, 1978
    - Tanzanapseudidae Bačescu, 1975
    - Whiteleggiidae Gutu, 1972

Chapter 9

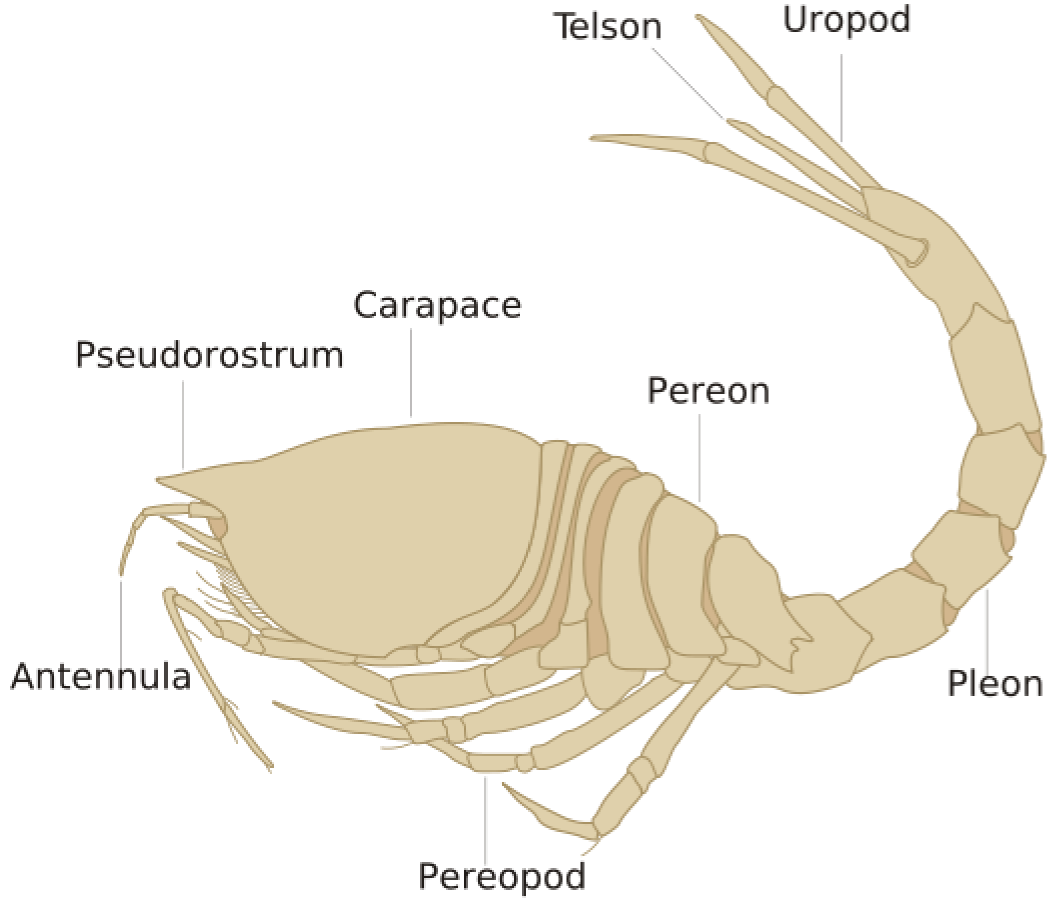
Cumacea and Amphionides

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 than 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)

Amphionides

Amphionides reynaudii	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Superorder:	Eucarida
Order:	**Amphionidacea** D. I. Williamson, 1973
Family:	**Amphionididae** Holthuis, 1955
Genus:	***Amphionides*** Zimmer, 1904
Species:	***A. reynaudii***
Binomial name	
Amphionides reynaudii (H. Milne–Edwards, 1833)	
Synonyms	
Amphion reynaudii H. Milne–Edwards, 1833	

Amphionides reynaudii is the sole representative of the Order **Amphionidacea**, and is a small (less than one inch long) planktonic crustacean found throughout the world's tropical oceans, mostly in shallow waters. Morphologically, *Amphionides* is somewhat unusual, with many body parts being reduced or absent. For example, it has only one pair of mouthparts — the maxillae — the mandibles and maxillules being absent.

