Animals that can Change Color

(Animal Diversity)

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Chapter 1

Polychrotidae

Polychrotidae

Carolina Anole with dewlap extended

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Reptilia
Order:	Squamata
Suborder:	Iguania
Family:	**Polychrotidae**

Genera

- *Anisolepis*
- *Anolis*
- *Chamaeleolis*
- *Chamaelinorops*
- *Ctenonotus* - Eastern Antillean Anoles, Eastern Antillian Anoles
- *Dactyloa* - South American anoles
- *Enyalius*
- *Norops*
- *Phenacosaurus*
- *Polychrus*
- *Urostrophus*
- *Xiphosurus* - Hispaniolan giant

anole, Puerto Rican giant anole

Polychrotidae is a family of lizards commonly known as **anoles**. NCBI places the anole in subfamily **Polychrotinae** of the family Iguanidae. Four genera are common: *Anolis*, *Norops*, *Phenacosaurus*, and *Polychrus*.

Anole lizards are frequently and incorrectly called American chameleons or geckos, although they are not closely related to either of those groups. In fact, they are more closely related to iguanas. These misconceptions are likely due to their ability to alter their skin color and run up walls.

Characteristics and distribution

Anoles are small and common lizards that can be found throughout the southeastern United States, the Caribbean, and various other regions of the Western world. A large majority of them sport a green coloration, including the only species native to North America, the aptly named Green anole, although the green anole can change its color based on its mood and surroundings. Anoles are an exorbitantly diverse and plentiful group of lizards. There are currently about 372 known species. The Knight, Green, Bark Anole, and Cuban brown anoles can all be found in the United States, primarily in Florida, although the most prevalent of these species by far is the Cuban brown anole, which has pushed the native green (or "Carolina") anole population farther north.

Interestingly, when green anoles and brown anoles cohabit the same area, the brown anoles are primarily terrestrial or restrict themselves to the lower branches of bushes, while the green anoles stay higher. Brown anoles have also spread into East Texas. At a nursery in the Heights neighborhood of Houston, Texas, a stable population has established itself, hatchlings having been observed in the Spring of 2005.

All species of anole in the U.S. except the green anole were introduced through eggs nested in imported plants. It is notable that while nearly all anoles can change their color, the extent and variations of this ability differ widely throughout the individual anole species. For example, the green anole can change its color from a bright, leafy green to a dull brown color, while the Cuban brown can only change its shade of brown, along with the patterns on its back.

Anole out of hiding

Many anoles are between 8 and 18 cm (3–7 inches) in length. Some larger species, such as the Knight Anole, can surpass 12 inches (300 mm); some males of the Knight Anole species can even reach 20 inches (510 mm) in length.

Anoles' diets include live insects and other invertebrates, with crickets , spiders , and moths being some of the most commonly consumed prey. Anoles are opportunistic feeders, and may attempt to eat any attractive meal that is small enough. The primary foods for captive anoles are small feeder crickets that can be purchased at most pet stores.

Green Anole on railing

These subtropical lizards are semi arboreal. They usually inhabit regions around 3–6 m (10–20 feet) high. Shrubs, walls, fences, bushes, and short trees are common hiding places.

Most anoles are said to live between 4 and 8 years. Even anoles captured from the wild can live for several years if given acceptable living space and cared for properly—a healthy anole in captivity, being free from predators and natural disaster, may live well beyond seven years. Some anoles may even reach 14 years with careful and proper care.

Green anoles mating

Breeding occurs for several months beginning in late spring. Males employ head bobbing and dewlap extension in courtship. 1–2 small, soft shell eggs are laid among leaf litter. More clutches may be laid before mating season has ended.

Anole populations in each of the Martinique islands, despite remaining separate for an estimated six to eight million years, have not experienced significant evolution, and many mixed-island couples have successfully reproduced.

Anoles have many features that make them readily identifiable. They have a dewlap, made of erectile cartilage, that extends from the neck/throat area. Their toes are covered with structures that allow them to cling to many different surfaces. Also, their tails have the ability to break off at special segments in order to escape predators or fights. The tail itself continues to wriggle strongly for some minutes after detaching. This ability is known as autotomy. Anoles are also diurnal, which means that they are active during the daytime.

Some species of anoles exhibit sexual dimorphism, which allows one to discern between males and females fairly easily with the naked eye. In green anoles, the females are characterized by a pale dorsal stripe extending from neck to tail, generally smaller body, and a smaller head with a shorter snout. Female brown anoles share these characteristics, although their dorsal stripe is oftentimes wider with diamond-shaped or squiggly edges. This stripe may be present sometimes in males, especially young ones not yet fully grown, but it is always fainter with less defined edges. Some females have a small dewlap (pale and much smaller than those of the males); others not at all.

Territory

Anoles are very territorial. Although the lizards are small, their territories are usually quite big: around three square yards, females' usually smaller. Their territories often contain a basking area, a shady area, a high lookout, and always a place to hide from predators. They do not take kindly to other anoles in their territory. Often when an intruder is in the area, the anole raises its spine, fans its dewlap, and does "push-ups" accompanied by intermittent ultrasonic hisses. If this does not scare off the intruder, a fight proceeds in which the two anoles bite at each other's necks. If the anole loses (gives up) the intruder gains entrance, otherwise he leaves. Females rarely fight. Anoles have a wide range of territorial behavior from one head bob to a pressurized bite usually aimed for the snout or jaw of the lizard. When caught by a person they will tend to bite if agitated and require some effort to remove from skin. They very rarely draw blood or cause injury.

Relationship with humans

Female Green Anole on fake plant in captivity

Anoles function well as a native pest control as they will eat spiders, cockroaches, and other bugs and will run from humans whenever possible.

Chapter 2

Cephalopod

Cephalopods
Temporal range: Devonian – Recent
(Stem-groups from Cambrian)

Bigfin reef squid (*Sepioteuthis lessoniana*)

Scientific classification [e]

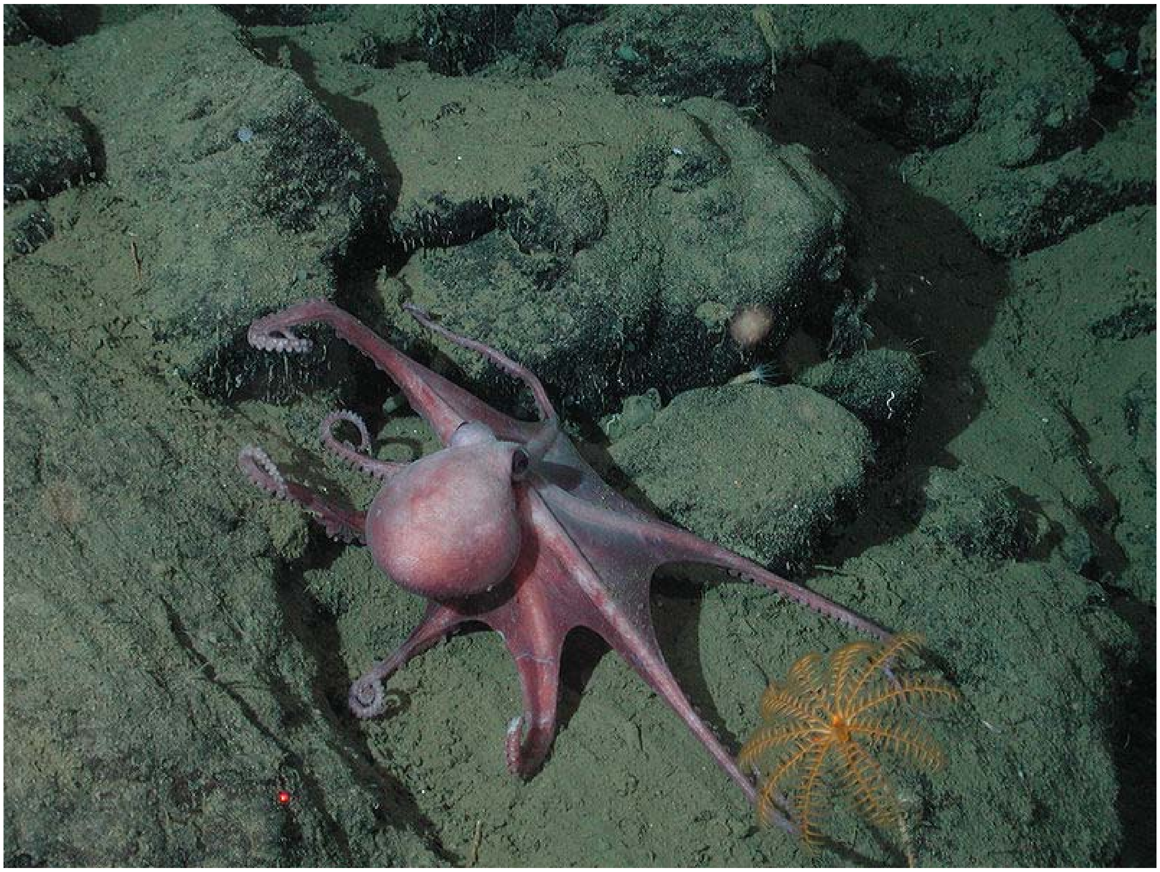
Kingdom:	Animalia
Phylum:	Mollusca
Class:	**Cephalopoda** Cuvier, 1797

A **cephalopod** is any member of the molluscan class **Cephalopoda**. These exclusively marine animals are characterized by bilateral body symmetry, a prominent head, and a set of arms or tentacles (muscular hydrostats) modified from the primitive molluscan foot.

Fishermen sometimes call them **inkfish**, referring to their common ability to squirt ink. The study of cephalopods is a branch of malacology known as **teuthology**.

Cephalopods became dominant during the Ordovician period, represented by primitive nautiloids. The class now contains two, only distantly related, extant subclasses: Coleoidea, which includes octopuses, squid, and cuttlefish; and Nautiloidea, represented by *Nautilus* and *Allonautilus*. In the Coleoidea, the molluscan shell has been internalized or is absent, whereas in the Nautiloidea, the external shell remains. About 800 living species of cephalopods have been identified. Two important extinct taxa are the Ammonoidea (ammonites) and Belemnoidea (belemnites).

Distribution



Left: A pair of *Sepia officinalis* in shallow water
Right: *Benthoctopus* sp. on the Davidson Seamount at 2,422 m depth

There are around 800 extant species of cephalopod, although new species continue to be described. An estimated 11,000 extinct taxa have been described, although the soft-bodied nature of cephalopods means they are not easily fossilised.

Cephalopods are found in all the oceans of Earth. None of them can tolerate freshwater, but the brief squid, *Lolliguncula brevis*, found in Chesapeake Bay may be a notable exception in that it tolerates brackish water.

Cephalopods occupy most of the depth of the ocean, from the abyssal plane to the sea surface. Their diversity is greatest near the equator (~40 species retrieved in nets at 11°N by a diversity study) and decreases towards the poles (~5 species captured at 60°N).

Nervous system and behaviour

Left: An octopus opening a container with a screw cap
Right: Hawaiian bobtail squid, *Euprymna scolopes*, burying itself in the sand, leaving only the eyes exposed

Cephalopods are widely regarded as the most intelligent of the invertebrates, and have well developed senses and large brains (larger than those of gastropods). The nervous system of cephalopods is the most complex of the invertebrates, and their brain-to-body-mass ratio falls between that of warm- and cold-blooded vertebrates. The giant nerve fibers of the cephalopod mantle have been widely used as experimental material in neurophysiology for many years; their large diameter (due to lack of myelination) makes them relatively easy to study.

Cephalopods are social creatures; when isolated from their own kind, they will take to shoaling with fish.

Some cephalopods are able to fly distances up to 50 m. While the organisms are not particularly aerodynamic, they achieve these rather impressive ranges by use of jet-propulsion; water continues to be expelled from the funnel while the organism is in flight.

Senses

Cephalopods have advanced vision, can detect gravity with statocysts, and have a variety of chemical sense organs. Octopuses use their tentacles to explore their environment and can use them for depth perception.

The primitive nautilus eye functions similarly to a pinhole camera.

Vision

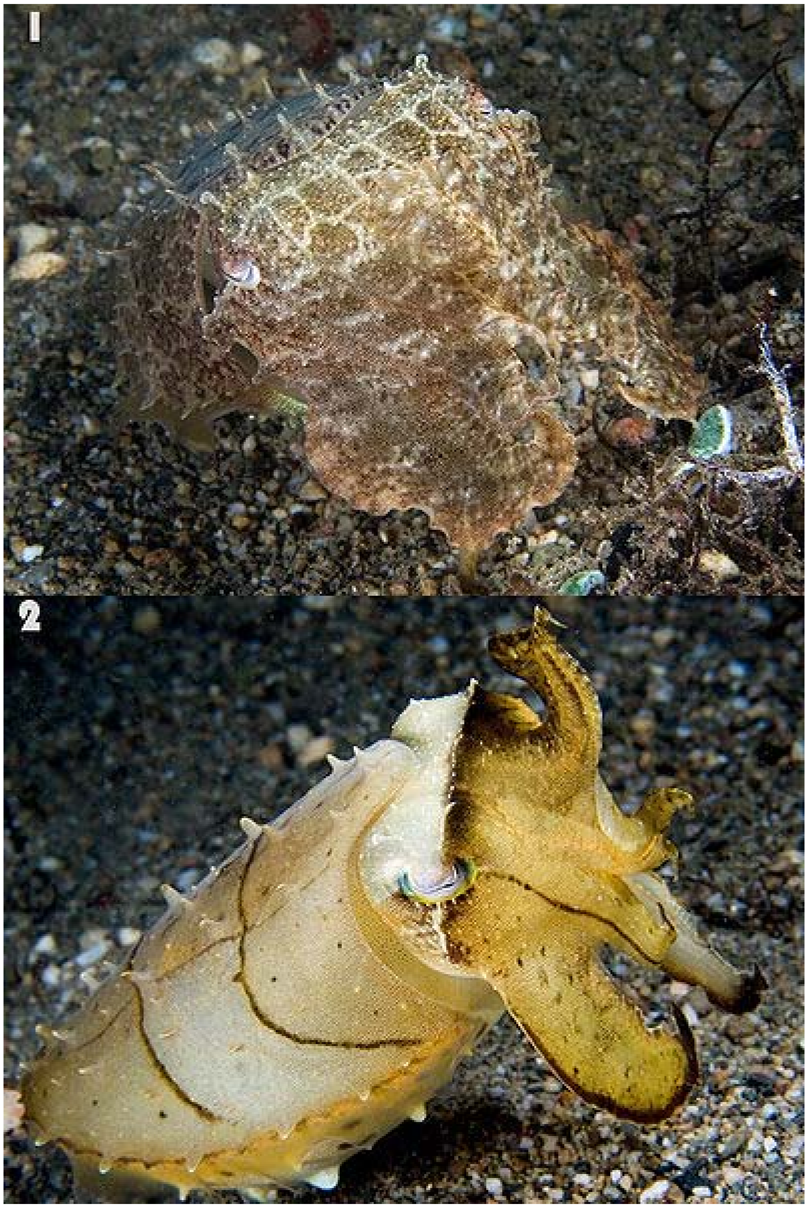
Most cephalopods rely on vision to detect predators and prey, and to communicate with one another. Consequently, cephalopod vision is acute: training experiments have shown that the common octopus can distinguish the brightness, size, shape, and horizontal or vertical orientation of objects. The morphological construction gives cephalopod eyes the same performance as sharks'; however, their construction differs, as cephalopods lack a cornea, and have an everted retina. Cephalopods' eyes are also sensitive to the plane of polarization of light. Surprisingly—given their ability to change color—all octopuses and most cephalopods are color blind. When camouflaging themselves, they use their chromatophores to change brightness and pattern according to the background they see, but their ability to match the specific color of a background may come from cells such as iridophores and leucophores that reflect light from the environment. They also produce visual pigments throughout their body, and may sense light levels directly from their body. Evidence of color vision has been found in the sparkling enope squid (*Watasenia scintillans*), which achieves color vision by the use of three distinct retinal molecules (A1, sensitive to red; A2, to purple, and A4, to yellow?) which bind to its opsin.

Unlike many other cephalopods, nautiluses do not have good vision; their eye structure is highly developed, but lacks a solid lens. They have a simple "pinhole" eye through which water can pass. Instead of vision, the animal is thought to use olfaction as the primary sense for foraging, as well as locating or identifying potential mates.

Hearing

Cephalopods can use their statocysts to detect sound.

Use of light



This broadclub cuttlefish (*Sepia latimanus*) can go from camouflage tans and browns (top) to yellow with dark highlights (bottom) in less than a second.

Most cephalopods possess chromatophores - that is, coloured pigments - which they can use in a startling array of fashions. As well as providing camouflage with their background, some cephalopods bioluminesce, shining light downwards to disguise their shadows from any predators that may lurk below. The bioluminescence is produced by bacterial symbionts; the host cephalopod is able to detect the light produced by these organisms. Bioluminescence may also be used to entice prey, and some species use colourful displays to impress mates, startle predators, or even communicate with one another. It is not certain whether bioluminescence is actually of epithelial origin or if it is a bacterial production.

Colouration

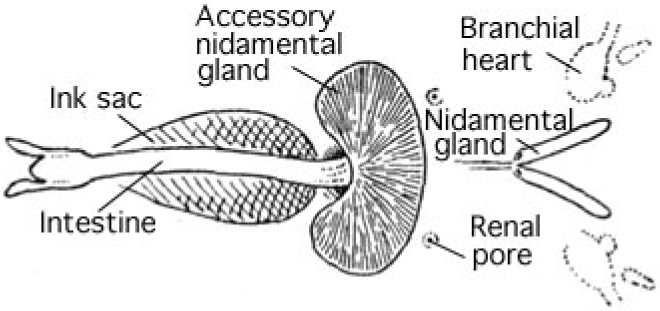
Colouration can be changed in milliseconds as they adapt to their environment, and the pigment cells are expandable by muscular contraction. Colouration is typically more pronounced in near-shore species than those living in the open ocean, whose functions tend to be restricted to camouflage by breaking their outline.

Evidence of original colouration has been detected in cephalopod fossils dating as far back as the Silurian; these orthoconic individuals bore concentric stripes, which are thought to have served as camouflage. Devonian cephalopods bear more complex colour patterns, whose function may be more complex.

