

The Encyclopedia of Life is an unprecedented effort to gather scientific knowledge about all life on earth—multimedia, information, facts, and more. [Learn more at eol.org](http://eol.org).

Crustaceans



Authors:

Simone Nunes Brandão,
Zoologisches Museum
Hamburg

Jen Hammock, National
Museum of Natural History,
Smithsonian Institution

Frank Ferrari, National
Museum of Natural History,
Smithsonian Institution

Photo credit: Blue Crab (*Callinectes sapidus*) by Jeremy Thorpe,
Flickr: EOL Images. CC BY-NC-SA

Defining the crustacean

The Latin root, crustaceus, "having a crust or shell," really doesn't entirely narrow it down to crustaceans. They belong to the phylum Arthropoda, as do insects, arachnids, and many other groups; all arthropods have hard exoskeletons or shells, segmented bodies, and jointed limbs. Crustaceans are usually distinguishable from the other arthropods in several important ways, chiefly:

Biramous appendages. Most crustaceans have appendages or limbs that are split into two, usually segmented, branches. Both branches originate on the same proximal segment.

Larvae. Early in development, most crustaceans go through a series of larval stages, the first being the nauplius larva, in which only a few limbs are present, near the front on the body; crustaceans add their more posterior limbs as they grow and develop further. The nauplius larva is unique to Crustacea.

Eyes. The early larval stages of crustaceans have a single, simple, median eye composed of three similar, closely opposed parts. This larval eye, or "naupliar eye," often disappears later in development, but on some crustaceans (e.g., the branchiopod Triops) it is retained even after the adult compound eyes have developed. In all copepod crustaceans, this larval eye is retained throughout their development as the

only eye, although the three similar parts may separate and each become associated with their own cuticular lens. In other crustaceans that retain the larval eye into adulthood, up to seven optical units may develop.

Labrum. Crustaceans have a lobe-like structure called the labrum anterior to the mouth that partially encloses it.

Head. Crustaceans are distinguished by a five-segmented head (cephalon), followed by a long trunk typically regionalized into a thorax and abdomen.

“Baby teeth.” Most crustaceans in their early larval stages chew their food with a unique structure called a naupliar arthrite, which is on the second antenna. This chewing tool is lost later in development, and chewing is taken over by the mandibular gnathobase.

Crustacean characters can reveal evolutionary history both by their presence and absence. The naupliar arthrite is one of several characters that are helping researchers to untangle the evolutionary history of crustaceans and other arthropods (Ferrari et al. 2011). Though it is present in larvae of many Crustacea, several groups have lost it over the course of their evolution, and the ostracods never inherited it. Other typical crustacean characters are confusing in a different way: they are shared with non-crustacean arthropods. This makes them handy for examining the relationships of the crustaceans to these other groups. For instance, horseshoe crabs, which are chelicerates, have several appendages that are biramous. These include the sixth (or digging) limb, and the eighth through thirteenth (the book gills or respiratory) limbs. In addition, the oldest living chelicerates, sea spiders, develop in a way very similar to crustaceans, suggesting a close relationship between crustaceans and chelicerates.

Habitat, physiological characteristics, and behavior

Crustaceans live in all kinds of habitats. Triops live in ephemeral pools. More familiar branchiopods that you may know as fairy shrimp do as well. Some copepods and ostracods can also be found in freshwater habitats, as well as crayfish and other decapods. Crustaceans can also be found on land; the most familiar are probably pillbugs, which are a type of isopod. (Not every organism with “bug” in its name is an insect.

Most crustaceans live in the ocean, and are one of the pillars of the global marine ecosystem. In much of the open ocean, the primary herbivores feeding on the phytoplankton are crustaceans. A diverse community of predators—from other crustaceans to squid, fish, and whales—can depend on this population of crustacean grazers: witness *Euphausia superba*, a euphausiid, without which the predator food web of the pelagic Southern Ocean would collapse. Euphausiids (order Euphausiacea) that school in large numbers are known as krill, and form the basis of marine food chains in much of the world’s oceans.

In the microzooplankton, marine fauna (less than a fifth of a millimeter in size) copepod larvae, and some adults, make up an important segment of the community (Landry and Hassett 1982). Only in recent years has this tiny-sized class of plankton been well accounted for, and it turns out to be a significant portion of the biomass in the open ocean. We know little about the role of small copepods in this community; however, recent studies have shown that they feed not only on phytoplankton but also on protozoans and bacteria (see Turner 2004 for review). Overall, the importance of small pelagic crustaceans in linking larger marine animals to the microscopic marine food web is very difficult to measure but hard to exaggerate.