Sexual dimorphism

Males and females differ in the form of the antennae, and also by the presence in males of the eighth thoracic appendage, albeit in a reduced form. This is the site of the male gonopore (the female's gonopore is on the sixth thoracic appendage). The first pleopod of the female is greatly enlarged and almost encloses the enlarged carapace. This is assumed to be a chamber in which the eggs are fertilised and retained until hatching. The more streamlined carapace and pleopods of the male make it more hydrodynamic, and so fewer males are caught than females.

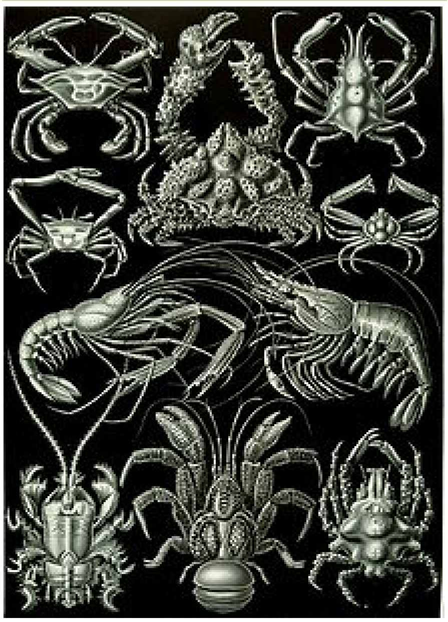
Classification

Originally described from its larvae, *Amphionides* was originally thought to be a shrimp. It was not until 1969 that the adult form was observed to be that described by Zimmer in 1904, and only in 1973 was *Amphionides* placed in its own order by Donald I. Williamson. The specific epithet *reynaudii* was given by Henri Milne-Edwards in honour of a friend of his, possibly Count François Dominique Reynaud de Montlosier.

Chapter 10

Decapoda

Decapoda **Temporal range: Devonian–Recent**	



"Decapoda" from Ernst Haeckel's *Kunstformen der Natur*, 1904

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Superorder:	Eucarida
Order:	**Decapoda** Latreille, 1802
Suborders	

Dendrobranchiata
Pleocyemata

The **decapods** or **Decapoda** (literally "ten-footed") are an order of crustaceans within the class Malacostraca, including many familiar groups, such as crayfish, crabs, lobsters, prawns and shrimp. Most decapods are scavengers. It is estimated that the order contains nearly 15,000 species in around 2,700 genera, with approximately 3,300 fossil species. Nearly half of these species are crabs, with the shrimp (c. 3000 species) and Anomura (including hermit crabs, porcelain crabs, squat lobsters: c. 2500 species), making up the bulk of the remainder. The earliest fossil decapod is the Devonian *Palaeopalaemon*.

Anatomy

As the name Decapoda implies, all decapods have ten legs. These are in the form of five pairs of thoracic appendages on the last five thoracic segments. The front three pairs function as mouthparts and are generally referred to as maxillipeds; the remainder are pereiopods. In many decapods, however, one pair of legs has enlarged pincers; the claws are called *chelae*, so those legs may be called *chelipeds*. Further appendages are found on the abdomen, with each segment capable of carrying a pair of biramous pleopods, the last of which form part of the tail fan (together with the telson) and are called uropods.

Classification

Classification within the order Decapoda depends on the structure of the gills and legs, and the way in which the larvae develop, giving rise to two suborders: Dendrobranchiata and Pleocyemata. Dendrobranchiata consists of prawns, including many species colloquially referred to as "shrimp", such as the Atlantic white shrimp. Pleocyemata includes the remaining groups, including true shrimp. Those groups which usually walk rather than swim (Pleocyemata, excluding Stenopodidea and Caridea) form a clade called Reptantia.