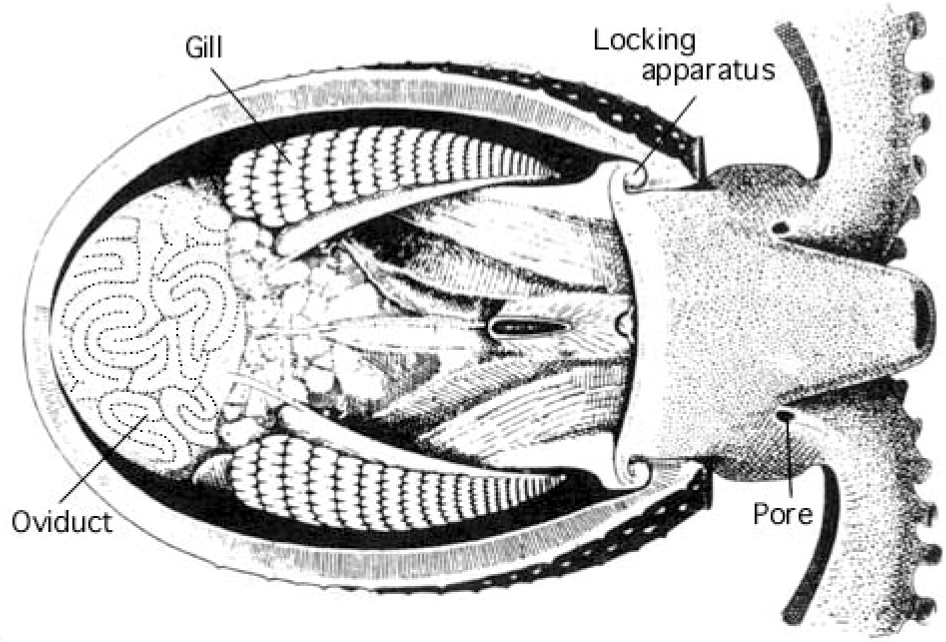
Ink

With the exception of the Nautilidae and the species of octopus belonging to the suborder Cirrina, all known cephalopods have an ink sac, which can be used to expel a cloud of dark ink to confuse predators. This sac is a muscular bag which originated as an extension of the hind gut. It lies beneath the gut and opens into the anus, into which its contents – almost pure melanin – can be squirted; its proximity to the base of the funnel means the ink can be distributed by ejected water as the cephalopod uses its jet propulsion. The ejected cloud of melanin is usually mixed, upon expulsion, with mucus, produced elsewhere in the mantle, and therefore forms a thick cloud, resulting in visual (and possibly chemosensory) impairment of the predator, like a smokescreen. However, a more sophisticated behaviour has been observed, in which the cephalopod releases a cloud, with a greater mucus content, that approximately resembles the cephalopod that released it (this decoy is referred to as a pseudomorph). This strategy often results in the predator attacking the pseudomorph, rather than its rapidly departing prey.

The inking behaviour of cephalopods has led to a common name of "inkfish", primarily used in fisheries science and the fishing industry, paralleling the terms white fish, oily fish, and shellfish.



Viscera of *Chtenopteryx sicula*



Viscera of *Ocythoe tuberculata*

Circulatory system

Cephalopods are the only mollusks with a closed circulatory system. Coleoids have two gill hearts (also known as branchial hearts) that move blood through the capillaries of the gills. A single systemic heart then pumps the oxygenated blood through the rest of the body.

Like most molluscs, cephalopods use hemocyanin, a copper-containing protein, rather than hemoglobin, to transport oxygen. As a result, their blood is colorless when deoxygenated and turns blue when exposed to air.

Respiration

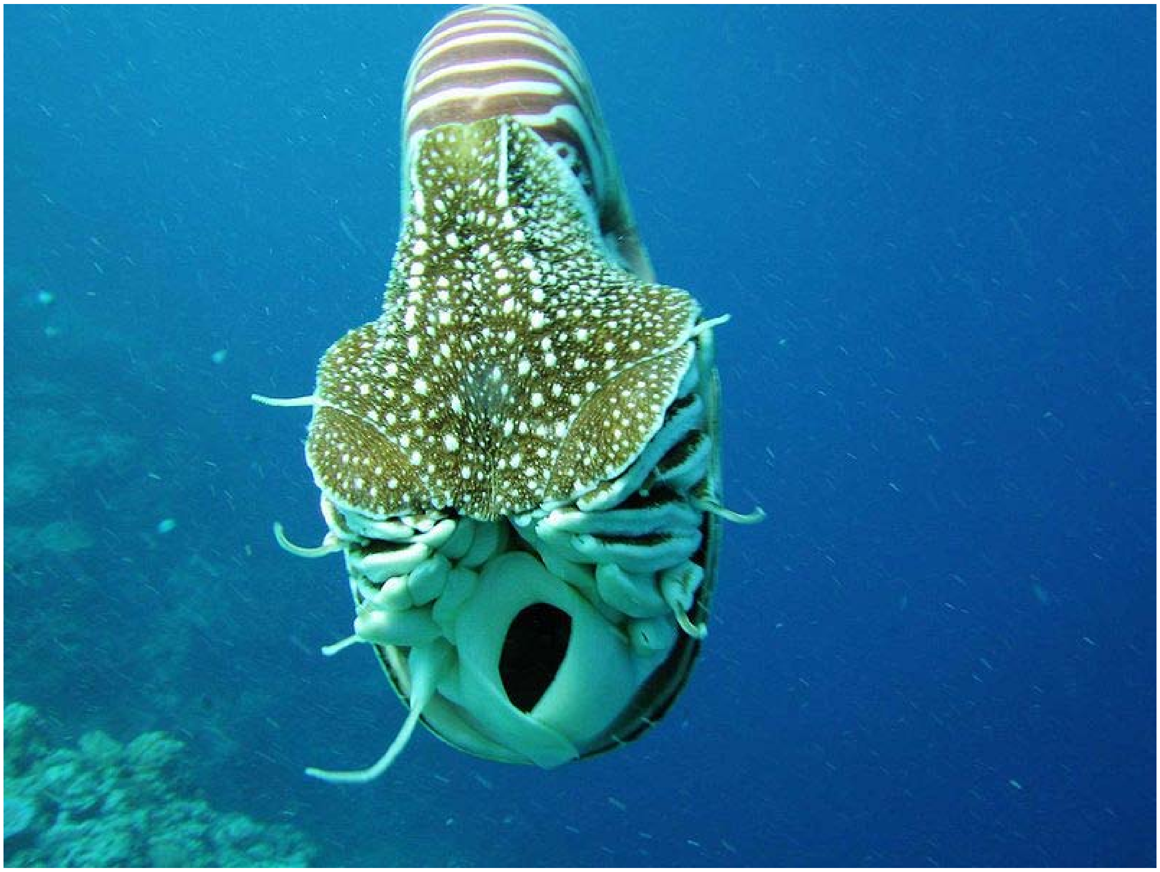
Cephalopods exchange gasses with the seawater by forcing water through their gills, which are attached to the roof of the organism. Water enters the mantle cavity on the outside of the gills, and the entrance of the mantle cavity closes. When the mantle contracts, water is forced through the gills, which lie between the mantle cavity and the funnel. The water's expulsion through the funnel can be used to power jet propulsion. The gills, which are much more efficient than those of other molluscs, are attached to the ventral surface of the mantle cavity. There is a trade-off with gill size regarding lifestyle. To achieve fast speeds, gills need to be small - water will be passed through them quickly when energy is needed, compensating for their small size. However, organisms which spend most of their time moving slowly along the bottom do not naturally pass much water through their cavity for locomotion; thus they have larger gills, along with complex systems to ensure that water is constantly washing through their gills, even when the organism is stationary. The water flow is controlled by contractions of the radial and circular mantle cavity muscles.

The gills of cephalopods are supported by a skeleton of robust fibrous proteins; the lack of mucopolysaccharides distinguishes this matrix from cartilage. The gills are also thought to be involved in excretion, with NH_4^+ being swapped with K^+ from the seawater.

Locomotion and buoyancy

Octopuses swim headfirst, with arms trailing behind

While all cephalopods can move by jet propulsion, this is a very energy-consuming way to travel compared to the tail propulsion used by fish. The relative efficiency of jet propulsion decreases further as animal size increases; paralarvae are far more efficient than juvenile and adult individuals. Since the Paleozoic era, as competition with fish produced an environment where efficient motion was crucial to survival, jet propulsion has taken a back role, with fins and tentacles used to maintain a steady velocity. Whilst jet propulsion is never the sole mode of locomotion, the stop-start motion provided by the jets continues to be useful for providing bursts of high speed - not least when capturing prey or avoiding predators. Indeed, it makes cephalopods the fastest marine invertebrates, and they can out-accelerate most fish. The jet is supplemented with fin motion; in the squid, the fins flap each time that a jet is released, amplifying the thrust; they are then extended between jets (presumably to avoid sinking). Oxygenated water is taken into the mantle cavity to the gills and through muscular contraction of this cavity, the spent water is expelled through the hyponome, created by a fold in the mantle. The size difference between the posterior and anterior ends of this organ control the speed of the jet the organism can produce. The velocity of the organism can be accurately predicted for a given mass and morhpology of animal. Motion of the cephalopods is usually backward as water is forced out anteriorly through the hyponome, but direction can be controlled somewhat by pointing it in different directions. Some cephalopods accompany this expulsion of water with a gunshot-like popping noise, thought to function to frighten away potential predators.



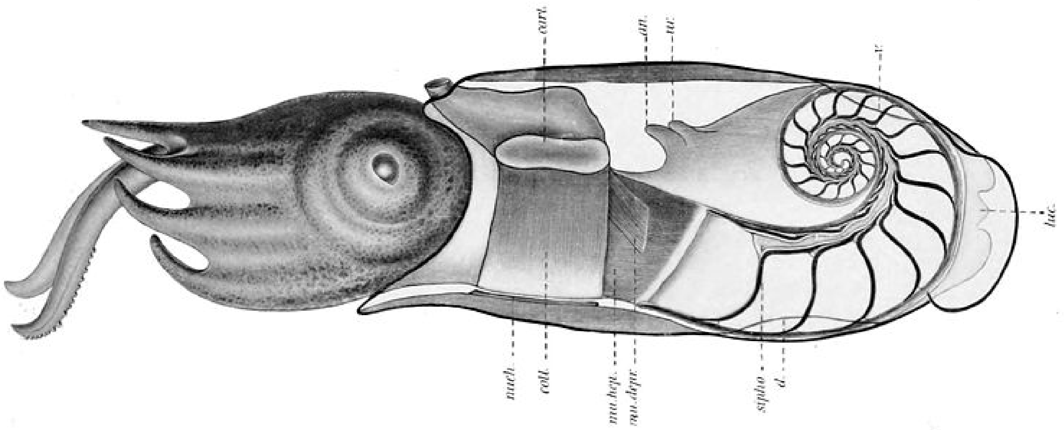
Nautilus belauensis seen from the front, showing the opening of the hyponome

Early cephalopods are thought to have produced jets by drawing their body into their shells, as *Nautilus* does today. *Nautilus* is also capable of creating a jet by undulations of its funnel; this slower flow of water is more suited to the extraction of oxygen from the water. The jet velocity in *Nautilus* is much slower than in coleoids, but less musculature and energy is involved in its production. Jet thrust in cephalopods is controlled primarily by the maximum diameter of the funnel orifice (or, perhaps, the average diameter of the funnel) and the diameter of the mantle cavity. Changes in the size of the orifice are used most at intermediate velocities. The absolute velocity achieved is limited by the cephalopod's requirement to inhale water for expulsion; this intake limits the maximum velocity to eight body-lengths per second, a speed which most cephalopods can attain after two funnel-blows. Water refills the cavity by entering not only through the orifices, but also though the funnel. To accommodate the rapid changes in water intake and expulsion, the orifices are highly flexible and can change their size by a factor of twenty; the funnel radius, conversely, changes only by a factor of around 1.5.

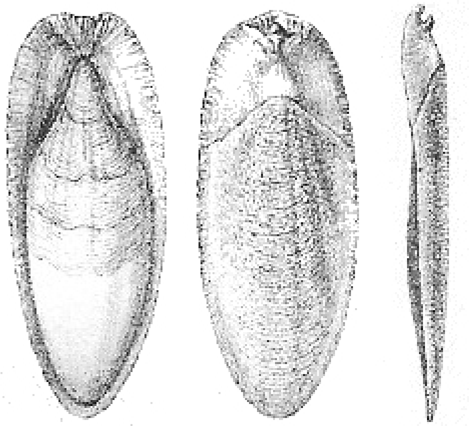
Some octopus species are also able to walk along the sea bed. Squids and cuttlefish can move short distances in any direction by rippling of a flap of muscle around the mantle.

While most cephalopods float (i.e. are neutrally buoyant or nearly so; in fact most cephalopods are about 2-3% denser than seawater), they achieve this in different ways. Some, such as *Nautilus*, allow gas to diffuse into the gap between the mantle and the shell; others allow purer water to ooze from their kidneys, forcing out denser salt water from the body cavity; others, like some fish, accumulate oils in the liver; and some octopuses have a gelatinous body with lighter chlorine ions replacing sulfate in the body chemistry.

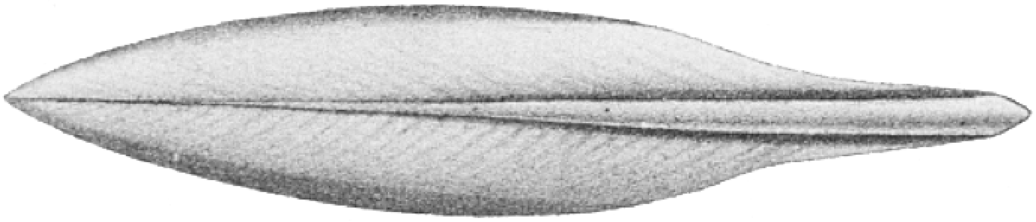
Shell



Cross section of *Spirula spirula*, showing the position of the shell inside the mantle



Cuttlebone of *Sepia officinalis*



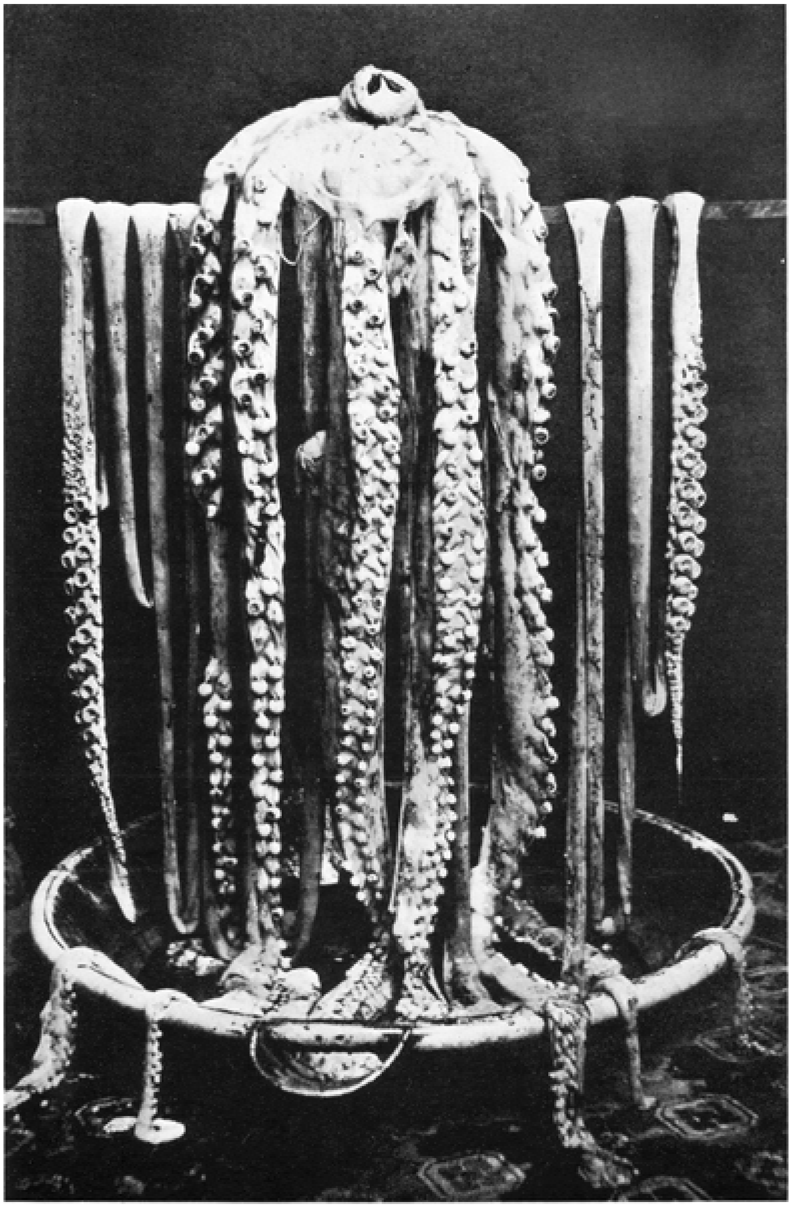
Gladius of *Sepioteuthis lessoniana*

Nautiluses are the only extant cephalopods with an external shell. However, all molluscan shells are formed from the ectoderm (outer layer of the embryo); in cuttlefish (*Sepia* spp.), for example, an invagination of the ectoderm forms during the embryonic period, resulting in a shell that is internal in the adult. The same is true of the chitinous gladius of squid and octopus. Cirrate octopuses have cartilaginous fin supports, which are sometimes referred to as a "shell vestige" or "gladius". The Incirrina have no vestige of an internal shell, and some squid also lack a gladius. Interestingly, the shelled coleoids do not form a clade or even a paraphyletic group. The *Spirula* shell begins as an organic structure, and is then very rapidly mineralized. Shells that are "lost" may be lost by resorption of the calcium carbonate component.

Females of the octopus genus *Argonauta* secrete a specialised paper-thin eggcase in which they reside, and this is popularly regarded as a "shell", although it is not attached to the body of the animal.

The largest group of shelled cephalopods, the ammonites, are extinct, but their shells are very common as fossils.

The deposition of carbonate, leading to a mineralized shell, appears to be related to the acidity of the organic shell matrix; shell-forming cephalopods have an acidic matrix, whereas the gladius of squid has a basic matrix.



Left: A giant squid found in Logy Bay, Newfoundland, in 1873. The two long feeding tentacles are visible on the extreme left and right.
Right: Detail of the tentacular club of *Abraliopsis morisi*

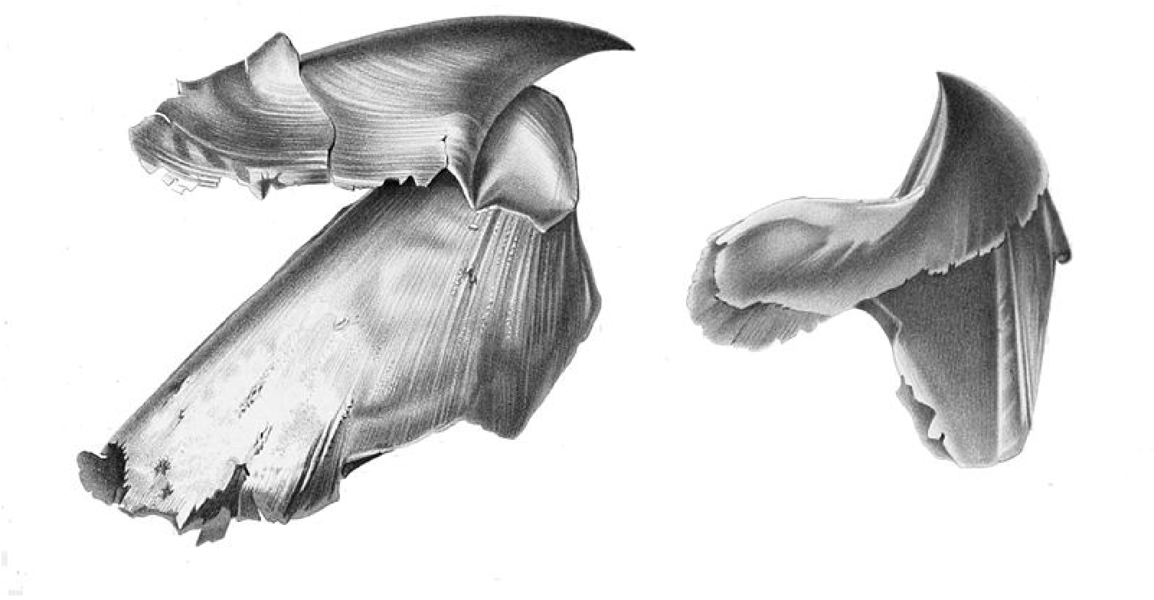
Head appendages

Cuttlefish and squid have five pairs of muscular appendages surrounding their mouths. The longer two, termed tentacles, are actively involved in capturing prey; they can lengthen rapidly (in as little as 15 milliseconds). In giant squid they may reach a length of 8 metres. They may terminate by broadening into a sucker-coated club.The shorter four pairs are termed arms, and are involved in holding and manipulating the captured organism. They too have suckers, on the side closest to the mouth; these help to hold onto the prey.