Crustaceans are also important members of benthic communities. They roam the seafloor and burrow in the sediment throughout the global ocean. Some benthic crustaceans are as microscopic and little studied as their pelagic kin, but there are also larger, more familiar groups that have been very well studied. From these more easily observed benthic representatives, we know that crustaceans pursue every imaginable survival strategy. Many have evolved intimate ecological relationships with a stunning array of other organisms.

From gammarid amphipods sheltering in the macroalgae they graze on to a multitude of crabs that wear other animals—everything from sponges to sea urchins—crustaceans are nothing if not neighborly. Did you think hermit crabs only carry snail shells? Sea anemones, hydrozoans, and zoanthid soft corals are also popular passengers. While many crustaceans carry their partners, others prefer to be carried. Some parasitic isopods ride around on fish, and of course barnacles ride around on practically everything, including turtles and whales (and drifting styrofoam!). Other crustaceans co-habitate with fish, like the goby shrimp *Alpheus bellulus*, which keeps house with several species of goby roommates, and contributes to keeping the burrow clean. Lots of crustaceans are in the cleaning business. They graze on filamentous algae growing on other plants, on sessile animals, or on other substrates, and many species of shrimp are active at “cleaning stations,” particular locations in reef habitats that fish know to visit in order to have parasites, dead skin, and other debris nibbled off their bodies. Cleaner shrimp even enter the mouths and gills of their associates in order to clean them.

Some types of crustaceans that may interest you

Branchiopods—including water fleas and the aquarium favorite, fairy shrimp—are usually small animals. A few live in the ocean, but most live in ponds, vernal pools and lakes, including salt lakes. They have many uses for their assorted appendages. They beat their legs rhythmically to cause a flow of water along their bodies, bringing them food particles and oxygen. They can wear their gills on their legs or on their mouthparts. Some use their antennae for swimming, or for grasping a mate during copulation.

Amphipods are shrimp-like in appearance, usually narrow bodied and curled in a distinct hump-backed shape. They inhabit marine water as well as fresh water, and very moist terrestrial habitat. The family Gammaridae is familiar to many aquarium owners; they often colonize aquarium filters, where they feed on detritus. Some can be important indicator species, disappearing at pollution thresholds in freshwater habitat like the Great Lakes. Most species are less than 2 cm long, but there are exceptions. Amphipods made the international news in February 2012 when a crew from the University of Aberdeen found seven huge specimens 7000 m down in a deep-sea trench off New Zealand. The 30-cm animals were nicknamed “supergiant” after *Alicella gigantea*, the largest known amphipod. That species has been found only a handful of times, in widely separated locations in the mid-Atlantic and North Pacific; it is not yet known whether the New Zealand supergiant is the same species, but it is certainly just as elusive. After their initial catch, the crew returned to the same site several times but sighted no others. This is an excellent example of how little we know the deep sea.

Cirripedians (or barnacles) are sessile animals in their adult phase, though they swim in the water column as larvae. Most barnacles live in relatively shallow water and many are famously well adapted for the rough and tumble of life in the shallows and the intertidal zone. They produce a very strong cement with which they attach securely to the substrate to weather the pounding of waves and current; when the receding tide leaves them high and dry, they close their shells to prevent dehydration. (In stalked barnacles, the shell-enclosed body dangles at the end of a long stalk, which is attached to the substrate.)

The substrate can be anything from rock to plants or other animals, and what goes around comes around: for instance, a barnacle growing on a mussel shell may find itself in turn serving as the substrate for a tube-dwelling worm. Most barnacles feed by extending feathery modified legs called setae into the water column to filter for food particles. There are exceptions: some deep sea hydrothermal vent barnacles are believed to “farm” chemosynthetic bacteria on their setae and then eat them. Other barnacles live parasitically in or on crabs.

Copepods, as mentioned above, are extremely abundant at sea and are also found in many freshwater habitats. Some drift with the plankton, others burrow in the sediment, and many parasitize other animals including fish, corals, mollusks, and other invertebrates.

Decapods are for most of us the most familiar crustaceans, at least at meal times. Most of the six million tons of crustaceans reported by the United Nations’ Food and Agricultural Organization (FAO) as harvested in 2010 were decapods—chiefly crabs, lobsters, and shrimp. This is also one of the largest crustacean groups, at approximately 15,000 known species. They inhabit marine and freshwater and a few live on land, but even the tree-climbing coconut crab releases its eggs into the water, where the larvae spend their first month.