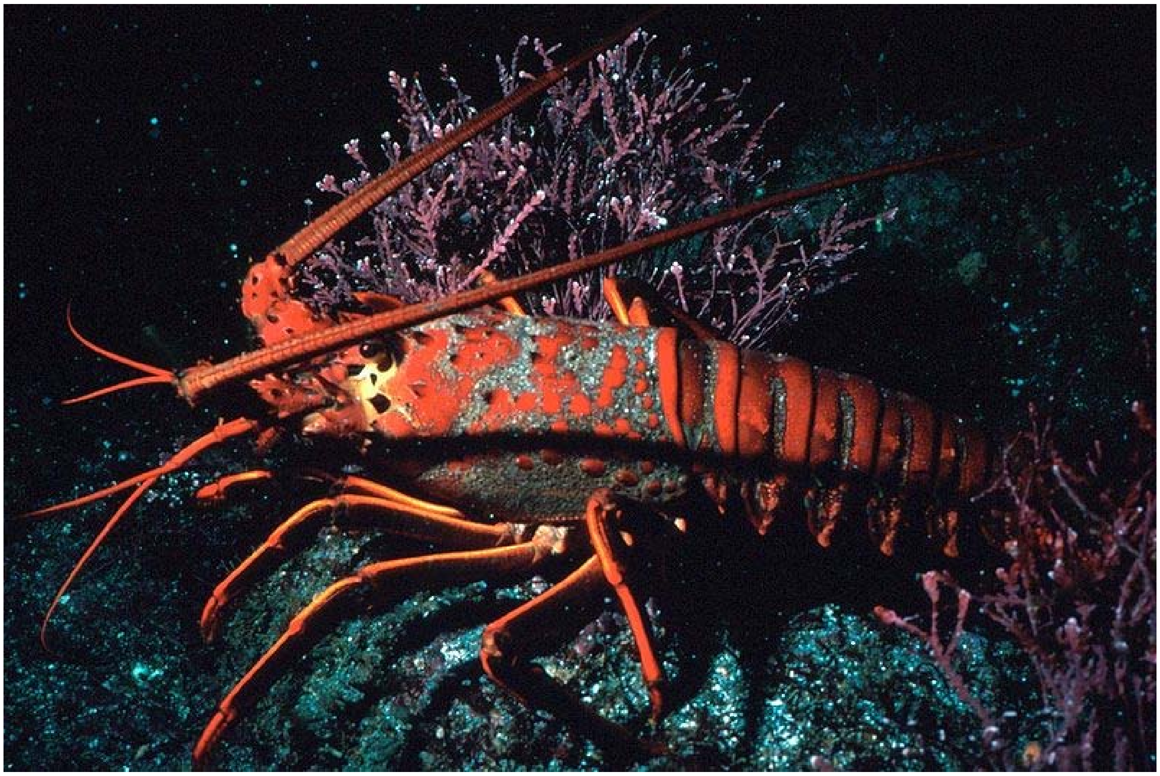
The following classification to the level of superfamilies follows De Grave *et al.*

Whiteleg shrimp, *Litopenaeus vannamei* (Dendrobranchiata: Penaeoidea)

Heterocarpus ensifer (Caridea: Pandaloidea)

Austropotamobius pallipes (Astacidea: Astacoidea)

Upogebia deltaura (Gebiidea: Upogebiidae)



California spiny lobster, *Panulirus interruptus* (Achelata: Palinuridae)

Polycheles sculptus (Polychelida: Polychelidae)

Atlantic blue crab, *Callinectes sapidus* (Brachyura: Portunoidea)

Order **Decapoda** Latreille, 1802

- Suborder **Dendrobranchiata** Bate, 1888
  - Penaeoidea Rafinesque, 1815
  - Sergestoidea Dana, 1852
- Suborder **Pleocyemata** Burkenroad, 1963
  - Infraorder **Stenopodidea** Bate, 1888
  - Infraorder **Caridea** Dana, 1852
    - Procaridoidea Chace & Manning, 1972
    - Galatheacaridoidea Vereshchaka, 1997
    - Pasiphaeoidea Dana, 1852
    - Oplophoroidea Dana, 1852
    - Atyoidea De Haan, 1849
    - Bresilioidea Calman, 1896
    - Nematocarcinoidea Smith, 1884

- • Psalidopodoidea Wood-Mason, 1874
- Stylodactyloidea Bate, 1888
- Campylonotoidea Sollaud, 1913
- Palaemonoidea Rafinesque, 1815

- Alpheoidea Rafinesque, 1815
- Processoidea Ortmann, 1896
- Pandaloidea Haworth, 1825
- Physetocaridoidea Chace, 1940
- Crangonoidea Haworth, 1825