The tentacle consists of a thick central nerve cord (which must be thick to allow each sucker to be controlled independently) surrounded by circular and radial muscles. Because the volume of the tentacle remains constant, contracting the circular muscles decreases the radius and permits the rapid increase in length. Typically a 70% lengthening is achieved by decreasing the width by 23%.

The size of the tentacle is related to the size of the buccal cavity; larger, stronger tentacles can hold prey as small bites are taken from it; with more numerous, smaller tentacles, prey is swallowed whole, so the mouth cavity must be larger.

Feeding



The two-part beak of the giant squid, *Architeuthis* sp.

All living cephalopods have a two-part beak; most have a radula, although it is reduced in most octopus and absent altogether in *Spirula*. They feed by capturing prey with their tentacles, drawing it in to their mouth and taking bites from it. They have a mixture of toxic digestive juices, some of which are manufactured by symbiotic algae, which they eject from their salivary glands onto their captured prey held in their mouth. These juices separate the flesh of their prey from the bone or shell. The salivary gland has a small tooth at its end which can be poked into an organism to digest it from within.

The digestive gland itself is rather short. It has four elements, with food passing through the crop, stomach and caecum before entering the intestine. Most digestion, as well as the absorption of nutrients, occurs in the digestive gland, sometimes called the liver. Nutrients and waste materials are exchanged between the gut and the digestive gland through a pair of connections linking the gland to the junction of the stomach and caecum. Cells in the digestive gland directly release pigmented excretory chemicals into the lumen of the gut, which are then bound with mucus passed through the anus as long dark strings, ejected with the aid of exhaled water from the funnel.

Radula

Amphioctopus marginatus eating a crab

The cephalopod radula consists of multiple symmetrical rows of up to nine teeth – thirteen in fossil classes. The organ is reduced or even vestigial in certain octopus species and is absent in *Spirula*. The teeth may be homodont (i.e. similar in form across a row), heterodont (otherwise), or ctenodont (comb-like). Their height, width and number of cusps is variable between species. The pattern of teeth repeats, but each row may not be identical to the last; in the octopus, for instance, the sequence repeats every five rows.

Cephalopod radulae are known from fossil deposits dating back to the Ordovician. They are usually preserved within the cephalopod's body chamber, commonly in conjunction with the mandibles; but this need not always be the case; many radulae are preserved in a range of settings in the Mason Creek. Radulae are usually difficult to detect, even when they are preserved in fossils, as the rock must weather and crack in exactly the right fashion to expose them; for instance, radulae have only been found in nine of the 43 ammonite genera, and they are rarer still in non-ammonoid forms: only three pre-Mesozoic species possess one.

Excretory system

Most cephalopods possess a single pair of large nephridia. Filtered nitrogenous waste is produced in the pericardial cavity of the branchial hearts, each of which is connected to a nephridium by a narrow canal. The canal delivers the excreta to a bladder-like renal sac, and also resorbs excess water from the filtrate. Several outgrowths of the lateral vena cava project into the renal sac, continuously inflating and deflating as the branchial hearts beat. This action helps to pump the secreted waste into the sacs, to be released into the mantle cavity through a pore.

Nautilus, unusually, possesses four nephridia, none of which are connected to the pericardial cavities.

Ammonium

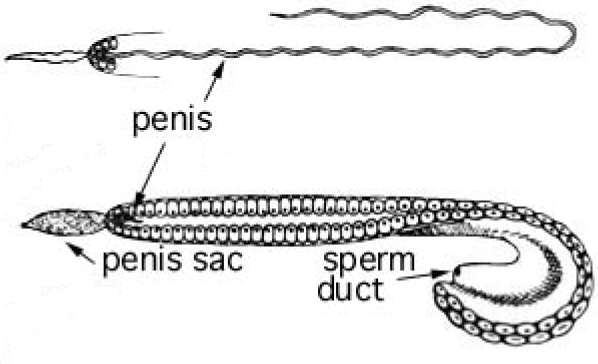
The handling of ammonia is thought to be important in shell formation in terrestrial molluscs, and in other nonmolluscan lineages.

Because protein (i.e. flesh) is a major constituent of the cephalopod diet, large amounts of ammonium are produced as waste. The main organs involved with the release of this excess ammonium are the gills.

The rate of this release is the lowest in the shelled cephalopods *Nautilus* and *Sepia*, probably as a result of their use of nitrogen to fill their shells with gas to produce buoyancy. Other cephalopods use ammonium in a similar way, storing the ions (as ammonium chloride) themselves to reduce their overall density and thus become more buoyant.

Reproduction and life cycle

Female *Argonauta argo* with eggcase and eggs



Detail of the hectocotylus of *Ocythoe tuberculata*

A dissected male specimen of *Onykia ingens*, showing a non-erect penis (the white tubular structure located below most of the other organs)

A specimen of the same species exhibiting elongation of the penis to 67 cm in length

With a few exceptions, Coleoidea live short lives with rapid growth. Most of the energy extracted from their food is used for growing. The penis in most male Coleoidea is a long and muscular end of the gonoduct used to transfer spermatophores to a modified arm called a hectocotylus. That, in turn, is used to transfer the spermatophores to the female. In species where the hectocotylus is missing, the penis is long and able to extend beyond the mantle cavity and transfers the spermatophores directly to the female. Deep water squid have the greatest known penis length relative to body size of all mobile animals, second in the entire animal kingdom only to certain sessile barnacles. Penis elongation in *Onykia ingens* may result in a penis that is as long as the mantle, head and arms combined.

Most cephalopods tend towards a semelparous reproduction strategy; they lay many small eggs in one batch and die afterwards. The Nautiloidea, on the other hand, stick to iteroparity; they produce a few large eggs in each batch and live for a long time.

External sexual characteristics are lacking in cephalopods, so cephalopods use colour communication. A courting male will approach a likely looking opposite number flashing his brightest colours, often in rippling displays. If the other cephalopod is female and receptive, her skin will change colour to become pale, and mating will occur. If the other cephalopod remains brightly coloured, it is taken as a warning.

The male has a sperm-carrying arm, known as the hectocotylous arm, with which to impregnate the female. In many cephalopods, mating occurs head to head and the male may simply transfer sperm to the female. Others may detach the sperm-carrying arm and leave it attached to the female. In the paper nautilus, this arm remains active and wriggling for some time, prompting the zoologists who discovered it to conclude it was some sort of worm-like parasite. It was duly given a genus name *Hectocotylus*, which held for some time until the mistake was discovered.

Nidamental glands are involved in the secretion of egg cases or the gelatinous substance comprising egg masses. The eggs may be brooded: female paper nautilus construct a shelter for the young, while Gonatiid squid carry a larva-laden membrane from the hooks on their arms. Other cephalopods deposit their young under rocks and aerate them with their tentacles hatching. Often, though, the eggs are left to their own devices; many squid lay sausage-like bunches of eggs in crevices or occasionally on the sea floor. Cuttlefish lay their eggs separately in cases and attach them to coral or algal fronds. Fossilised egg clutches show that ammonites also laid clutches of eggs.

Cephalopods are occasionally long-lived, especially in the deep water or polar forms, but most of the group live fast and die young, maturing rapidly to their adult size. Some may gain as much as 12% of their body mass each day. Most live for one to two years, reproducing and then dying shortly thereafter.

To free up resources for reproduction, many squid are known to resorb the muscle tissue of their mantle and tentacles, breaking down the tissue and using the energy contained therein to produce more gametes.

Egg cases laid by a female squid

Embryology

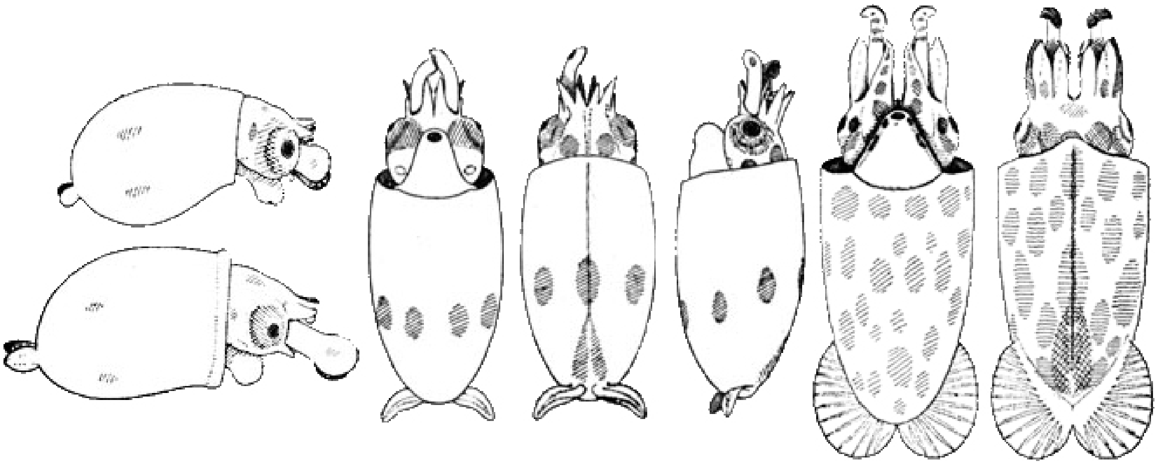
Unlike most other molluscs, cephalopods do not have a distinct larval stage. The fertilised ovum initially divides to produce a disc of germinal cells at one pole, with the yolk remaining at the opposite pole. The germinal disc grows to envelop and eventually absorb the yolk, forming the embryo. The tentacles and arms first appear at the hind part of the body, where the foot would be in other molluscs, and only later migrate towards the head.

The funnel of cephalopods develops on the top of their head, whereas the mouth develops on the opposite surface. The early embryological stages are reminiscent of ancestral gastropods and extant Monoplacophora.

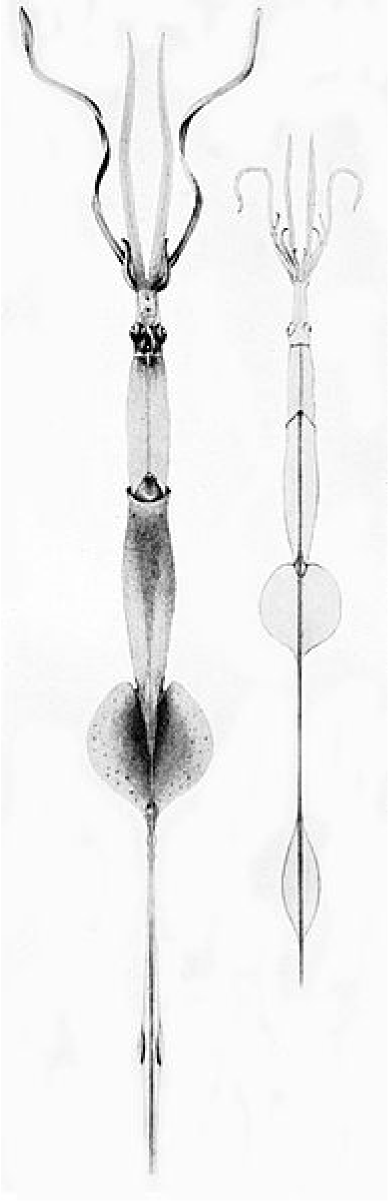
The shells develop from the ectoderm as an organic framework which is subsequently mineralised. In *Sepia*, which has an internal shell, the ectoderm forms an invagination whose pore is sealed off before this organic framework is deposited.

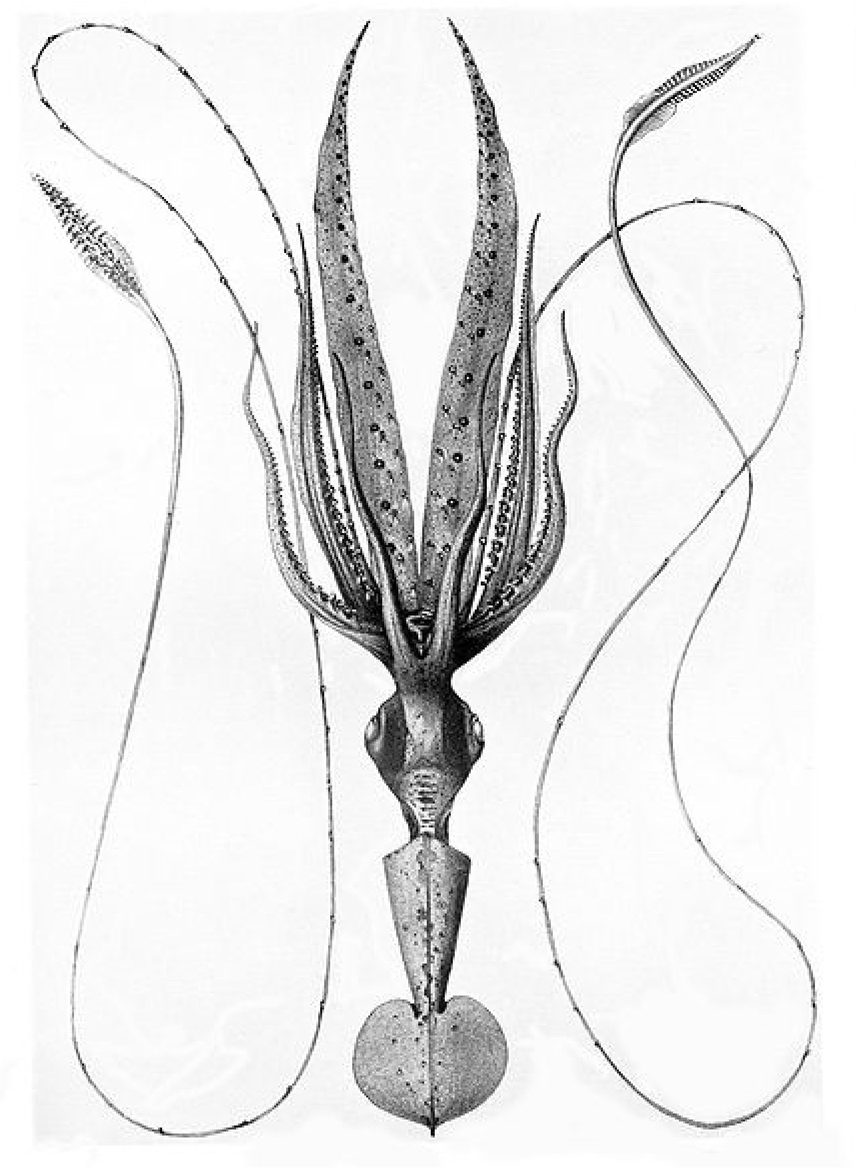
The gene *engrailed* is expressed first in the arms, funnel and optic vesicles, and is only later present in the tentacles and eyelids. It is expressed in embryonic stages 17–19 in all arm buds, and subsequently in the future-tentacles in stages 24–5, suggesting that it may serve a role in the differential development of tentacles. Sequential expression of Hox genes is also observed in cephalopod arms.

Development



Chtenopteryx sicula paralarvae. **Left:** Two very young paralarvae. The circular tentacular clubs bear approximately 20 irregularly arranged suckers. Two chromatophores are present on each side of the mantle. **Centre:** Ventral, dorsal and side views of a more advanced paralarva. An equatorial circulet of seven large yellow-brown chromatophores is present on the mantle. Posteriorly the expanded vanes of the gladius are visible in the dorsal view. **Right:** Ventral and dorsal views of a very advanced paralarva.





Left: Immature specimens of *Chiroteuthis veranyi*. In this paralarval form, known as the doratopsis stage, the pen is longer than the mantle and 'neck' combined

Right: A mature *Chiroteuthis veranyi*. This species has some of the longest tentacles in proportion to its size of any known cephalopod.

Cephalopod eggs span a large range of sizes, from 1 to 30 mm in diameter. The length of time before hatching is highly variable; smaller eggs in warmer waters are the fastest to hatch, and newborns can emerge after as little as a few days. Larger eggs in colder waters can develop for over a year before hatching.

The process from spawning to hatching follows a similar trajectory in all species, the main variable being the amount of yolk available to the young and when it is absorbed by the embryo.

Young do not pass through a larval stage, strictly speaking. They quickly learn how to hunt, using encounters with prey to refine their strategies.

Growth in juveniles is usually allometric, whilst adult growth is isometric.

Evolution

The traditional view of cephalopod evolution holds that they evolved in the Late Cambrian from a monoplacophoran-like ancestor with a curved, tapering shell, which was closely related to the gastropods (snails). The similarity of the early shelled cephalopod *Plectronoceras* to some gastropods was used in support of this view. The development of a siphuncle would have allowed the shells of these early forms to become gas-filled (thus buoyant) in order to support them and keep the shells upright while the animal crawled along the floor, and separated the true cephalopods from putative ancestors such as *Knightoconus*, which lacked a siphuncle. Neutral or positive buoyancy (i.e. the ability to float) would have come later, followed by swimming in the Plectronocerida and eventually jet propulsion in more derived cephalopods.

However, some morphological evidence is difficult to reconcile with this view, and the redescription of *Nectocaris pteryx*, which did not have a shell and appeared to possess jet propulsion in the manner of "derived" cephalopods, complicated the question of the order in which cephalopod features developed – provided *Nectocaris* is a cephalopod at all.

Early cephalopods were likely predators near the top of the food chain. They underwent pulses of diversification during the Ordovician period to become diverse and dominant in the Paleozoic and Mesozoic seas. In the Early Palaeozoic, their range was far more restricted than today; they were mainly constrained to sublittoral regions of shallow shelves of the low latitudes, and usually occur in association with thrombolites. A more pelagic habit was gradually adopted as the Ordovician progressed. Deep-water cephalopods, whilst rare, have been found in the Lower Ordovician - but only in high-latitude waters. The mid Ordovician saw the first cephalopods with septa strong enough to cope with the pressures associated with deeper water, and could inhabit depths greater than 100–200 m. The direction of shell coiling would prove to be crucial to the future success of the lineages; endogastric coiling would only permit large size to be attained with a straight shell, whereas exogastric coiling - initially rather rare - permitted the spirals familiar from the fossil record to develop, with their corresponding large size and diversity. (Endogastric mean the shell is curved so as the ventral or lower side is longitudinally concave (belly in); exogastric means the shell is curve so as the ventral side is longitudinally convex (belly out) allowing the funnel to be pointed backwards beneath the shell.)

An ammonitic ammonoid with the body chamber missing, showing the septal surface (especially at right) with its undulating lobes and saddles

The ancestors of coleoids (including most modern cephalopods) and the ancestors of the modern nautilus, had diverged by the Floian Age of the Early Ordovician Period, over 470 million years ago. The Bactritida, an Silurian–Triassic group of orthocones, are widely held to be paraphyletic to the coleoids and ammonoids – that is, the latter groups arose from within the Bactritida. An increase in the diversity of the coleoids and ammonoids is observed around the start of the Devonian period, and corresponds with a profound increase in fish diversity. This could represent the origin of the two derived groups.

Unlike most modern cephalopods, most ancient varieties had protective shells. These shells at first were conical but later developed into curved nautiloid shapes seen in modern nautilus species. Competitive pressure from fish is thought to have forced the shelled forms into deeper water, which provided an evolutionary pressure towards shell loss and gave rise to the modern coleoids, a change which led to greater metabolic costs associated with the loss of buoyancy, but which allowed them to recolonise shallow waters. However, some of the straight-shelled nautiloids evolved into belemnites, out of which some evolved into squid and cuttlefish. The loss of the shell may also have resulted from evolutionary pressure to increase manoeuvrability, resulting in a more fish-like habit.