Euphausiids (or krill) superficially resemble decapod shrimp, but their appendages appear quite different. Krill lack maxillipeds, and they carry their thoracic gills outside the carapace instead of inside, giving them a feathery appearance. They are abundant throughout the global oceans. Most species feed on algae and are in turn eaten by a wide variety of predators, including fish and baleen whales. Thus they form a critical link between the primary producers and the larger predators in the marine food web.

Isopods are a cosmopolitan group with representatives in most habitats. Half a millimeter to over half a meter long (don’t worry—that one’s a harmless scavenger, and lives only in the deep sea), they also subscribe to a wide variety of survival strategies. They are unusually diverse and successful on land for a crustacean group, with about 4000 species of pillbugs (or woodlice). Most of these prefer moist habitats, and they tend to be nocturnal scavengers. Marine isopods, of which about 5000 have been described, are more diverse in their diets and even a single species can run the gamut from scavenging through hunting to cannibalism. Many marine isopods are parasitic, perhaps none more sophisticated than the infamous *Cymothoa exigua*, which shrivels the tongue of its host, the spotted rose snapper, and then functionally replaces it. That’s right—apparently an isopod makes a perfectly adequate tongue for this fish. At least, the snapper makes do.

Ostracods inhabit virtually all environments where there is water: deep sea; high altitude lakes; tropical sandy beaches and coral reefs; very cold water around the Antarctic continent; temporary ponds. They are mostly aquatic organisms, though there are some species that live in very humid habitats in tropical forests. They are not only very abundant and diverse (10,000 described species), but they have left an impressive fossil record from the last 450 million years (other 20,000 species). This is due to their calcified carapace, which stays in the sediment after the animal dies and is easily fossilized.

Paleontologists study these fossils to understand our planet’s ecological past and how it changed through time. The ostracods are like sages; they’ve lived a very long time, have seen many things and are able to tell us a lot about the past and the future, including climate change. Morphologically, ostracods are very diverse, but all types have their entire body enclosed in a bivalved carapace and all have a reduced number of legs. They reproduce mostly sexually, but a few freshwater species may also reproduce parthenogenetically. They feed mostly on the organic matter on sediment, but some species specialize in grazing holes in algae, while others have become voraciously carnivorous.

Remipedians were discovered in 1979; there were 20 known species at last count. They usually live in submerged coastal caves with connections to freshwater lakes at one end and to the ocean at the other. The animals are typically found in the lower part of the cave, in salt water. They live in total darkness and have no eyes; they depend on highly developed organs and neural centers for smell as their sensory functions. They are 1–4 cm long and swim on their backs, using up to 42 pairs of swimming appendages. They are known to filter feed and scavenge, and may also be predatory. They are hermaphrodites. (Koenemann et al. 2007, 2009).

Stomatopods (or mantis shrimp) are the terror of many an aquarium where they are accidentally introduced, often in live rock. It's not their fault that they like to hide in holes and burrows, and frequently go unnoticed in shipments of rock. They also happen to be predatory and territorial, so they are inclined to either eat or intimidate many of their neighbors. Their powerful forelimbs can be used for spearing or crushing, and have earned them the nickname "thumbsplitters" among fishermen unlucky enough to encounter them from time to time without warning. Some aquarists as well as many divers and snorklers find them beautiful and fascinating for their bright colors and quirky behavior. Mantis shrimp are highly visual, can see 12 colors and polarized light, and address potential mates as well as rivals with elaborate gestures and posturing.

What's with all the -pods?

Those groups (and the –pedians) are all named for characters regarding their feet, from the latin *poda*. Feet are very important to crustaceans and other arthropods. Can you guess the translated names? Ten-foot, oar-feet, mouth-feet, gill-feet, jaw-feet, tendril-feet, one-kind-of-feet, both-kinds-of-feet...)

If you're familiar with all of those groups, you're doing pretty well, but let's not forget the rest of the crustaceans. This incredibly diverse group includes many more subgroups than most of us suspect. New species are discovered every year, and new groupings and divisions are made as researchers tease apart the evolutionary history of these lineages. Here are some more crustaceans you may not have heard of:

Amphionidacea. *Amphionides reynaudii* is the only species in this order, a small (less than one inch long) planktonic crustacean found throughout the world's tropical oceans. The larvae live mostly in shallow waters, the adults in greater depth.

Acrothoracica. Burrowing parasites, related to copepods and barnacles that favor mollusk and coral hosts.

Ascothoracida. Parasites, related to copepods and barnacles that favor echinoderm and coral hosts.

Brachypoda. Blind burrowers in seafloor mud, they feed on detritus and are sometimes known as horseshoe shrimp.

Branchiura. Aptly named "fish lice," these flat-bodied parasites cling to host fish with their maxillae and feed on their blood.