- Infraorder **Astacidea** Latreille, 1802

  - Enoplometopoidea de Saint Laurent, 1988
  - Nephropoidea Dana, 1852
  - Astacoidea Latreille, 1802
  - Parastacoidea Huxley, 1879

- Infraorder Glypheidea Winckler, 1882

  - Glypheoidea Winckler, 1882

- Infraorder **Axiidea** de Saint Laurent, 1979b
- Infraorder **Gebiidea** de Saint Laurent, 1979
- Infraorder **Achelata** Scholtz & Richter, 1995
- Infraorder **Polychelida** Scholtz & Richter, 1995
- Infraorder **Anomura** MacLeay, 1838

  - Aegloidea Dana, 1852
  - Galatheoidea Samouelle, 1819
  - Hippoidea Latreille, 1825a
  - Kiwaoidea Macpherson, Jones & Segonzac, 2005
  - Lithodoidea Samouelle, 1819
  - Lomisoidea Bouvier, 1895
  - Paguroidea Latreille, 1802

Infraorder **Brachyura** Linnaeus, 1758

- Section Dromiacea De Haan, 1833
  - Dromioidea De Haan, 1833
  - Homolodromioidea Alcock, 1900
  - Homoloidea De Haan, 1839
- Section Raninoida De Haan, 1839
- Section Cyclodorippoida Ortmann, 1892
- Section Eubrachyura de Saint Laurent, 1980
  - Subsection Heterotremata Guinot, 1977
    - Aethroidea Dana, 1851
    - Bellioidea Dana, 1852
    - Bythograeoidea Williams, 1980
    - Calappoidea De Haan, 1833
    - Cancroidea Latreille, 1802

        - Carpilioidea Ortmann, 1893
        - Cheiragonoidea Ortmann, 1893
        - Corystoidea Samouelle, 1819
        - Dairoidea Serène, 1965
        - Dorippoidea MacLeay, 1838
        - Eriphioidea MacLeay, 1838
        - Gecarcinucoidea Rathbun, 1904

- Goneplacoidea MacLeay, 1838
- Hexapodoidea Miers, 1886
- Leucosioidea Samouelle, 1819
- Majoidea Samouelle, 1819
- Orithyioidea Dana, 1852c
- Palicoidea Bouvier, 1898
- Parthenopoidea MacLeay,
- Pilumnoidea Samouelle, 1819
- Portunoidea Rafinesque, 1815
- Potamoidea Ortmann, 1896
- Pseudothelphusoidea Ortmann, 1893
- Pseudozioidea Alcock, 1898
- Retroplumoidea Gill, 1894
- Trapezioidea Miers, 1886
- Trichodactyloidea H. Milne-Edwards, 1853
- Xanthoidea MacLeay, 1838

Subsection Thoracotremata Guinot, 1977

- Cryptochiroidea Paul'son, 1875
- Grapsoidea MacLeay, 1838
- Ocypodoidea Rafinesque, 1815
- Pinnotheroidea De Haan, 1833