Phylogeny

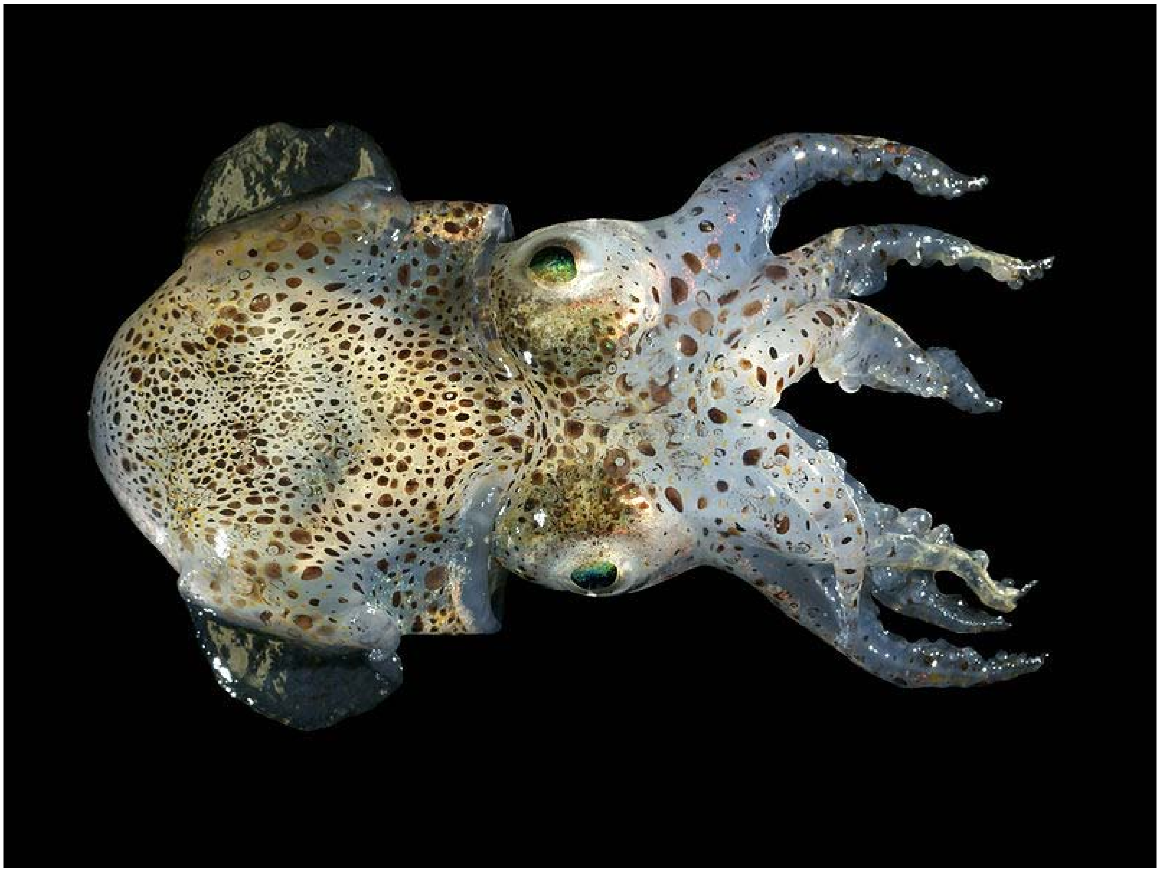
The internal phylogeny of the cephalopods is difficult to constrain; many molecular techniques have been adopted, but the results produced are conflicting. *Nautilus* tends to be considered an outgroup, with *Vampyroteuthis* forming an outgroup to other squid; however in one analysis the nautiloids, octopus and teuthids plot as a polytomy. Some molecular phylogenies do not recover the mineralized coleoids (*Spirula*, *Sepia*, and *Metasepia*) as a clade; however, others do recover this more parsimonious-seeming clade, with *Spirula* as a sister group to *Sepia* and *Metasepia* in a clade that had probably diverged before the end of the Triassic.

Molecular estimates for clade divergence vary. One 'statistically robust' estimate has *Nautilus* diverging from *Octopus* at 415 ± 24 million years ago.

Taxonomy

Chambered Nautilus (*Nautilus pompilius*)

Common Cuttlefish (*Sepia officinalis*)



Atlantic Bobtail (*Sepiola atlantica*)

European Squid (*Loligo vulgaris*)

Common Octopus (*Octopus vulgaris*)

The classification presented here, for recent cephalopods, follows largely from Current Classification of Recent Cephalopoda (May 2001), for fossil cephalopods takes from Arkell et al. 1957, Teichert and Moore 1964, Teichert 1988, and others. The three subclasses are traditional, corresponding to the three orders of cephalopods recognized by Bather.

Class Cephalopoda († indicates extinct groups)

- Subclass Nautiloidea: Fundamental ectocochliate cephalopods that provided the source for the Ammonoidea and Coleoidea.
    - Order † Plectronocerida: the ancestral cephalopods from the Cambrian Period
    - Order † Ellesmerocerida (500 to 470 Ma)
    - Order † Endocerida (485 to 430 Ma)
    - Order † Actinocerida (480 to 312 Ma)
    - Order † Discosorida (482 to 392 Ma)
    - Order † Pseudorthocerida (432 to 272 Ma)
    - Order † Tarphycerida (485 to 386 Ma)
    - Order † Oncocerida (478.5 to 324 Ma)
    - Order Nautilida (extant; 410.5 to 0 Ma)
    - Order † Orthocerida (482.5 to 211.5 Ma)
    - Order † Ascocerida (478 to 412 Ma)
    - Order † Bactritida (418.1 to 260.5 Ma)

- Subclass † Ammonoidea: Ammonites (479 to 65 Ma)
    - Order † Goniatitida (388.5 to 252 Ma)
    - Order † Ceratitida (254 to 200 Ma)
    - Order † Ammonitida (215 to 66 Ma)
- Subclass Coleoidea (410.0 Ma-Rec)
    - Cohort † Belemnoidea: Belemnites and kin
        - Genus † *Jeletzkya*
        - Order † Aulacocerida (265 to 183 Ma)
        - Order † Phragmoteuthida (189.6 to 183 Ma)
        - Order † Hematitida (339.4 to 318.1 Ma)
        - Order † Belemnitida (339.4 to 65.5 Ma)
        - Genus † *Belemnoteuthis* (189.6 to 183 Ma)
    - Cohort Neocoleoidea
        - Superorder Decapodiformes (also known as Decabrachia or Decembranchiata)
            - ?Order † Boletzkyida
            - Order Spirulida: Ram's Horn Squid
            - Order Sepiida: cuttlefish
            - Order Sepiolida: pygmy, bobtail and bottletail squid
            - Order Teuthida: squid
        - Superorder Octopodiformes (also known as Vampyropoda)
            - Family † Trachyteuthididae
            - Order Vampyromorphida: Vampire Squid
            - Order Octopoda: octopus

Other classifications differ, primarily in how the various decapod orders are related, and whether they should be orders or families.

Suprafamilial classification of the Treatise

This is the older classification that combines those found in parts K and L of the Treatise on Invertebrate Paleontology, which forms the basis for and is retained in large part by classifications that have come later.

Nautiloids in general, (Teichert and Moore 1964) Sequence as given.

> Subclass † Endoceratoidea. Not used by Flower, e.g. Flower and Kummel 1950, interjocerids included in the Endocerida.
> Order † Endocerida
> Order † Intejocerida
> Subclass † Actinoceratoidea Not used by Flower, ibid
> Order † Actinocerida
> Subclass † Nautiloidea Nautiloidea in the restricted sense.
> Order † Ellesmerocerida Plectronocerida subsequently split off as separate order.
> Order † Orthocerida Includes orthocerids and pseudorthocerids
> Order † Ascocerida

Order † Oncocerida
Order † Discosorida
Order † Tarphycerida
Order † Barrandeocerida A polyphyletic group now included in the Tarphycerida
Order Nautilida
Subclass † Bactritoidea
Order † Bactritida

Paleozoic Ammonoidea (Miller, Furnish, and Schindewolf, 1957)

Suborder † Anarcestina
Suborder † Clymeniina
Suborder † Goniatitina
Suborder † Prolecanitina

Mesozoic Ammonoidea (Arkel et al., 1957)

Suborder † Ceratitina
Suborder † Phylloceratina
Suborder † Lytoceratina
Suborder † Ammonitina

Subsequent revisions include the establishment of three Upper Cambrian orders, the Plectronocerida, Protactinocerida and Yanhecerida; separation of the pseudorthocerids as the Pseudorthocerida, and elevating orthoceritoids as the Subclass Orthoceratoidea.

Shevyrev classification

Shevyrev (2005) suggested a division into eight subclasses, mostly comprising the more diverse and numerous fossil forms, although this classification has been criticized as arbitrary.

Various species of ammonites

Holotype of *Ostenoteuthis siroi* from family Ostenoteuthidae.

A fossilised belemnite

Class Cephalopoda

- Subclass † Ellesmeroceratoidea
    - Order † Plectronocerida (501 to 490 Ma)
    - Order † Protactinocerida

    - Order † Yanhecerida
    - Order † Ellesmerocerida (500 to 470 Ma)
- Subclass † Endoceratoidea (485 to 430 Ma)
    - Order † Endocerida (485 to 430 Ma)
    - Order † Intejocerida (485 to 480 Ma)
- Subclass † Actinoceratoidea
    - Order † Actinocerida (480 to 312 Ma)
- Subclass Nautiloidea (490.0 Ma- Rec)
    - Order † Basslerocerida (490 to 480 Ma)
    - Order † Tarphycerida (485 to 386 Ma)
    - Order † Lituitida (485 to 480 Ma)
    - Order † Discosorida (482 to 392 Ma)
    - Order † Oncocerida (478.5 to 324 Ma)
    - Order Nautilida (410.5 Ma-Rec)
- Subclass † Orthoceratoidea (482.5 to 211.5 Ma)
    - Order † Orthocerida (482.5 to 211.5 Ma)
    - Order † Ascocerida (478 to 412 Ma)
    - Order † Dissidocerida (479 to 457.5 Ma)
    - Order † Bajkalocerida
- Subclass † Bactritoidea (422 to 252 Ma)
- Subclass † Ammonoidea (410 to 66 Ma)
- Subclass Coleoidea (410.0 Ma-rec)

Cladistic classification

Pyritized fossil of *Vampyronassa rhodanica*, a vampyromorphid from the Lower Callovian (164.7 million years ago)

Another recent system divides all cephalopods into two clades. One includes nautilus and most fossil nautiloids. The other clade (Neocephalopoda or Angusteradulata) is closer to modern coleoids, and includes belemnoids, ammonoids, and many orthocerid families. There are also stem group cephalopods of the traditional Ellesmerocerida that belong to neither clade.

Monophyly of coeloids

The coeloids have been thought to possibly represent a polyphyletic group, although this has not been supported by the rising body of molecular data.

Post-mortem decay

After death, if undisturbed, cephalopods decay relatively quickly. Their muscle softens within a couple of days, and may swell; egg sacs can swell so much that they rip through the mantle. Subsequently, the organs shrink again; at this point the organism may start to break up into fragments. The eyes retain their size while the head shrinks around them. The gills may remain swollen at this point. After around a week, the carcass collapses in on itself and begins to disintegrate. The ink sac solidifies around this point. After a fortnight little is left but a blob with eyes, arms and ink sac visible. After a couple of months, these are only recognisable as flattened dark stains - although in some cases the eye lenses can remain intact for up to a year.

Chapter 3

Acanthuridae

Acanthuridae

Sohal surgeonfish, *Acanthurus sohal*

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Actinopterygii
Order:	Perciformes
Suborder:	Acanthuroidei
Family:	**Acanthuridae**

Genera

Acanthurus
Ctenochaetus
Naso (unicornfishes)
Paracanthurus
Prionurus
Zebrasoma

Acanthuridae ("thorn tail") is the family of **surgeonfishes**, **tangs**, and **unicornfishes**. The family includes about 80 species in six genera, all of which are marine fish living in tropical seas, usually around coral reefs. Many of the species are brightly colored and popular for aquaria.

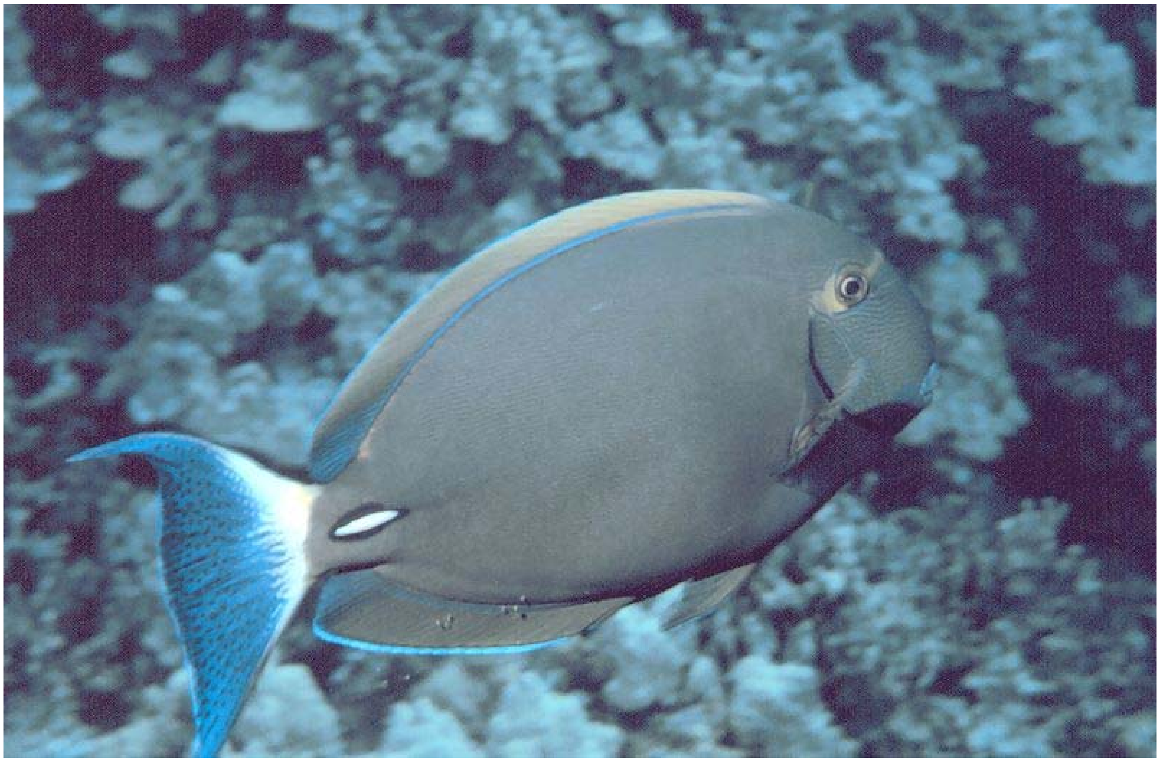
The distinctive characteristic of the family is the spines, one or more on either side of the tail, which are dangerously sharp. The dorsal, anal and caudal fins are large, extending for most of the length of the body. The small mouths have a single row of teeth used for grazing on algae.

Surgeonfishes sometimes feed as solitary individuals, but they also often travel and feed in schools. It has been suggested that feeding in schools is a mechanism for overwhelming the highly aggressive defense responses of small territorial damselfishes that vigorously guard small patches of algae on coral reefs.

Most species are relatively small and have a maximum length of 15–40 cm (6–16 in), but some members of the genus *Acanthurus*, some members of the genus *Prionurus*, and most members of the genus *Naso* can grow larger, with the whitemargin unicornfish (*N. annulatus*), the largest species in the family, reaching a length of up to a metre (3,3 ft). These fishes can grow quickly in aquariums so it is advisable to check the average growth size and suitability before adding to a marine aquarium.

Species

Achilles tang, *Acanthurus achilles*



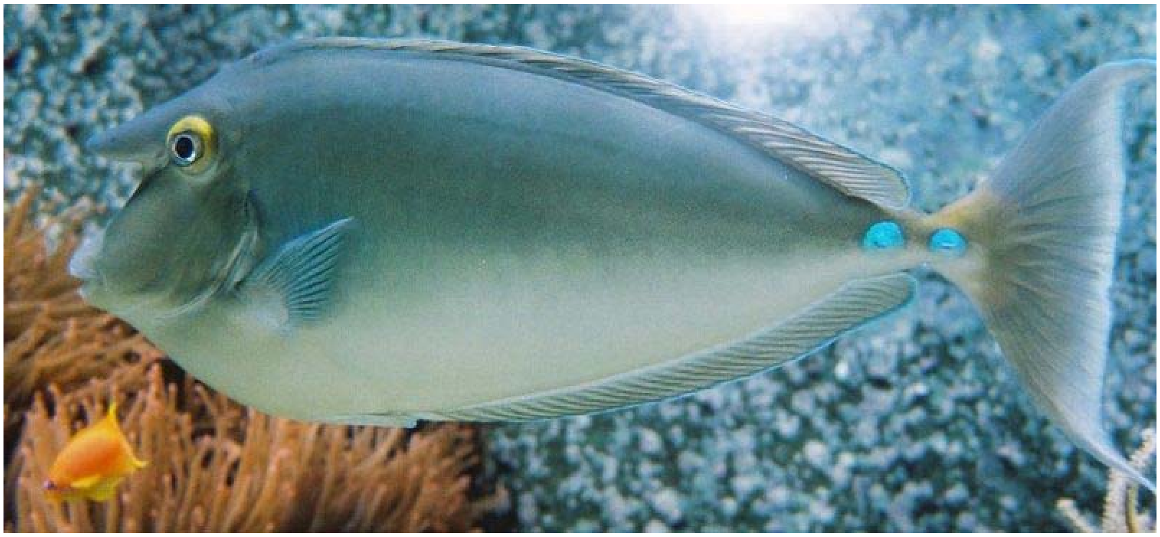
Eyestripe surgeonfish, *Acanthurus dussumieri*

Powderblue surgeonfish, *Acanthurus leucosternon*

Doubleband surgeonfish, *Acanthurus tennenti*

Kole Tang, *Ctenochaetus strigosus*

Elongate unicornfish, *Naso lopezi*



Bluespine unicornfish, *Naso unicornis*

Red Sea sailfin tang, *Zebrasoma desjardinii*

Orangespot surgeonfish, *Acanthurus olivaceus*, is being cleaned by two Hawaiian cleaner wrasse, *Labroides phthirophagus*

Regal Tang, *Paracanthurus hepatus* in an aquarium

- Genus *Acanthurus*
    - Achilles tang, *Acanthurus achilles* Shaw, 1803.
    - Whitefin surgeonfish, *Acanthurus albipectoralis* Allen & Ayling, 1987.
    - Orange-socket surgeonfish, *Acanthurus auranticavus* Randall, 1956.
    - Ocean surgeon, *Acanthurus bahianus* Castelnau, 1855.
    - Black-spot surgeonfish, *Acanthurus bariene* Lesson, 1831.
    - Ringtail surgeonfish, *Acanthurus blochii* Valenciennes, 1835.
    - Doctorfish tang, *Acanthurus chirurgus* (Bloch, 1787).
    - Chronixis surgeonfish, *Acanthurus chronixis* Randall, 1960.
    - Atlantic Blue tang surgeonfish, *Acanthurus coeruleus* Bloch & Schneider, 1801.
    - Eyestripe surgeonfish, *Acanthurus dussumieri* Valenciennes, 1835.
    - Fowler's surgeonfish, *Acanthurus fowleri* de Beaufort, 1951.
    - Black surgeonfish, *Acanthurus gahhm* (Forsskål, 1775).
    - Finelined surgeonfish, *Acanthurus grammoptilus* Richardson, 1843.
    - Whitespotted surgeonfish, *Acanthurus guttatus* Forster, 1801.
    - Japan surgeonfish, *Acanthurus japonicus* (Schmidt, 1931).
    - Palelipped surgeonfish, *Acanthurus leucocheilus* Herre, 1927.
    - Whitebar surgeonfish, *Acanthurus leucopareius* (Jenkins, 1903).
    - Powderblue surgeonfish, *Acanthurus leucosternon* Bennett, 1833.
    - Lined surgeonfish, *Acanthurus lineatus* (Linnaeus, 1758).