Cumacea. Distributed throughout the global ocean, these animals generally graze on algae, detritus, and microbes in the sediment. Most species are less than 1 cm long.

Facetotecta. This little known group contains only a handful of species in a single genus. They are a sister group to the barnacles and are believed to be parasitic as adults, but we're guessing about that because no adults have ever been observed. This group is known entirely from its larvae.

Leptostraca. Only a few dozen species of these small marine crustaceans are known, but they are distributed among many habitats, from the intertidal to the bathypelagic zone, 1000–4000 meters down in the water column. Most live near the bottom and stir up the sediment to filter for food particles.

Lophogastrida. Most of these pelagic swimmers are a few centimeters long and hunt zooplankton. There are only about 40 species known but they're widely distributed through the world's oceans.

Mictacea. The only fairly well-known species in this very small order inhabits marine caves and has stalked eyes, but may nevertheless be blind.

Mysida. Mysid shrimp resemble krill in general appearance, and can be 2 mm to 8 cm long. Most are omnivores and sift food particles from the water. They are widely distributed and can be found in the water column or on the seafloor at all depths.

Mystacocarida. These tiny crustaceans (less than 1 mm long) are well adapted to live in interstitial habitats between grains of sediment. There are only about a dozen known species. Like most interstitial organisms, they are not well studied, but are believed to scrape food from the surface of sand grains with their abrasive mouthparts.

Pentastomida. Tongue worms are obligate parasites that live in the respiratory tracts of vertebrates, usually reptiles in the tropics, but also other vertebrates such as fish and mammals (including humans). Their life cycle generally involves at least two hosts: an intermediate host in which the eggs develop into larvae and then nymphs, and a definitive host, which is infected by eating the intermediate host. The Pentastomida adults mature and breed in the lungs of the definitive host. The “worms” moniker describes the long, soft body of the animal (2–15 cm in length).

Spelaeogriffacea. These aquatic cave dwellers have only a handful of species known from isolated habitats, but these are very widely spaced: they've been found in Brazil, South Africa and Australia!

Syncarida. Some 200 known species of syncarids can be found in freshwater sediment all over the world. Most are less than a centimeter long. Unlike most crustaceans, they do not carry their eggs but lay them on the substrate or scatter them in the water column after mating.

Tanaidacea. Most of the 1500 known tanaid species are marine. They usually live on the seafloor, often in burrows or tubes. Most are filter feeders, scavengers, or predators, but there is at least one known parasite, which digs its way into the body wall of its sea cucumber host.

Tantulocarida. Crustaceans that parasitize other crustaceans! These animals are among the smallest arthropods, and can be less than a tenth of a millimeter long.

Thermosbaenacea. There are only about a dozen known species, from a range of habitats including North African hot springs, freshwater, and brackish underwater caves. They are not well studied but may feed on dead plant matter.

References

1. Barnard, J.L. and Camilla L. Ingram, 1986. *The Supergiant Amphipod Alicella gigantea Chevreaux from the North Pacific Gyre*. Journal of Crustacean Biology 6(4):825–839.
2. Brusca, R. C. and G. J. Brusca. 2003. The Crustacea. In: Brusca R.C. and G. J. Brusca, Invertebrates. Sunderland, MD: Sinauer Associates; pp. 511–587.
3. Ferrari, F., Fornshell, J., Vagelli, A., Ivanenko, V., and Dahms, H. 2011. *Early Post-Embryonic Development of Marine Chelicerates and Crustaceans with a Nauplius*. Crustaceana 84 (7): 869–893.
4. Koenemann, S., Hoenemann, M., and T. Stemme (Eds). 2009. World Remipedia Database. Available online at <http://www.marinespecies.org/remipedia>. Accessed May 24, 2012.
5. Koenemann, S., Schram, F., Iliffe, T., Hinderstein, L., and A. Bloechl. 2007. *Behavior of Remipedia in the Laboratory, with Supporting Field Observations*. Journal of Crustacean Biology 27(4):534–542.
6. Landry, M. and R. Hassett. 1982. *Estimating the grazing impact of marine micro-zooplankton*. Marine Biology, 67(3): 283–288.
7. Martin, J., Davis, G. 2001. *An Updated Classification of the Recent Crustacea*. Los Angeles, CA: Natural History Museum of Los Angeles County. Science Series 39.
8. Smith, J. S. *Some amazing facts about ostracods*. Online. Accessed July 3, 2012.
9. Smith, J. S. *Ostracod Biology*. Online. Accessed July 3, 2012.
10. Turner, J. 2004. *The Importance of Small Planktonic Copepods and Their Roles in Pelagic Marine Food Webs*. Zoological Studies 43(2): 255–266.