Chapter 11

Phylogeny of Malacostraca

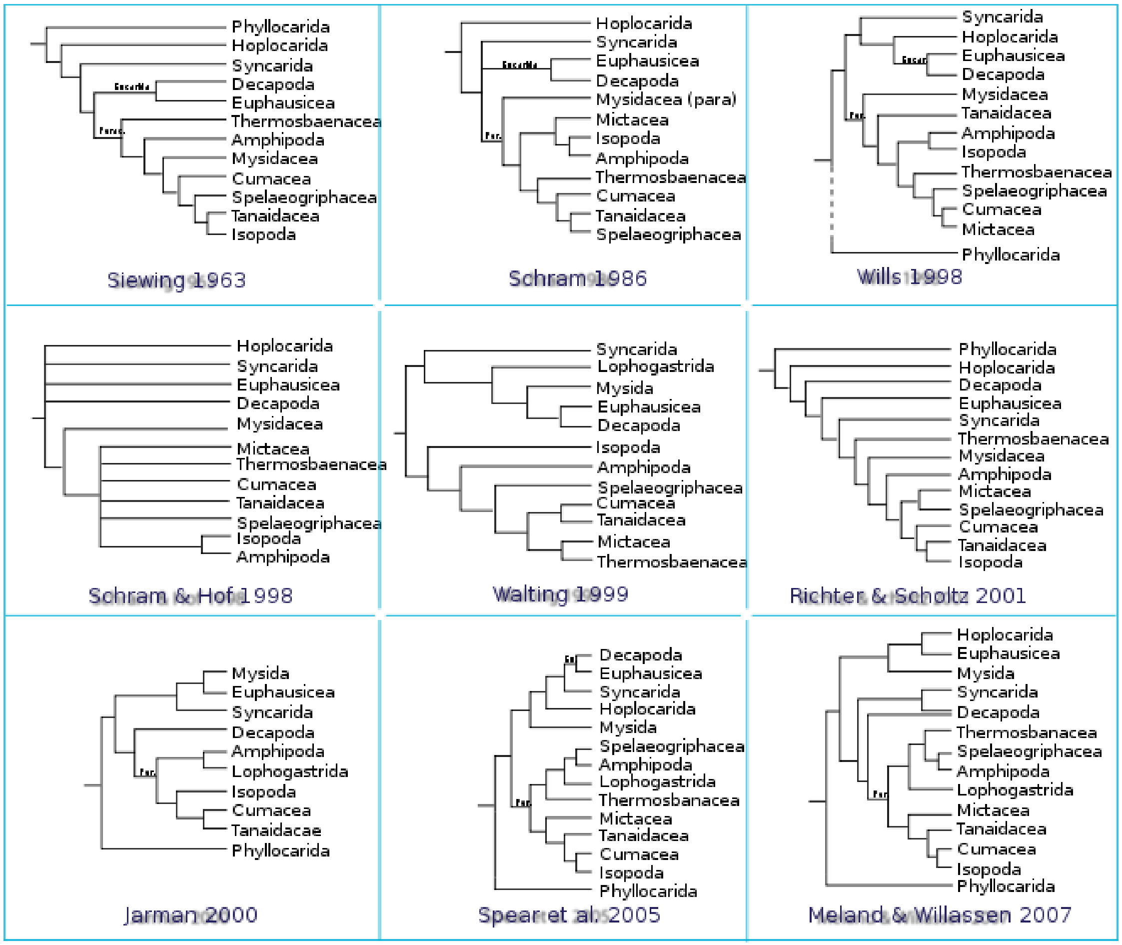
The **phylogeny of Malacostraca** is the arrangement of the Malacostraca classes in the Crustacea subphylum and the relationship of the malacostracan orders.

Introduction

Although this class is united by a number of well defined and documented features, which were recognised a century ago by Calman (1904), the phylogenetic relationship (the evolutionary tree) of the orders which compose this class is unclear due to the vast diversity present in their morphology. Recently molecular studies have attempted to infer the phylogeny of this clade , resulting in phylogenies which have a limited amount of morphological support , to resolve a well-supported eumalacostracan phylogeny,it will be necessary to look beyond the most commonly utilized sources of data (nuclear ribosomal and mitochondrial sequences) to obtain a robust tree in the future.

Features

The Malacostraca is assumed to be monophyletic due to several common morphological traits which are present throughout the group and due to molecular studies that have also confirmed it . William T. Calman in 1904 and 1909 described these common morphological features and introduced the major taxonomic subdivisions of the Malacostraca which are still in use today: he divided the Malacostraca in two subclasses the Phyllocarida and the Eumalacostraca, which is further subdivided into four superorders: Eucarida, Peracarida, Hoplocarida and Syncarida. W.T. Calman coined the term *caridoid facies* for the common eumalacostracan (shrimp-like) features; the most important of these is the constant number of segments in each tagma: members of this class have five segments in the cephalon, eight thoracic segments (thoracomeres) and six segments in the pleon and possess a telson, which forms a characteristic tail fan when the uropods are present. Many other characteristic features are present but their presence varies amongst lineages; one notable ancestral feature which varies is the carapace, which may be absent, reduced or well developed covering the whole cephalothorax. Furthermore, Richter, S., & Scholtz, G. (2001) list five separate unique eumalacostracan features which taken together form a strong argument in favour of the monophyly of the Eumalacostraca. However debate arises in the relationship between the subdivisions of the Malacostraca, due to the presence of several contrasting features.