    - White-freckled surgeonfish, *Acanthurus maculiceps]* (Ahl, 1923).
    - Elongate surgeonfish, *Acanthurus mata* (Cuvier, 1829).
    - Monrovia doctorfish, *Acanthurus monroviae* Steindachner, 1876.
    - Whitecheek surgeonfish, *Acanthurus nigricans* (Linnaeus, 1758).
    - Epaulette surgeonfish, *Acanthurus nigricauda* Duncker & Mohr, 1929.
    - Brown surgeonfish, *Acanthurus nigrofuscus* (Forsskål, 1775).
    - Bluelined surgeonfish, *Acanthurus nigroris* Valenciennes, 1835.
    - Bluelined surgeon, *Acanthurus nubilus* (Fowler & Bean, 1929).
    - Orangespot surgeonfish, *Acanthurus olivaceus* Bloch & Schneider, 1801.
    - Black-barred surgeonfish, *Acanthurus polyzona* (Bleeker, 1868).
    - Chocolate surgeonfish, *Acanthurus pyroferus* Kittlitz, 1834.
    - Gulf surgeonfish, *Acanthurus randalli* Briggs & Caldwell, 1957.
    - *Acanthurus reversus* Randall & Earle, 1999.
    - Sohal surgeonfish, *Acanthurus sohal* (Forsskål, 1775).
    - Doubleband surgeonfish, *Acanthurus tennentii* Günther, 1861.
    - Thompson's surgeonfish, *Acanthurus thompsoni* (Fowler, 1923).
    - Convict surgeonfish, *Acanthurus triostegus* (Linnaeus, 1758).
    - Indian Ocean mimic surgeonfish, *Acanthurus tristis* Randall, 1993.
    - Yellowfin surgeonfish, *Acanthurus xanthopterus* Valenciennes, 1835.
- Genus *Ctenochaetus*
    - Twospot surgeonfish, *Ctenochaetus binotatus* Randall, 1955.
    - *Ctenochaetus cyanocheilus* Randall & Clements, 2001.
    - *Ctenochaetus flavicauda* Fowler, 1938.
    - *Ctenochaetus hawaiiensis*
    - Striped-fin surgeonfish, *Ctenochaetus marginatus* (Valenciennes, 1835).
    - Striated surgeonfish, *Ctenochaetus striatus* (Quoy & Gaimard, 1825).
    - Kole Tang, *Ctenochaetus strigosus* (Bennett, 1828).
    - Tomini surgeonfish, *Ctenochaetus tominiensis* Randall, 1955.
    - *Ctenochaetus truncatus* Randall & Clements, 2001.
- Genus *Naso*
    - Whitemargin unicornfish, *Naso annulatus* (Quoy & Gaimard, 1825).
    - Humpback unicornfish, *Naso brachycentron* (Valenciennes, 1835).
    - Spotted unicornfish, *Naso brevirostris* (Cuvier, 1829).
    - *Naso caeruleacauda* Randall, 1994.
    - Gray unicornfish, *Naso caesius* Randall & Bell, 1992.
    - Elegant unicornfish, *Naso elegans* (Rüppell, 1829).
    - Horseface unicornfish, *Naso fageni* Morrow, 1954.
    - Sleek unicornfish, *Naso hexacanthus* (Bleeker, 1855).
    - Orangespine unicornfish, *Naso lituratus* (Forster, 1801).
    - Elongate unicornfish, *Naso lopezi* Herre, 1927.
    - *Naso maculatus* Randall & Struhsaker, 1981.
    - Squarenose unicornfish, *Naso mcdadei* Johnson, 2002.
    - Slender unicorn, *Naso minor* (Smith, 1966).
    - *Naso reticulatus* Randall, 2001.
    - Oneknife unicornfish, *Naso thynnoides* (Cuvier, 1829).
    - Bulbnose unicornfish, *Naso tonganus* (Valenciennes, 1835).

    - Humpnose unicornfish, *Naso tuberosus* Lacépède, 1801.
    - Bluespine unicornfish, *Naso unicornis* (Forsskål, 1775).
    - Bignose unicornfish, *Naso vlamingii* (Valenciennes, 1835).
- Genus *Paracanthurus*
    - Palette surgeonfish, *Paracanthurus hepatus* (Linnaeus, 1766).
- Genus *Prionurus*
    - Biafra doctorfish, *Prionurus biafraensis* (Blache & Rossignol, 1961).
    - *Prionurus chrysurus* Randall, 2001.
    - Razor surgeonfish, *Prionurus laticlavius* (Valenciennes, 1846).
    - Yellowspotted sawtail, *Prionurus maculatus* (Randall & Struhsaker, 1981).
    - Sixplate sawtail, *Prionurus microlepidotus* Lacépède, 1804.
    - Yellowtail surgeonfish, *Prionurus punctatus* Gill, 1862.
    - Scalpel sawtail, *Prionurus scalprum* Valenciennes, 1835.
- Genus *Zebrasoma*
    - Red Sea sailfin tang, *Zebrasoma desjardinii* (Bennett, 1836).
    - Yellow tang, *Zebrasoma flavescens* (Bennett, 1828).
    - Spotted tang, *Zebrasoma gemmatum* (Valenciennes, 1835).
    - Longnose surgeonfish, *Zebrasoma rostratum* (Günther, 1875).
    - Twotone tang, *Zebrasoma scopas* (Cuvier, 1829).
    - Sailfin tang, *Zebrasoma veliferum* (Bloch, 1795).
    - Purple tang, *Zebrasoma xanthurum* (Blyth, 1852).
    - *Zebrasoma xanthurus*

Etymology and taxonomic history

The name of the family is derived from the Greek words *akantha* and *oura*, which loosely translate to "thorn" and "tail", respectively. This refers to the distinguishing characteristic of the family, the "scalpel" found each member's caudal peduncle.

In the early 1900s, the family was called **Hepatidae**.

In the aquarium

Tangs are very sensitive to disease in the home aquarium. However if the tang is fed enough algae and the aquarium is properly maintained disease should not be a problem. It is usually necessary to quarantine the animals for a period before introducing them to the aquarium.

Adults range from 15–40 cm (6-15 in.) in length and most grow quickly even in aquariums. When considering a tang for an aquarium it is important to consider the size to which these fish can grow. Larger species such as the popular **Pacific Blue tang surgeonfish** (of *Finding Nemo* fame), Naso or **lipstick tang**, clown and sohal tangs can grow to 40 cm (15 in.) and require swimming room and hiding places.

Many also suggest adding aggressive tangs to the aquarium last as they are territorial and may fight and possibly kill other fish.

Tangs primarily graze on macroalgae, such as caulerpa and gracilias, although they have been observed in an aquarium setting to eat meat-based fish foods. A popular technique for aquarists, is to grow macroalgae in a sump or refugium. This technique not only is economically beneficial, but serves to promote enhanced water quality through nitrate absorption. The growth of the algae can then be controlled by feeding it to the tang.

Chapter 4

Chameleon

Chameleon

Common Chameleon, *Chamaeleo chamaeleon*

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Reptilia
Order:	Squamata
Suborder:	Lacertilia
Infraorder:	Iguania
Family:	**Chamaeleonidae**

Subfamilies and Genera

- Chamaeleoninae
    - *Bradypodion*
    - *Calumma*
    - *Chamaeleo*
    - *Furcifer*
    - *Kinyongia*
    - *Nadzikambia*
- Brookesiinae
    - *Brookesia*
    - *Rieppeleon*
    - *Rhampholeon*

Chameleons (family Chamaeleonidae) are a distinctive and highly specialized clade of lizards. They are distinguished by their parrot-like zygodactylous feet, their separately mobile and stereoscopic eyes, their very long, highly modified, and rapidly extrudable tongues, their swaying gait, the possession by many of a prehensile tail, crests or horns on their distinctively shaped heads, and the ability of some to change color. Uniquely adapted for climbing and visual hunting, the approximately 160 species of chameleon range from Africa, Madagascar, Spain and Portugal, across south Asia, to Sri Lanka, have been introduced to Hawaii, California and Florida, and are found in warm habitats that vary from rain forest to desert conditions.

Etymology

The English word *chameleon* (also *chamaeleon*) derives from Latin *chamaeleō*, a borrowing of the Ancient Greek χαμαιλέων (*khamailéōn*), a compound of χαμαί (*khamaí*) "on the ground" and λέων (*léōn*) "lion". The Greek word is a calque translating the Akkadian *nēš qaqqari*, "ground lion".

Evolution

The oldest known chameleon fossil is that of *Chamaeleo caroliquarti*, found in Europe and dated to about 26 mya. However the chameleons are probably far older than that, perhaps sharing a common ancestor with iguanids and agamids more than 100 mya (agamids being more closely related). Fossil evidence has also been found in Africa and Asia, and suggests that chameleons were once more widespread than they are today. They may have their origins in Madagascar, which today is home to nearly half of all the 150 or more known species in this family, and later dispersed to other areas. Monophyly of the family is supported by several studies.

Description

Cape Dwarf Chameleon, Tokai, South Africa

Chameleons vary greatly in size and body structure, with maximum total length varying from 3.3 cm (1.3 in.) in *Brookesia minima* (one of the world's smallest reptiles) to 68.5 cm (27 in.) in the male *Furcifer oustaleti*. Many have head or facial ornamentation, such as nasal protrusions, or horn-like projections in the case of *Chamaeleo jacksonii*, or large crests on top of their head, like *Chamaeleo calyptratus*. Many species are sexually dimorphic, and males are typically much more ornamented than the female chameleons. Chameleons are often sold at pet stores and are not rare to have as household pets. Below is a table of common pet chameleons:

Species' Scientific Name	Species' Common Name	Typical Total Length (Male)	Typical Total Length (Female)	Color	Typical Lifespan (Years)
Chamaeleo calyptratus	Veiled Chameleon	14"-24"	10-13"	Green & Light Colors	≈5
Chamaeleo jacksonii	Jackson's Chameleon	9"-13"	10"-13"	Green & Light Colors	≈5-10

Furcifer pardalis	Panther Chameleon	15"-21"	9"-13"	Darker Colors	≈5 (2-3 for birthing females)
Rhampholeon brevicaudatus	Bearded Pygmy Chameleon	2"-3"	2"-3"	Brown, Beige, Green	≈3-5
Rhampholeon spectrum	Spectral Pygmy Chameleon	3"-4"	2"-4"	Tan & Gray	Unknown
Rhampholeon temporalis	Pygmy Chameleon	2.5"-4"	2"-3.5"	Gray & Brown	Unknown

Chameleon species have in common their foot structure, eyes, tongues and a lack of ears.

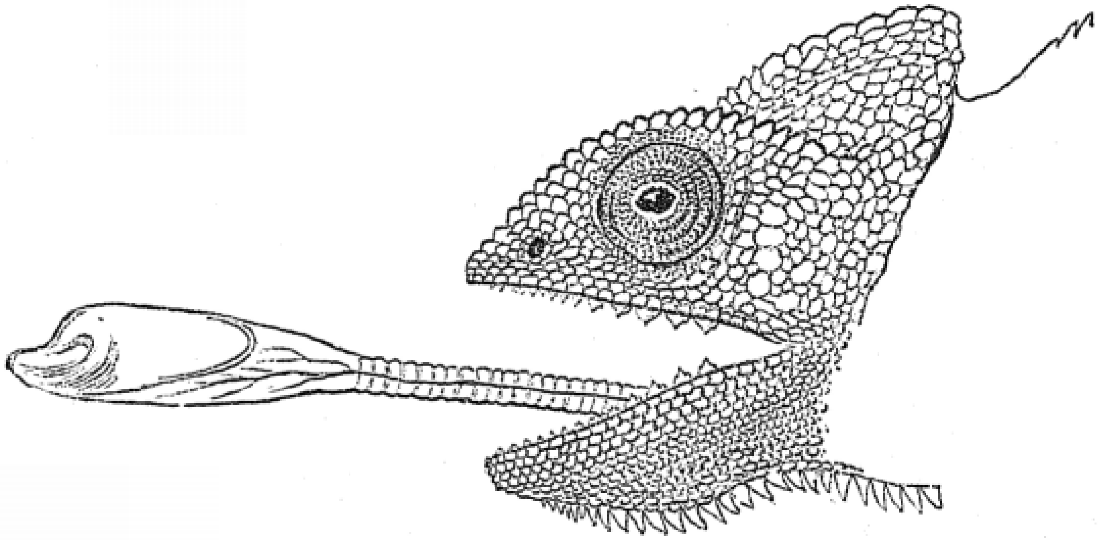
Oustalet's Chameleon, Ambalavao, Madagascar

Chameleons are didactyl: on each foot the five toes are fused into a group of two and a group of three, giving the foot a tongs-like appearance. These specialized feet allow chameleons to grip tightly to narrow branches. Each toe is equipped with a sharp claw to gain traction on surfaces such as bark when climbing. The claws make it easy to see how many toes are fused into each part of the foot — two toes on the outside of each front foot and three on the inside.

Their eyes are the most distinctive among the reptiles. The upper and lower eyelids are joined, with only a pinhole large enough for the pupil to see through. They can rotate and focus separately to observe two different objects simultaneously, this lets their eyes move independently from each other. It in effect gives them a full 360-degree arc of vision around their body. When prey is located, both eyes can be focused in the same direction, giving sharp stereoscopic vision and depth perception. They have very good eyesight for reptiles, letting them see small insects from a long (5–10 m) distance.

They lack a vomeronasal organ. Also, like snakes, they do not have an outer or a middle ear. This suggests that chameleons might be deaf, although snakes can sense vibration using a bone called the quadrate. Furthermore, some or maybe all chameleons, can communicate via vibrations that travel through solid substrates such as branches.

Chameleons have very long tongues (sometimes longer than their own body length) which they are capable of rapidly extending out of the mouth.



Head of *Chamæleon calcaratus*, with projected tongue.

Tongue structure

The tongue extends out faster than human eyes can follow, at around 26 body lengths per second. The tongue hits the prey in about 30 thousandths of a second. The tongue of the chameleon is a complex arrangement of bone, muscle and sinew. At the base of the tongue there is a bone and this is shot forward giving the tongue the initial momentum it needs to reach the prey quickly. At the tip of the elastic tongue there is a muscular, club-like structure covered in thick mucus that forms a suction cup. Once the tip sticks to a prey item, it is drawn quickly back into the mouth, where the chameleon's strong jaws crush it and it is consumed. Ultraviolet light is part of the visible spectrum for chameleons. Chameleons exposed to ultraviolet light show increased social behavior and activity levels, are more inclined to bask and feed and are also more likely to reproduce as it has a positive effect on the pineal gland.

Distribution and habitat

The tiny, usually brown-colored *Brookesia* chameleons are mainly terrestrial

Chameleons are primarily found in the mainland of sub-Saharan Africa and on the island of Madagascar, although a few species are also found in northern Africa, southern Europe, the Middle East, southern India, Sri Lanka and several smaller islands in the western Indian Ocean. There are introduced, feral populations of veiled and Jackson's chameleons in Hawaii and isolated pockets of feral Jackson's chameleons have been reported in California and Florida.

Chameleons inhabit all kinds of tropical and mountain rain forests, savannas and sometimes deserts and steppes. The "typical" chameleons from the subfamily Chamaeleoninae are arboreal and usually found in trees or bushes, although a few (notably the Namaqua Chameleon) are partially or largely terrestrial. Most species from the subfamily Brookesiinae, which includes the genera *Brookesia*, *Rieppeleon* and *Rhampholeon*, live low in vegetation or on the ground among leaf litter.

Reproduction

West Usambara Two-Horned Chameleon (*Kinyongia multituberculata*) in the Usambara mountains, Tanzania.

Chameleons are mostly oviparous, some being ovoviviparous.

The oviparous species lay eggs after a 3–6 week gestation period. The female will climb down to the ground and begin digging a hole, anywhere from 10–30 cm (4–12 in.) deep depending on the species. The female turns herself around at the bottom of the hole and deposits her eggs. Once finished, the female buries lina and leaves the nesting site. Clutch sizes vary greatly with species. Small *Brookesia* species may only lay 2–4 eggs, while large Veiled Chameleons (*Chamaeleo calyptratus*) have been known to lay clutches of 80–100 eggs. Clutch sizes can also vary greatly among the same species. Eggs generally hatch after 4–12 months, again depending on species. The eggs of Parson's Chameleon (*Calumma parsonii*), a species which is rare in captivity, are believed to take upwards of 24 months to hatch.

The ovoviviparous species, such as the Jackson's Chameleon (*Chamaeleo jacksonii*) have a 5–6 month gestation period. The newborn are in a transparent membrane and they are still sleeping, once they touch the ground or branch, they will wake up and attempt to crawl out of the membrane. The female can have 8–31 live young at once.

Feeding behavior

Chameleons generally eat locusts, mantis, crickets, grasshopper and other insects, but larger chameleons have been known to eat small birds and other lizards. A few species, such as Jackson's Chameleon (*C. jacksonii*) and the Veiled Chameleon (*C. calyptratus*) will consume small amounts of plant matter. Chameleons prefer running water to still water.

Chameleons require lots of vitamins and minerals. To ensure sufficient nutrients, zoo-keepers "gut-load" insects before feeding them to chameleons, by rearing them on a diet of potatoes, fish flakes (tropical), dry puppy food, dark leafy greens, etc. and dusting them with vitamin and mineral powders.

Change of color

Camouflage of a Common Chameleon in its natural environment (vicinity of Oueslatia, Tunisia)

This Common Chameleon (*Chamaeleo chamaeleon*) turned black

Some chameleon species are able to change their skin colors. Different chameleon species are able to change different colors which can include pink, blue, red, orange, green, black, brown, light blue, yellow, turquoise and purple.

The primary purpose of color change has been found to be due to social signalling, as opposed to camouflage, although both social signalling color change, and color change for purposes of camouflage do occur in most chameleons, to some extent. Color change is also used as an expression of the physiological condition of the lizard, and as a social indicator to other chameleons. Research suggests that social signaling was the primary driving force behind the evolution of color change, and that camouflage evolved as a secondary concern. Chameleons tend to show darker colors when angered, or attempting to scare or intimidate others, and males show lighter, multi-colored patterns when courting females.

Some varieties of chameleon - such as the Smith's dwarf chameleon - use their color-changing ability to blend in with their surroundings, as an effective form of camouflage.

The desert dwelling Namaqua Chameleon also uses color change as an aid to thermoregulation, becoming black in the cooler morning to absorb heat more efficiently, then a lighter grey colour to reflect light during the heat of the day - or showing both colours at the same time, neatly separated left from right by the spine.

Chameleons have specialized cells, collectively called chromatophores, that lie in layers under their transparent outer skin. The cells in the upper layer, called xanthophores and erythrophores, contain yellow and red pigments respectively. Below these is another layer of cells called iridophores or guanophores, and they contain the colorless crystalline substance guanine. These are particularly strong reflectors of the blue part of incident light. If the upper layer of chromatophores appears mainly yellow, the reflected light becomes green (blue plus yellow). A layer of dark melanin contained in melanophores is situated even deeper under the reflective iridophores. The melanophores determine the 'lightness' of the reflected light. These specialized cells are full of pigment granules, which are located in their cytoplasm. Dispersion of the pigment granules in the cell grants the intensity of appropriate color. If the pigment is equally distributed in the cell, the whole cell has the intensive color, which depends on the type of chromatophore cell. If the pigment is located only in the centre of the cell, cell appears to be transparent. All these pigment cells can rapidly relocate their pigments, thereby influencing the color of the chameleon.

Chamaeleo melleri

Parasites

A number of monoxenous coccidia are known to infect these species including species of the genera *Choleoeimeria*, *Eimeria* and *Isospora*.

Recognised parasites include:

- *Choleoeimeria bohemii* - Meller's chameleon (*Chamaeleo melleri*)
- *Choleoeimeria brookesiae* - spiny leaf chameleon (*Brookesia decaryi*)
- *Choleoeimeria glawi* - panther chameleon (*Furcifer pardalis*)
- *Choleoeimeria hirbayah* - veiled chameleon (*Chamaeleo calyptratus*)
- *Choleoeimeria largeni* - graceful chameleon (*Chamaeleo gracilis*)
- *Choleoeimeria tilburyi* - Jackson's chameleon (*Chamaeleo jacksonii*)

- *Eimeria hajeki* - pygmy chameleon (*Rampholeon temporalis*)
- *Eimeria vencesi* - panther chameleon (*Furcifer pardalis*)
- *Eimeria worthi* - Oustalet's chameleon (*Furcifer oustaleti*)

- *Isospora brygooi* - panther chameleon (*Furcifer pardalis*)
- *Isospora jaracimrmani* - veiled chameleon (*Chamaeleo calyptratus*)

Chapter 5

Cuttlefish

Cuttlefish

Sepia latimanus, East Timor

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Superorder:	Decapodiformes
Order:	**Sepiida** Zittel, 1895

Suborders and Families

- †Vasseuriina
    - †Vasseuriidae
    - †Belosepiellidae
- Sepiina
    - †Belosaepiidae
    - Sepiadariidae
    - Sepiidae

Cuttlefish are marine animals of the order **Sepiida**. They belong to the class Cephalopoda (which also includes squid, octopuses, and nautiluses). Despite their name, cuttlefish are not fish but molluscs. Recent studies indicate that cuttlefish are among the most intelligent invertebrates. Cuttlefish also have one of the largest brain-to-body size ratios of all invertebrates.

The origin of the word cuttlefish can be found in the old English term *cudele*, which derived in the 15th century from the Norwegian *koddi* (cushion, testicle) and the Middle German *kudel* (pouch), a good description of the cephalopod's shape. The Greco-Roman world valued the cephalopod as a source of the unique brown pigment that the creature releases from its siphon when it is alarmed. The word for it in Greek and Latin, *sepia* (later *seppia* in Italian), is used to refer to a brown pigment in English.

Cuttlefish have an internal shell (the cuttlebone), large W-shaped pupils, and eight arms and two tentacles furnished with denticulated suckers, with which they secure their prey. They generally range in size from 15 cm (5.9 in) to 25 cm (9.8 in), with the largest species, *Sepia apama*, reaching 50 cm (20 in) in mantle length and over 10.5 kg (23 lb) in weight.

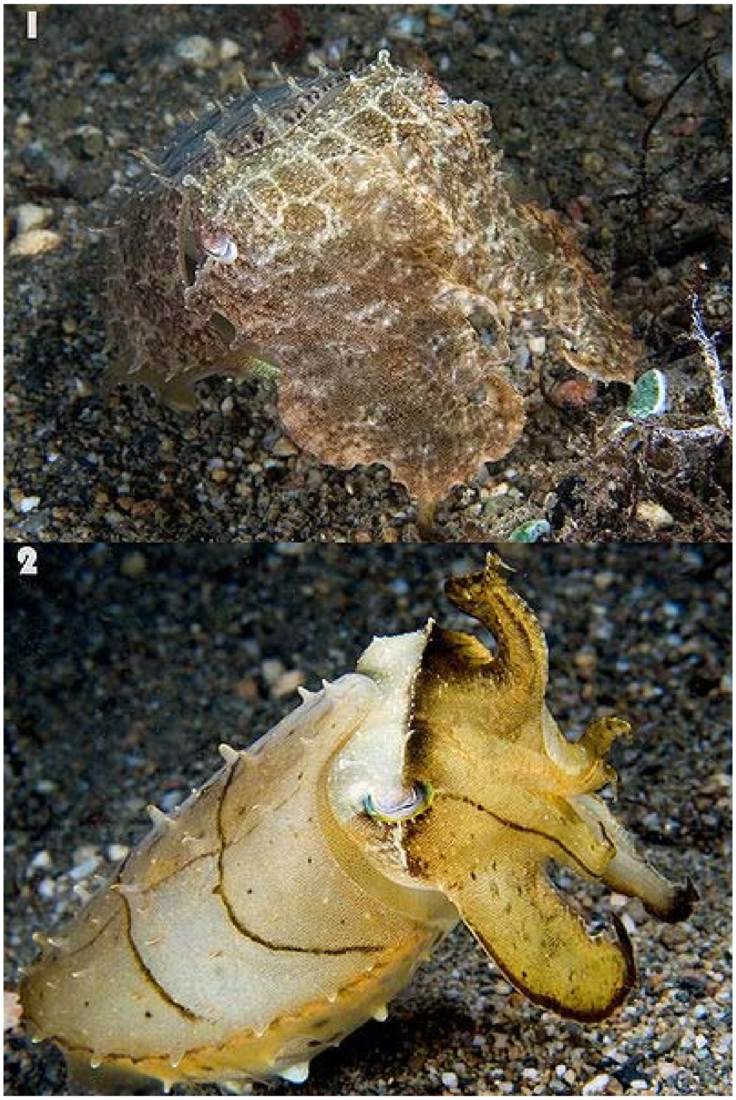
Cuttlefish eat small molluscs, crabs, shrimp, fish, octopuses, worms, and other cuttlefish. Their predators include dolphins, sharks, fish, seals and other cuttlefish. Their life expectancy is about one to two years.

Cuttlefish in its natural habitat

Physiology

Cuttlebone

Cuttlefish possess an internal structure called the cuttlebone, which is porous and is made of aragonite. This provides the cuttlefish with buoyancy. Buoyancy can be regulated by changing the gas-to-liquid ratio in the chambered cuttlebone via the ventral siphuncle. Each species has a distinct shape, size, and pattern of ridges or texture on the cuttlebone. The cuttlebone is unique to cuttlefish, one of the features that distinguishes them from their squid relatives. Jewelers and silversmiths traditionally use cuttlebones as moulds for casting small objects but they are probably better known as the tough material given to parakeets and other caged birds as a source of dietary calcium.



This Broadclub Cuttlefish (*Sepia latimanus*) can go from camouflage tans and browns (top) to yellow with dark highlights (bottom) in less than a second.

Skin

An infant cuttlefish protects itself with camouflage

Cuttlefish are sometimes referred to as the chameleon of the sea because of their remarkable ability to rapidly alter their skin color at will. Cuttlefish change color and light polarity to communicate to other cuttlefish and to camouflage themselves from predators.

This color-changing function is produced by groups of red, yellow, brown, and black pigmented chromatophores above a layer of reflective iridophores and leucophores, with up to 200 of these specialized pigment cells per square millimeter, which corresponds to about 359 DPI. The pigmented chromatophores have a sac of pigment and a large membrane that is folded when retracted. There are 6-20 small muscle cells on the sides which can contract to squash the elastic sac into a disc against the skin. Yellow chromatophores (xanthophores) are closest to the surface of the skin, red and orange are below (erythrophores), and brown or black are just above the iridophore layer (melanophores). The iridophores reflect blue and green light. Iridophores are plates of chitin or protein, which can reflect the environment around a cuttlefish. They are responsible for the metallic blues, greens, golds, and silvers often seen on cuttlefish. All of these cells can be used in combinations. For example, orange is produced by red and yellow chromatophores, while purple can be created by a red chromatophore and an iridophore. The cuttlefish can also use an iridophore and a yellow chromatophore to produce a brighter green. As well as being able to influence the color of light as it reflects off their skin, cuttlefish can also affect the light's polarization, which can be used to signal to other marine animals, many of which can also sense polarization.

Eyes

Close up of a cuttlefish eye

Cuttlefish eyes are among the most developed in the animal kingdom. The organogenesis of cephalopod eyes differs fundamentally from that of vertebrates like humans. Superficial similarities between cephalopod and vertebrate eyes are thought to be examples of convergent evolution. The cuttlefish pupil is a smoothly-curving W shape. Although they cannot see color, they can perceive the polarization of light, which enhances their perception of contrast. They have two spots of concentrated sensor cells on their retina (known as foveae), one to look more forward, and one to look more backward. The lenses, instead of being reshaped as they are in humans, are pulled around by reshaping the entire eye to change focus. Unlike the vertebrate eye, there is no blind spot as the optic nerve is positioned behind the retina.

Scientists have speculated that cuttlefish's eyes are fully developed before birth and start observing their surroundings while still in the egg. One team of French researchers has additionally suggested that cuttlefish prefer to hunt the prey they saw before hatching.

Circulation

The blood of a cuttlefish is an unusual shade of green-blue because it uses the copper-containing protein hemocyanin to carry oxygen instead of the red iron-containing protein hemoglobin that is found in vertebrates' blood. The blood is pumped by three separate hearts: two branchial hearts pump blood to the cuttlefish's pair of gills (one heart for each), and the third pumps blood around the rest of the body. Cuttlefish blood must flow more rapidly than most other animals because hemocyanin carries substantially less oxygen than hemoglobin.

Ink

Cuttlefish have ink, like squid and octopuses, which they use to help evade predators.

Toxicity

Like octopuses and some squid, all cuttlefish have bacterially-produced neurotoxins in their saliva.

Pfeffer's Flamboyant Cuttlefish from Sipadan, Malaysia

The muscles of Pfeffer's Flamboyant Cuttlefish contain a highly toxic compound that is yet to be identified. Mark Norman with Museum Victoria in Victoria, Australia, has shown the toxin to be as lethal as that of a fellow cephalopod, the blue-ringed octopus.

Ecology

Diet

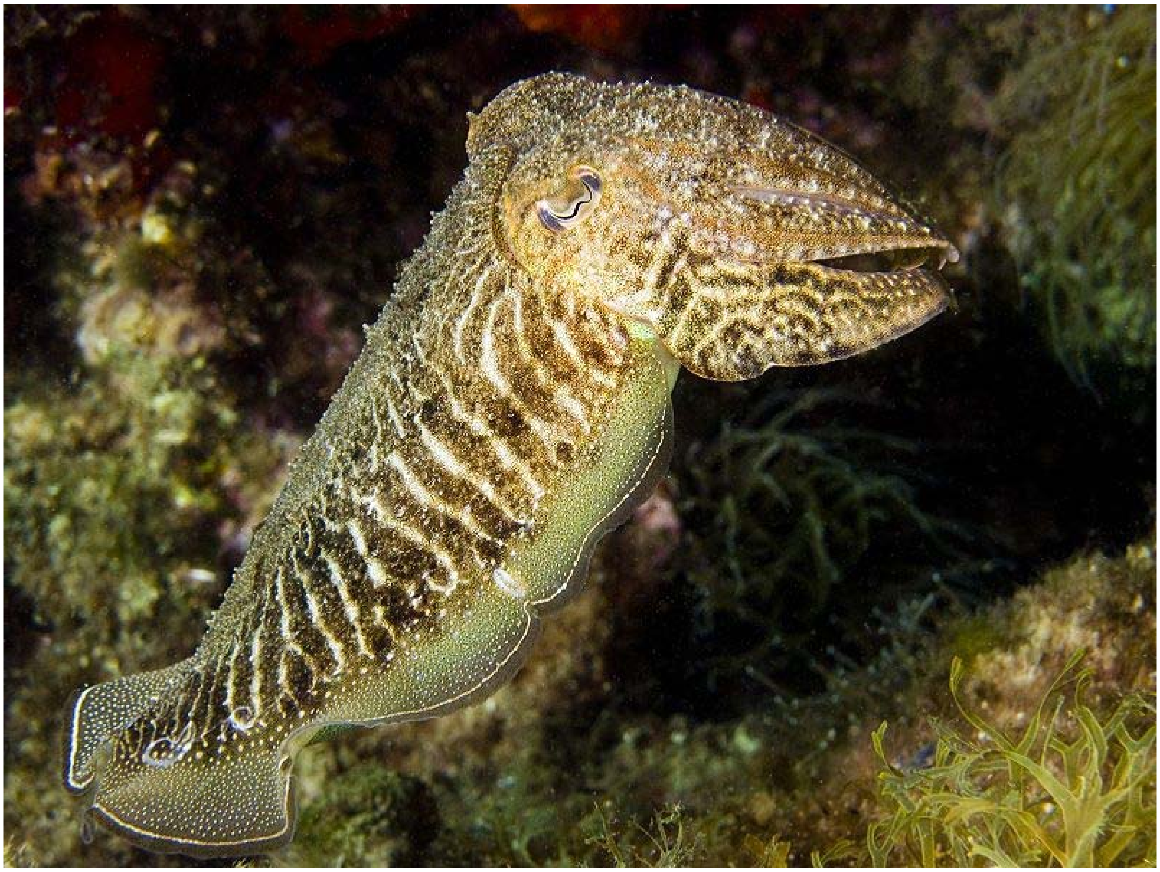
The preferred diet of the cuttlefish is crabs and fish. They feed on small shrimp shortly after hatching.

The cuttlefish uses its camouflage to hunt and sneak up on its prey. When it gets close enough, it opens its eight arms and shoots out two long feeding tentacles. On the end of each is a pad covered in suckers that grabs and pulls prey toward its beak.

Range and habitat

Family Sepiidae, which contains all cuttlefish, inhabit tropical/temperate ocean waters. They are mostly shallow-water animals although they are known to go to depths of about 600 metres (2,000 ft). They have an unusual biogeographic pattern: totally absent from the Americas, but present along the coasts of east and south Asia, western Europe, the Mediterranean, as well as all coasts of Africa and Australia. By the time the family evolved, ostensibly in the Old World, the north Atlantic possibly had become too cold and deep for these warm water species to cross.

Taxonomy



Sepia officinalis from Turkish waters

There are over 120 species of cuttlefish currently recognised, grouped into 5 genera. Sepiadariidae contains seven species and 2 genera; all the rest are in Sepiidae.

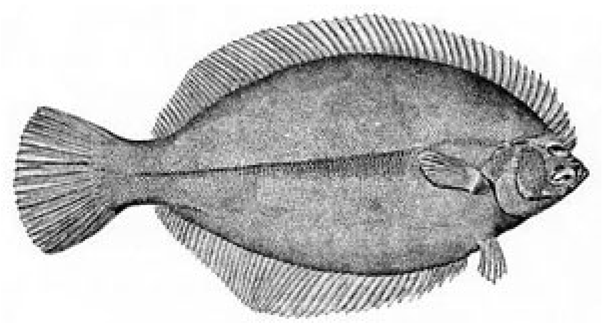
- CLASS CEPHALOPODA
    - Subclass Nautiloidea: nautilus
    - Subclass Coleoidea: squid, octopus, cuttlefish
        - Superorder Octopodiformes
        - Superorder Decapodiformes
            - ?Order †Boletzkyida
            - Order Spirulida: Ram's Horn Squid
            - Order **Sepiida**: cuttlefish
                - Suborder †Vasseuriina
                    - Family †Vasseuriidae
                    - Family †Belosepiellidae
                - Suborder Sepiina
                    - Family †Belosaepiidae

    - Family Sepiadariidae
    - Family Sepiidae
- Order Sepiolida: bobtail squid
- Order Teuthida: squid

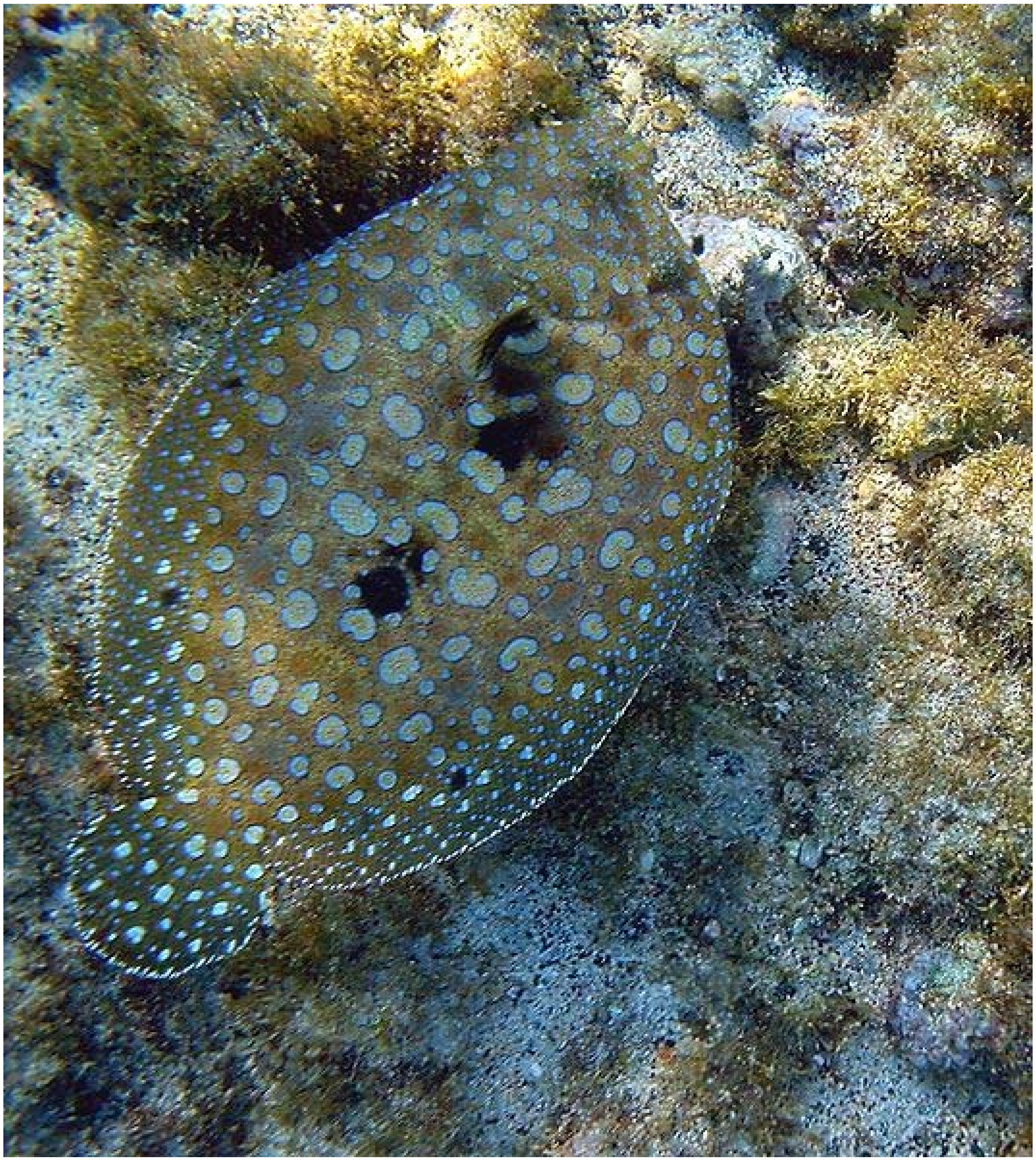
Chapter 6

Flounder and Four-Spotted flounder

Flounder



Winter flounder, *Pseudopleuronectes americanus*



Flowery flounder, *Bothus mancus*, Bahía de la Chiva, at Hawaii

The **flounder** is an ocean-dwelling flatfish species that is found in coastal lagoons and estuaries of the Northern Atlantic and Pacific Oceans.