Phylogenetic trees from several published studies. The first six were obtained via morphological data whereas the last three were obtained with molecular data using a GTR+Γ+I model (General time reversible + gamma distribution+independent frequencies).

The traditional basal malacostracans

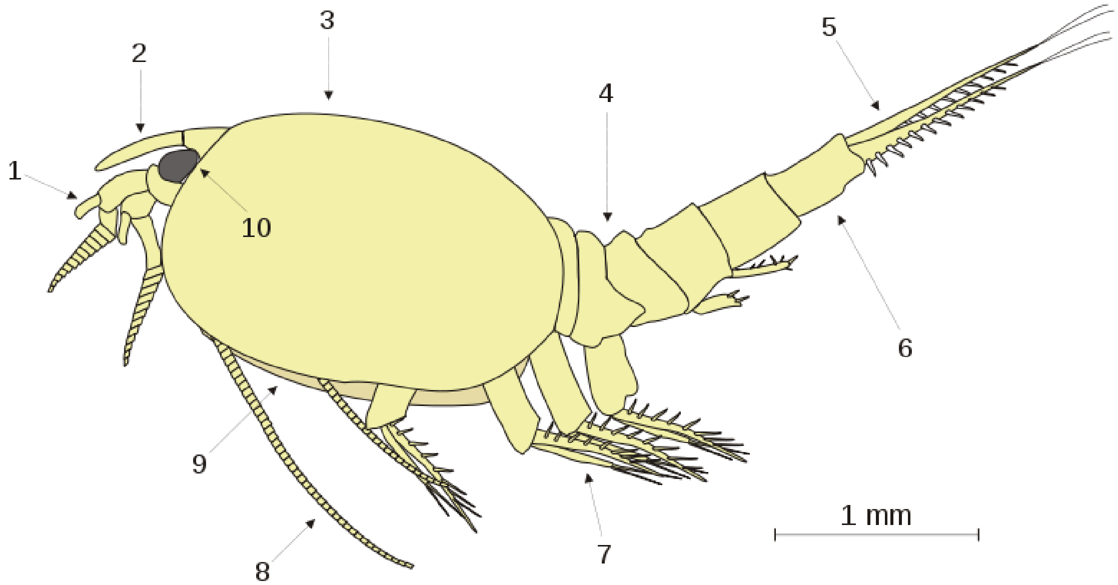


Diagram of *Nebalia bipes* showing the major features of the external anatomy: **1**: antennule; **2**: rostrum; **3**: carapace; **4**: abdomen / pleon; **5**: furca; **6**: telson; **7**: pleopods; **8**: antenna; **9**: thoracopods; **10**: eye

The Phyllocarida is a group of about 36 small marine species that are distributed across planet and possess a characteristic large bivalve carapace and an elongated abdomen with no uropods. This group is believed to be the most primitive malacostracan group, because they lack some of the caridoid facies, such as the presence of seven abdominal segments (eight if telson is included). Furthermore one study by Wills, M.A. places them as a sister branch to the Cephalocarida and basal to a Maxillopoda + Eumalacostraca clade and therefore making the Malacostraca paraphyletic. The Eumalacostraca — the malacostraca minus the phyllocarida — were subdivided on the basis of several features, although which group is basal is unclear. Several authors, such as Siewin (1963), believe that the Syncarida is the most basal group due to the absence of morphological traits that are present in the remaining eumalacostracans; in addition, the Syncarida are distributed worldwide in reclusive habitats such as interstitial and groundwater, whereas their extensive fossil record shows that they were once marine, implying that the species present today are remnants of a more abundant group. A second problematic group often attributed to be basal in the Eumalacostraca clade is the Hoplocarida. This group is composed of 200 species commonly called mantis shrimps, which are found in shallow tropical and subtropical marine habitats that have adapted to a predatorial life thanks to their specialized large second pair of thoracopods (thoracic appendices), raptorial legs, which are used to capture prey, in fact their name is a combination of Greek words meaning “armed shrimp”. Its precise location amongst the Malacostraca is unclear and has been proposed to be a sister group to the remaining eumalacostracans due to its ancient fossil record but it has also been placed either sister to the Eucarida or even inside the Eucarida by molecular studies. In fact, the Malacostracan has a well-documented fossil record, that, although patchy or missing entirely (ghost lineage) for certain clades, offer a unique opportunity to analyse the morphology of the ancestral taxa of a clade or a dead-end sister taxa (plesion), whose age (determined by its stratigraphy) gives an estimate of how long has a group been around. However, the major limitation to fossilized samples is that typically the soft parts do not fossilize and are therefore lost, as a consequence a much more limited amount of information that can be gathered. Furthermore some taxa may not fossilize well, and therefore leave no trace even though they existed, when this occurs in the fossil record, the period were the taxa are expected to appear is called a ghost range.