Taxonomy

There are a number of geographical and taxonomical species to which flounder belong.

- Western Atlantic
    - Summer flounder (also known as *fluke*) - *Paralichthys dentatus*
    - Southern flounder - *Paralichthys lethostigma*
    - Winter flounder - *Pseudopleuronectes americanus*

- European waters
    - European flounder - *Platichthys flesus*

- Off the coast of Japan
    - Olive flounder - *Paralichthys olivaceus*

Eye migration

In its life cycle, an adult flounder has two eyes situated on one side of its head, where at hatching one eye is located on each side of its brain. One eye migrates to the other side of the body as a process of metamorphosis as it grows from larval to juvenile stage. As an adult, a flounder changes its habits and camouflages itself by lying on the bottom of the ocean floor as protection against predators. As a result, the eyes are then on the side which faces up. The side to which the eyes migrate is dependent on the species type.

Habitat

Flounder ambush their prey, feeding at soft muddy areas of the sea bottom, near bridge piles, docks and coral reefs, and have been also found at the bottom of the Mariana trench, the deepest known ocean canyon. Swiss scientist Jacques Piccard and US Navy Lt. Don Walsh reached a depth of 10,916 meters (35,814 ft) and were surprised to discover sole or flounder about 30 cm long.

A flounder's diet consists mainly of fish spawn, crustaceans, polychaetes and small fish. Flounder typically grow to a length of 12.5–37.5 centimetres (4.9–14.8 in), and as large as 60 centimeters (23.6 in). Their width is about half their length.

Threats

A flounder blending into its environment

World stocks of large predatory fish and large ground fish such as sole and flounder were estimated in 2003 to be only about 10% of pre-industrial levels, largely due to overfishing. Most overfishing is due to the extensive activities of the fishing industry. Current estimates suggest that approximately 30 million flounder (excluding sole) are alive in the world today. In the Gulf of Mexico, along the coast of Texas, research indicates the flounder population could be as low as 15 million due to heavy overfishing and industrial pollution.

According to Seafood Watch, Atlantic flounder and sole are currently on the list of seafood that sustainability-minded consumers should avoid.

Four-Spotted flounder

Four-Spotted Flounder	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Actinopterygii
Order:	Pleuronectiformes
Family:	Paralichthyidae
Genus:	*Paralichthys*
Species:	***P. oblongus***
Binomial name	
Paralichthys oblongus (Jordan & Evermann, 1896)	

The **Four-Spotted Flounder**, *Paralichthys oblongus* (Jordan and Evermann, 1896), also called American Four-Spotted Flounder or simply Four-Spot, is a flatfish and member of the left-eyed flounder family Paralichthyidae.

Description

As with most members of the left-eye flounders they can change the color and pattern of their dark side to match the surrounding bottom, and are also capable of rapidly burrowing into muddy or sandy bottoms. The back, which may vary in overall color from light brown to dark gray, is marked with four large and quite conspicuous black "eye-like" spots edged with a much lighter color, two of them situated at each margin of the body. The teeth are sharp and well developed. The underside is pale pinkish, almost translucent in certain areas. Data collected from fishing trawlers suggests adults average about 10 to 12 inches long with 16 inches likely being the maximum size. Adults are predatory and mostly piscivorous, preying on any small fish such as sand lance and Atlantic silverside, as well as squid.

Habitat

A range in the western Atlantic from the Gulf of Maine, and perhaps as far north as Nova Scotia, south to Florida, preferring water depths of at least 12 fathoms and as far out as to the continental shelf. Little is documented of the breeding and seasonal migratory habits of this fish.

Commercial fishing, angling, and food quality

The Four-spotted flounder is most often taken commercially by fishing trawlers. Due to its small size and lack of abundance inshore it is not prized or even well known by recreational anglers who may often mistake this flounder for its relative the Summer Flounder *Paralichthys dentatus*, as it shares a similar offshore range, appearance, and feeding habits. In addition to the obvious four spots and more translucent underside, the Four-Spot can also be identified from the Summer Flounder by its slightly more elongated shape and proportionately larger eyes. The meat is white and considered to have a very mild taste like that of the Summer flounder and Southern flounder *Paralichthys lethostigma*.

Chapter 7

Frog

Frogs
Temporal range: Triassic–present

Australian Green Tree Frog (*Litoria caerulea*)

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Amphibia
Subclass:	Lissamphibia
Order:	**Anura** Merrem, 1820

Suborders

Archaeobatrachia
Mesobatrachia
Neobatrachia

Native distribution of frogs (in black)

Frogs are amphibians in the order Anura (meaning "tail-less", from Greek *an-,* without + *oura*, tail), formerly referred to as *Salientia* (Latin *salere* (*salio*), "to jump"). Most frogs are characterized by a short body, webbed digits (fingers or toes), protruding eyes and the absence of a tail. Frogs are widely known as exceptional jumpers, and many of the anatomical characteristics of frogs, particularly their long, powerful legs, are adaptations to improve jumping performance. Due to their permeable skin, frogs are often semi-aquatic or inhabit humid areas, but move easily on land. They typically lay their eggs in puddles, ponds or lakes, and their larvae, called tadpoles, have gills and develop in water. Adult frogs follow a carnivorous diet, mostly of arthropods, annelids and gastropods. Frogs are most noticeable by their call, which can be widely heard during the night or day, mainly in their mating season.

The distribution of frogs ranges from tropic to subarctic regions, but most species are found in tropical rainforests. Consisting of more than 5,000 species described, they are among the most diverse groups of vertebrates. However, populations of certain frog species are declining significantly.

A popular distinction is often made between frogs and toads on the basis of their appearance, but this has no taxonomic basis. (Members of the anuran family Bufonidae are called true toads, but many species from other families are also called toads.) In addition to their ecological importance, frogs have many cultural roles, such as in literature, symbolism and religion, and they are also valued as food and as pets.

Etymology and terminology

The name frog derives from Old English *frogga*, (compare Old Norse *frauki*, German *Frosch*, older Dutch spelling *kikvorsch*), cognate with Sanskrit *plava* (frog), probably deriving from Proto-Indo-European *praw* = "to jump".

A distinction is often made between frogs and toads on the basis of their appearance, caused by the convergent adaptation among so-called toads to dry environments; however, this distinction has no taxonomic basis. The only family exclusively given the common name "toad" is Bufonidae, but many species from other families are also called "toads," and the species within the toad genus *Atelopus* are referred to as "harlequin frogs".

Taxonomy

The order *Anura* contains 4,810 species in 33 families, of which the Leptodactylidae (1100 spp.), Hylidae (800 spp.) and Ranidae (750 spp.) are the richest in species. About 88% of amphibian species are frogs.

European Fire-bellied Toad (*Bombina bombina*)

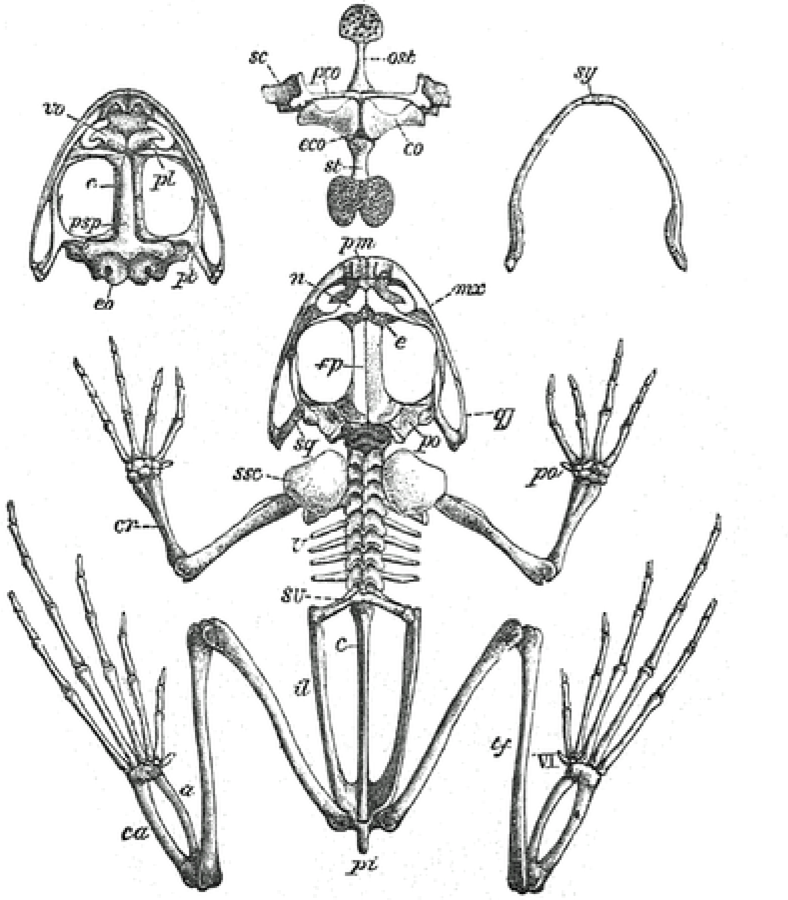
Young American bullfrog found in a stream in New Jersey

The use of the common names "frog" and "toad" has no taxonomic justification. From a taxonomic perspective, all members of the order Anura are frogs, but only members of the family Bufonidae are considered "true toads". The use of the term "frog" in common names usually refers to species that are aquatic or semi-aquatic with smooth and/or moist skins, and the term "toad" generally refers to species that tend to be terrestrial with dry, warty skin. An exception is the fire-bellied toad (*Bombina bombina*): while its skin is slightly warty, it prefers a watery habitat.

Frogs and toads are broadly classified into three suborders: Archaeobatrachia, which includes four families of primitive frogs; Mesobatrachia, which includes five families of more evolutionary intermediate frogs; and Neobatrachia, by far the largest group, which contains the remaining 24 families of "modern" frogs, including most common species throughout the world. Neobatrachia is further divided into the Hyloidea and Ranoidea. This classification is based on such morphological features as the number of vertebrae, the structure of the pectoral girdle, and the morphology of tadpoles. While this classification is largely accepted, relationships among families of frogs are still debated. Future studies of molecular genetics should soon provide further insights to the evolutionary relationships among anuran families.

Some species of anurans hybridise readily. For instance, the Edible Frog (*Rana esculenta*) is a hybrid of the Pool Frog (*R. lessonae*) and the Marsh Frog (*R. ridibunda*). *Bombina bombina* and *Bombina variegata* similarly form hybrids, although these are less fertile, giving rise to a hybrid zone.

Morphology and physiology



Skeleton of *Rana esculenta*. (Guide to Reptile Gallery B.M.)

a. Astragalus.
c. Coccyx.
ca. Calcaneum.
co. Coracoid.
cr. Radius-ulna.
e. Ethmoid.
eco. Epicoracoid.
eo. Exoccipital.
fp. Frontoparietal.
il. Ilium.
mx. Maxillary.
n. Nasal.
ost. Omosternum.
pco. Præcoracoid.
pl. Palatine.
pi. Pubis-ischium.
pm. Præmaxillary.
po. Prootic.
po'. Pollex.
psp. Parasphenoid.
pt. Pterygoid.
qj. Quadratojugal.
sc. Scapula.
sq. Squamosal.
ssc. Suprascapula.
st. Sternum.
sv. Sacral vertebra.
sy. Symphysial.
tf. Tibia-fibula.
v. Dorsal vertebræ.
vo. Vomer.
VI. Rudiment of sixth toe.

Skeleton of *Rana*

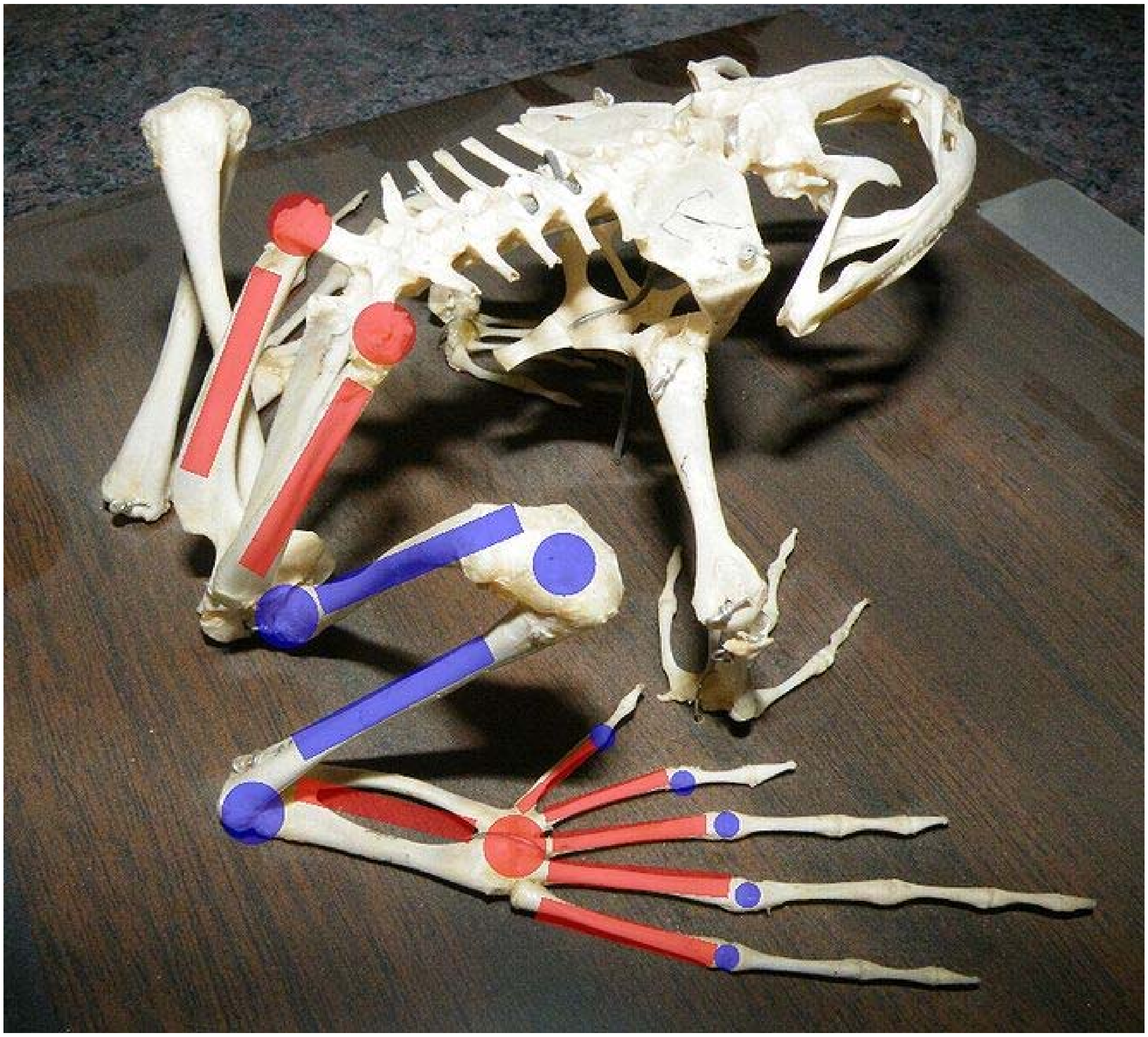
The morphology of frogs is unique among amphibians. Compared with the other two groups of amphibians, (salamanders and caecilians), frogs are unusual because they lack tails as adults and their legs are more suited to jumping than walking. The physiology of frogs is generally like that of other amphibians (and differs from other terrestrial vertebrates) because oxygen can pass through their highly permeable skin. This unique feature allows frogs to "breathe" largely through their skin. Because the oxygen is dissolved in an aqueous film on the skin and passes from there to the blood, the skin must remain moist at all times; this makes frogs susceptible to many toxins in the environment, some of which can similarly dissolve in the layer of water and be passed into their bloodstream. This may be the cause of the decline in frog populations.

Many characteristics are not shared by all of the approximately 5,250 described frog species. However, some general characteristics distinguish them from other amphibians. Frogs are usually well suited to jumping, with long hind legs and elongated ankle bones. They have a short vertebral column, with no more than ten free vertebrae, followed by a fused tailbone (urostyle or coccyx), typically resulting in a tailless phenotype.

Frogs range in size from 10 mm (0.39 in) (*Brachycephalus didactylus* of Brazil and *Eleutherodactylus iberia* of Cuba) to 300 mm (12 in) (goliath frog, *Conraua goliath*, of Cameroon). The skin hangs loosely on the body because of the lack of loose connective tissue. Skin texture varies: it can be smooth, warty or folded. Frogs have three eyelid membranes: one is transparent to protect the eyes underwater, and two vary from translucent to opaque. Frogs have a tympanum on each side of the head, which is involved in hearing and, in some species, is covered by skin. Most frogs have teeth, specifically pedicellate teeth in which the crow is separated from the root by fibrous tissue. Most only have teeth on the edge of the upper jaw (*maxillary teeth*) as well as *vomerine teeth* on the roof of their mouth. They do not have any teeth on their lower jaw, so they usually swallow their food whole. The teeth are mainly used to hold the prey and keep it in place till they can get a good grip on it and swallow their meal, assisted by retracting their eyes into their head. True toads lack any teeth at all, and some species (Pyxicephalus) which prey on relatively large organisms (including mice and other frogs) have cone shaped projections of bone, called odontoid processes, at the front of the lower jaw which function like teeth.

Feet and legs

Tyler's Tree Frog (*Litoria tyleri*) illustrates large toe pads and webbed feet



A bullfrog skeleton, showing elongate limb bones and extra joints. Red marks indicate bones which have been substantially elongated in frogs and joints which have become mobile. Blue indicates joints and bones which have not been modified or only somewhat elongated.

The structure of the feet and legs varies greatly among frog species, depending in part on whether they live primarily on the ground, in water, in trees, or in burrows. Frogs must be able to move quickly through their environment to catch prey and escape predators, and numerous adaptations help them do so.

Many frogs, especially those that live in water, have webbed toes. The degree to which the toes are webbed is directly proportional to the amount of time the species lives in the water. For example, the completely aquatic African dwarf frog (*Hymenochirus sp.*) has fully webbed toes, whereas the toes of White's tree frog (*Litoria caerulea*), an arboreal species, are only a half or a quarter webbed.

Arboreal frogs have "toe pads" to help grip vertical surfaces. These pads, located on the ends of the toes, do not work by suction. Rather, the surface of the pad consists of interlocking cells, with a small gap between adjacent cells. When the frog applies pressure to the toe pads, the interlocking cells grip irregularities on the substrate. The small gaps between the cells drain away all but a thin layer of moisture on the pad, and maintain a grip through capillarity. This allows the frog to grip smooth surfaces, and does not function when the pads are excessively wet.

In many arboreal frogs, a small "intercalary structure" in each toe increases the surface area touching the substrate. Furthermore, since hopping through trees can be dangerous, many arboreal frogs have hip joints that allow both hopping and walking. Some frogs that live high in trees even possess an elaborate degree of webbing between their toes, as do aquatic frogs. In these arboreal frogs, the webs allow the frogs to "parachute" or control their glide from one position in the canopy to another.

Ground-dwelling frogs generally lack the adaptations of aquatic and arboreal frogs. Most have smaller toe pads, if any, and little webbing. Some burrowing frogs have a toe extension—a metatarsal tubercle—that helps them to burrow. The hind legs of ground dwellers are more muscular than those of aqueous and tree-dwelling frogs.