Eucarida

Eucarida is a diverse and abundant group, whose members have a carapace which is fused to the thoracic segments to form a cephalothorax. The Eucarida is divided into three orders, the Euphausiacea, the Decapoda and the Amphionidacea.
The members of the Euphausiacea are commonly called krill and are all marine shrimp-like species whose pleopods (abdominal appendages) function as swimmerets, they swarm and mostly feed on plankton, this group is composed of only 90 species, but some of these are one of the most abundant species on the planet, in fact, it is estimated that the biomass of the Antarctic krill*Euphausia superba'* is 500 million tons .
The Decapoda is a group with 18,000 species which have 5 pairs of thoracopods and a well developed carapace that covers the gills (which are exposed in krill). Many of these species have common names and are often eaten. The decapods are further subdivided on the basis of the gill structure into two suborders Dendrobranchiata (prawns) and Pleocyemata, which is further subdivided into several infraorders, such as the Caridea (true shrimps), the Stenopodidea (boxer shrimp) and the Anomura and the Brachyura (Crabs) and so forth, although some authors use alternative groupings for these three, Eukyphida, Euzygida and Reptantia (crabs and other decapods), respectively. In addition, there is an enigmatic eucarid species, *Amphionides reynaudii*, which is the sole representative of its order, but due to the loss of several features resulting from its small size, its classification has been unclear.

Peracarida

The other major malacostracan superorder, the Peracarida, is highly diverse in habit, size and shape and contains 21,500 species, but this number is a gross underestimate as the number of described species has tripled in the past 20 years. Most authors studying morphological characters propose a monophyletic Peracarida which forms a well supported subtree that is sister to a Eucarida subtree, one paper is an exception and proposes that the Peracarida is derived from a polyphyletic Eucarida. With the exception of thermosbaenacean species, a characteristic of the members of this group is that they brood their young in a marsupium formed by branches (endites) of their thoracopods, called oostegites . The Peracarida is divided into nine orders (Isopoda, Amphipoda, Mysida, Lophogastrida, Cumacea, Tanaidacea, Mictacea, Thermosbaenacea and Spelaeogriphacea), although some authors prefer to unite two pairs of orders with similar organisms, which are the Mysidacea, formed by the Mysida and the Lophogastrida, and the Edriophthalma, formed by the Isopoda and the Amphipoda . The members of the Mysida and the Lophogastrida have several common features: they are shrimp-like with compound stalked eyes and have a carapace which covers most of the thorax but does not fuse with the last four thoracic segments (as instead is seen in the Eucarida), they possess well developed thoracopods (for swimming) and tail fan, they also have similar behaviour (swarming) and foregut structure ; Pygocephalomorph, a fossil from the Permian, appears similar to the Lophogastrida, which in addition to other factors, has traditionally allowed the Lophogastrida to be identified as the more primitive Mysidacea. However, the monophyly of the Mysidacea been recently disputed , due to molecular data and several differences, one profound difference between the two taxa is that in the Mysida the carapace acts as a respiratory surface due to the absence of gills, which are however present in the Lophogastrida. When they are considered together many authors have put Mysidacea basal to the remaining peracarids ((paraphyletic)Ruppert & Barnes, 1994; ; (monophyletic)), others have even either grouped them with Euphausiacea to form the Schizopoda or made them basal to a eucarid subtree (paraphyletic).

The Isopoda and the Amphipoda are two of the largest pericarid groups, they both lack a carapace, possess sessile compound eyes and lack a sharp demarcation between thoracic and abdominal segments, but however differ in several features, such as gills.
The Isopoda contains 10,000 species, the organisms are dorsoventrally flattened and occupy not only marine and freshwater habitats, but even terrestrial (woodlice) for which they developed a thickened cuticle and gas exchange organs, allowing them to live even in arid regions. The Amphipoda is a highly diverse group of 8,000 species, ranging from the Caprellida with a long and narrow body shape (skeleton shrimp) to the shrimp-like Gammaridea (scuds and sand hoppers). The position of the Isopoda and the Amphipoda amongst the Peracarida is also debated, some authors support a derived united group (Edriophthalma) which is either monophyletic or paraphyletic (Wheeler, 1998), others support a basal paraphyletic Isopoda and Amphipoda group (Watling, 1999); however, other authors believe that several features that unite the Isopoda and the Amphipoda are homoplasious and that the two groups reside with different groups: one proposed a basal Amphipoda to a clade formed from Isopoda + Tanaidacea and Cumacea + Mictacea + Speleogriphacea , while some older phylogenetic trees place the Amphipoda and the Mysidacea basal to the Peracarida (without the Thermosbaenacea) either as a polyphyletic or a monophyletic group, whereas the Isopoda are in a derived clade with Tanaidacea. Recent molecular studies by Jarman et al. (2000), Spears et al. (2005) and Meland & Willassen (2007) (which was derived from Spears et al., (2005) by adding 22 mysidacean taxa to those 26 taxa) suggest a phylogeny with some elements similar to that proposed by Richter & Scholtz (2001), but disprove the monophyly of both the Edriophthalma and the Mysidacea and do not possess a basal eumalacostracan taxa or a basal peracarid taxa (the Hoplocarida and the Syncarida, respectively in): The Amphipoda (with Spleogriphacea) form a clade with the Lophogastrida, the Isopoda are in a derived clade with the Cumacea and Tanaidacea, while most importantly the Mysida in all three analyses falls basal to the non-Peracarida subtree , which however has a limited morphological support (Poore, 2005). The remaining Peracarida orders are the cryptic and either moderately abundant, Cumacea and Tanaidacea, or are extremely rare and relictual, Mictacea, Spelaeogriphacea, and Thermosbaenacea. There are about 1,600

members of the Cumacea, these are small burrowing crustaceans which have a characteristic large bulbous carapace (covering three thoracic segments) and an elongated abdomen which finishes in a pleotelson with stylus-like uropods, in fact due to their peculiar shape they are sometimes called hooded shrimp. Tanaidacea is a group of 1,500 species which are small burrowing or tube-dwelling crustaceans with a short carapace (covering two thoracic segments) that possess a pair of chelate second thoracopods (gnathopods). Only three extant and two fossil speleogriphacean species have been found, these are blind cave-dwelling species with a short carapace (one thoracic segment); while the Mictacea is a group erected only two decades ago, and to date, five species have been found, *Mictocaris halope* (cave dwelling) and four species in the Hursutiidae family, in the genera *Hirsutia* (at 1,000 meter depths) and *Thetispelecaris* (submarine caves), these blind species lack a carapace but have a well developed headshield, and have reduced pleopods. This enigmatic group is believed by some authors not to be monophyletic, in fact one author proposed that *Mictocaris halope* should be grouped with the Spelaeogriphacea, forming the Cosinzeneacea. The Thermosbaenacea is a group of 11 species found in hot springs, caves and groundwater that has the peculiarity that its brooding pouch is formed by its extended carapace and not by modified thoracopod endites as occurs in the remaining peracarids, for this reason some authors have removed this group from the Peracarida and placed it in its own superorder, the Pancarida, basal to the Pericarida .

Molecular studies

The major feature that emerges from the picture of the phylogeny of the Malacostraca is that their diversity has resulted in several studies proposing dramatically different phylogenetic trees. With the advent of DNA sequencing, molecular studies have not helped a particular evolutionary model based on morphology to become the accepted one, but rather they have added more uncertainty to the accepted phylogenetic relationships: in fact not only they contradicted several morphological studies, but they also questioned the monophyly of the Eucarida and the Peracarida, in particular regarding the positions of the Mysida the Syncarida and the Hoplocarida, furthermore the molecular studies to date are only three, two of which overlap and concentrate on the Peracarida, while the third uses a limited amount of taxa.