Sometimes during the tadpole stage, one of the animal's rear leg stubs is eaten by a dragonfly nymph. In some of these cases, the full leg grows anyway, and in other cases, it does not, although the frog may still live out its normal lifespan with only three legs. Other times, a parasitic flatworm called *Riberoria trematodes* digs into the rear of a tadpole, where it rearranges the limb bud cells, which sometimes causes the frog to have extra legs.

Jumping

Rainforest Rocket Frog jumping

Frogs are generally recognized as exceptional jumpers, and the best jumper of all vertebrates. The Australian rocket frog, *Litoria nasuta*, can leap over 50 times its body length (5.5 cm), resulting in jumps of over 2 meters. The acceleration of the jump may be up to twice gravity. There are tremendous differences between species in jumping capability, but within a species, jump distance increases with increasing size, but relative jumping distance (body-lengths jumped) decreases.

While frog species can use a variety of locomotor modes (running, walking, gliding, swimming, and climbing), more are either proficient at jumping or descended from ancestors who were, with much of the musculo-skeletal morphology modified for this purpose. The tibia, fibula and tarsals have been fused into a single, strong bone, as have the radius and ulna in the forelimbs (which must absorb the impact of landing). The metatarsals have become elongated to add to the leg length and allow the frog to push against the ground for longer during a jump. The illium has elongated and formed a mobile joint with the sacrum which, in specialist jumpers such as Ranids or Hylids, functions as an additional limb joint to further power the leaps. This elongation of the limbs results in the frog being able to apply force to the ground for longer during a jump, which in turn results in a longer, faster jump.

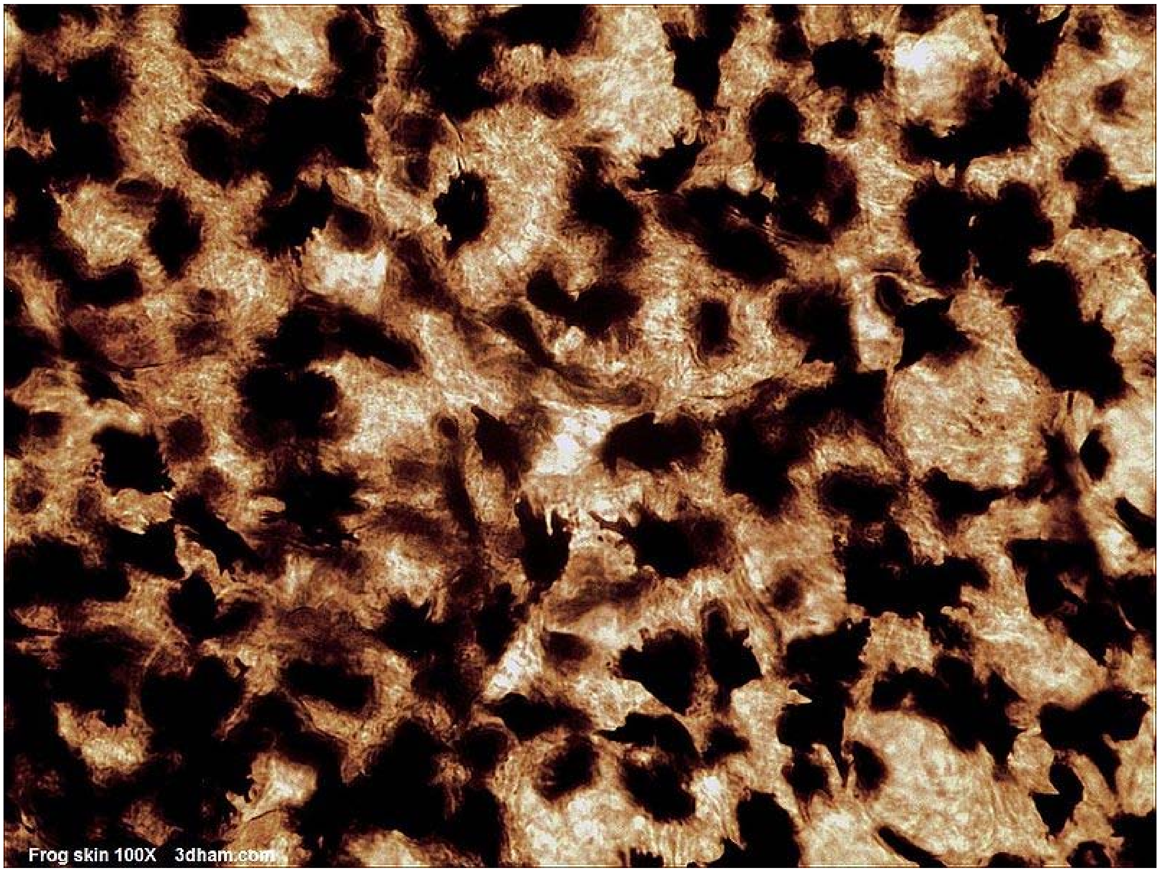
The muscular system has been similarly modified. The hind limbs of the ancestor of frogs presumably contained pairs of muscles which would act in opposition (one muscle to flex the knee, a different muscle to extend it), as is seen in most other limbed animals.

However, in modern frogs, almost all muscles have been modified to contribute to the action of jumping, with only a few small muscles remaining to bring the limb back to the starting position and maintain posture. The muscles have also been greatly enlarged, with the muscles involved in jumping accounting for over 17% of the total mass of the frog.

In some extremely capable jumpers, such as the cuban tree frog, the peak power exerted during a jump can exceed what muscle is capable of producing. Currently, it is hypothesized that frogs are storing muscular energy by stretching their tendons like springs, then triggering the release all at once, allowing the frog to increase the energy of its jump beyond the limits of muscle-powered acceleration. A similar mechanism has already been documented in locusts and grasshoppers.

Skin

Pouched Frog (*Assa darlingtoni*) camouflaged against leaf litter.



Microscopic view of frog skin

Many frogs are able to absorb water and oxygen directly through the skin, especially around the pelvic area. However, the permeability of a frog's skin can also result in water loss. Some tree frogs reduce water loss with a waterproof layer of skin. Others have adapted behaviours to conserve water, including engaging in nocturnal activity and resting in a water-conserving position. This position involves the frog lying with its toes and fingers tucked under its body and chin, respectively, with no gap between the body and substrate. Some frog species will also rest in large groups, touching the skin of the neighbouring frog. This reduces the amount of skin exposed to the air or a dry surface, and thus reduces water loss. These adaptations only reduce water loss enough for a predominantly arboreal existence, and are not suitable for arid conditions.

Camouflage is a common defensive mechanism in frogs. Most camouflaged frogs are nocturnal, which adds to their ability to hide. Nocturnal frogs usually find the ideal camouflaged position during the day to sleep. Some frogs have the ability to change colour, but this is usually restricted to shades of one or two colours. For example, White's tree frog varies in shades of green and brown. Features such as warts and skin folds are usually found on ground-dwelling frogs, where a smooth skin would not disguise them effectively. Arboreal frogs usually have smooth skin, enabling them to disguise themselves as leaves.

Certain frogs change colour between night and day, as light and moisture stimulate the pigment cells and cause them to expand or contract.

Poison

Many frogs contain mild toxins that make them unpalatable to potential predators. For example, all toads have large poison glands—the parotoid glands—located behind the eyes, on the top of the head. Some frogs, such as some poison dart frogs, are especially toxic. The chemical makeup of toxins in frogs varies from irritants to hallucinogens, convulsants, nerve poisons, and vasoconstrictors. Many predators of frogs have adapted to tolerate high levels of these poisons. Others, including humans, may be severely affected.

Oophaga pumilio, a poison dart frog, contains numerous alkaloids which deter predators

Some frogs obtain poisons from the ants and other arthropods they eat; others, such as the Australian Corroboree Frogs (*Pseudophryne corroboree* and *Pseudophryne pengilleyi*), can manufacture an alkaloid not derived from their diet. Some native people of South America extract poison from the poison dart frogs and apply it to their darts for hunting, although few species are toxic enough to be used for this purpose. It was previously a misconception the poison was placed on arrows rather than darts. The common name of these frogs was thus changed from "poison arrow frog" to "poison dart frog" in the early 1980s. Poisonous frogs tend to advertise their toxicity with bright colours, an adaptive strategy known as aposematism. There are at least two non-poisonous species of frogs in tropical America (*Eleutherodactylus gaigei* and *Lithodytes lineatus*) that mimic the colouration of dart poison frogs' coloration for self-protection (Batesian mimicry).

Because frog toxins are extraordinarily diverse, they have raised the interest of biochemists as a "natural pharmacy". The alkaloid epibatidine, a painkiller 200 times more potent than morphine, is found in some species of poison dart frogs. Other chemicals isolated from the skin of frogs may offer resistance to HIV infection. Arrow and dart poisons are under active investigation for their potential as therapeutic drugs.

The skin secretions of some toads, such as the Colorado River toad and cane toad, contain bufotoxins, some of which, such as bufotenin, are psychoactive, and have therefore been used as recreational drugs. Typically, the skin secretions are dried and smoked. Skin licking is especially dangerous, and appears to constitute an urban myth.

Respiration and circulation

The skin of a frog is permeable to oxygen and carbon dioxide, as well as to water. There are a number of blood vessels near the surface of the skin. When a frog is underwater, oxygen is transmitted through the skin directly into the bloodstream. On land, adult frogs use their lungs to breathe. Their lungs are similar to those of humans, but the chest muscles are not involved in respiration, and there are no ribs or diaphragm to support breathing. Frogs breathe by taking air in through the nostrils (which often have valves which close when the frog is submerged), causing the throat to puff out, then compressing the floor of the mouth, which forces the air into the lungs. In August 2007 an aquatic frog named *Barbourula kalimantanensis* was discovered in a remote part of Indonesia. The Bornean Flat-headed Frog (*B. kalimantanensis*) is the first species of frog known to science without lungs.

Frogs are known for their three-chambered heart, which they share with all tetrapods except birds, crocodilians and mammals. In the three-chambered heart, oxygenated blood from the lungs and de-oxygenated blood from the respiring tissues enter by separate atria, and are directed via a spiral valve to the appropriate vessel—aorta for oxygenated blood and pulmonary artery for deoxygenated blood. This special structure is essential to keeping the mixing of the two types of blood to a minimum, which enables frogs to have higher metabolic rates, and to be more active than otherwise.

Some species of frog have remarkable adaptations that allow them to survive in oxygen deficient water. The lake titicaca frog (*Telmatobius culeus*) is one such species and to survive in the poorly oxygenated waters of Lake Titicaca it has incredibly wrinkly skin that increases its surface area to enhance gas exchange. This frog will also do 'push-ups' on the lake bed to increase the flow of water around its body.

Digestion and excretion

The frog's digestive system begins with the mouth. Frogs have teeth along their upper jaw called the maxillary teeth, which are used to grind food before swallowing. These teeth are very weak, and cannot be used to catch or harm agile prey. Instead, the frog uses its sticky tongue to catch food (such as flies or other insects). The food then moves through the esophagus into the stomach. The food then proceeds to the small intestine (duodenum and ileum) where most digestion occurs. Frogs carry pancreatic juice from the pancreas, and bile (produced by the liver) through the gallbladder from the liver to the small intestine, where the fluids digest the food and extract the nutrients. When the food passes into the large intestine, the water is reabsorbed and wastes are routed to the cloaca. All wastes exit the body through the cloaca and the cloacal vent.

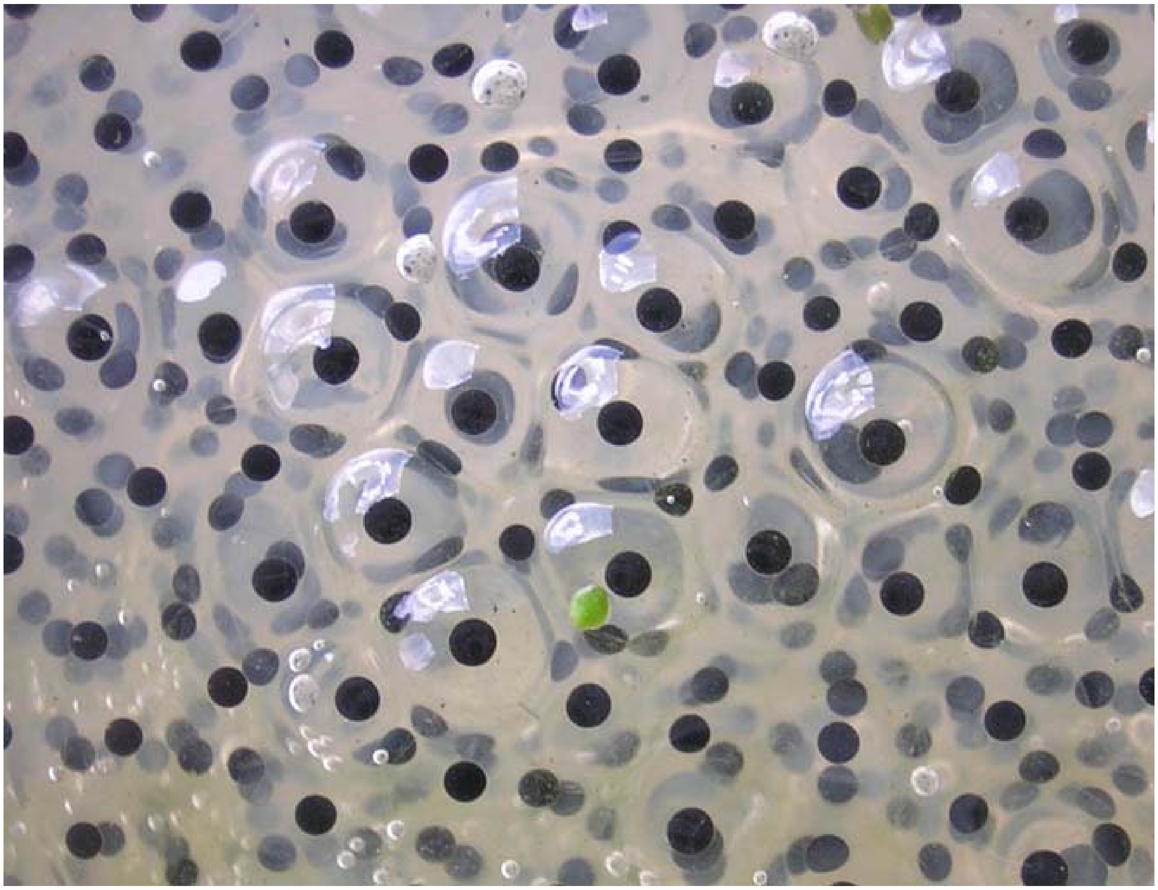
Nervous system

The frog has a highly developed nervous system which consists of a brain, spinal cord and nerves. Many parts of the frog's brain correspond with those of humans. The medulla oblongata regulates respiration, digestion, and other automatic functions. Muscular coordination and posture are controlled by the cerebellum. The relative size of the cerebrum of a frog is much smaller than that of a human. Frogs have ten cranial nerves (nerves which pass information from the outside directly to the brain) and ten pairs of spinal nerves (nerves which pass information from extremities to the brain through the spinal cord). By contrast, all amniotes (mammals, birds and reptiles) have twelve cranial nerves. Frogs do not have external ears; the eardrums (tympanic membranes) are directly exposed. As in all animals, the ear contains semicircular canals which help control balance and orientation. Due to their short cochlea, frogs use electrical tuning to expand their range of audible frequencies.

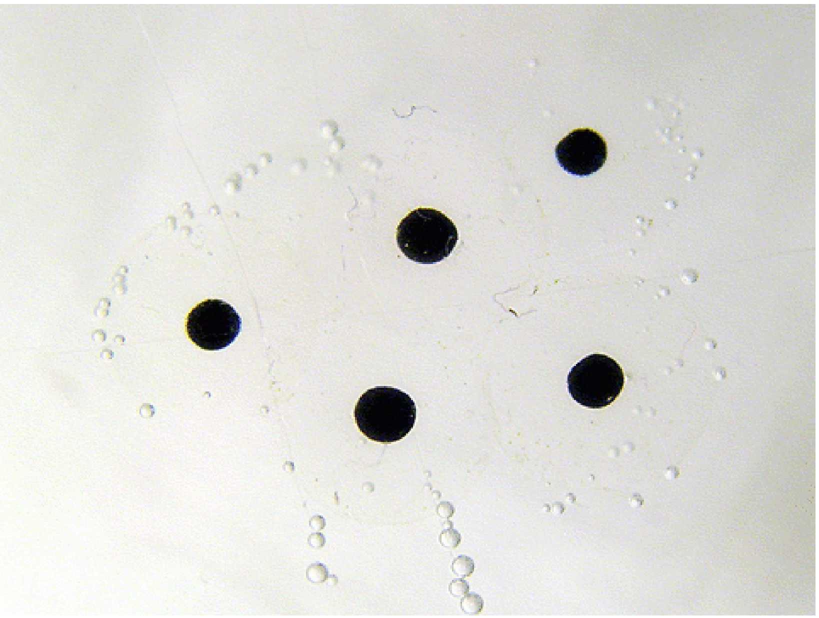
Natural history

The life cycle of frogs, like that of other amphibians, consists of four main stages: egg, tadpole, metamorphosis and adult. The reliance of frogs on an aquatic environment for the egg and tadpole stages gives rise to a variety of breeding behaviours that include the well-known mating calls used by the males of most species to attract females to the bodies of water that they have chosen for breeding. Some frogs also look after their eggs—and in some cases even the tadpoles—for some time after laying.

Life cycle



Frogspawn



Frogspawn development

Tadpole of Haswell's Froglet (*Paracrinia haswelli*

The life cycle of a frog starts with an egg. A female generally lays gelatinous egg masses containing thousands of eggs, in water. Each anuran species lays eggs in a distinctive, identifiable manner. An example are the long strings of eggs laid by the common American toad. The eggs are highly vulnerable to predation, so frogs have evolved many techniques to ensure the survival of the next generation. In colder areas the embryo is black to absorb more heat from the sun, which speeds up the development. Most commonly, this involves synchronous reproduction. Many individuals will breed at the same time, overwhelming the actions of predators; the majority of the offspring will still die due to predation, but there is a greater chance some will survive. Another way in which some species avoid the predators and pathogens eggs are exposed to in ponds is to lay eggs on leaves above the pond, with a gelatinous coating designed to retain moisture. In these species the tadpoles drop into the water upon hatching. The eggs of some species laid out of water can detect vibrations of nearby predatory wasps or snakes, and will hatch early to avoid being eaten. Some species, such as the Cane Toad (*Bufo marinus*), lay poisonous eggs to minimise predation. While the length of the egg stage depends on the species and environmental conditions, aquatic eggs generally hatch within one week. Other species go through their whole larval phase inside the eggs or the mother, or they have direct development. Unlike salamanders and newts, frogs and toads never become sexually mature while still in their larval stage.

Eggs hatch and continue life as tadpoles (occasionally known as polliwogs), which typically have oval bodies and long, vertically flattened tails. At least one species (Nannophrys ceylonensis) has tadpoles that are semi-terrestrial and live among wet rocks, but as a general rule, free living larvae are fully aquatic. They lack eyelids and have a cartilaginous skeleton, a lateral line system, gills for respiration (external gills at first, internal gills later) and tails with dorsal and ventral folds of skin for swimming. From pretty early onward they develop a gill pouch that covers the gills and the front legs and also the lungs are developed in an early stage as an accessory breathing organ. Some species which go through the metamorphosis inside the egg and hatch to small frogs never develop gills, instead there are specialised areas of skin that takes care of the respiration. Tadpoles also lack true teeth, but the jaws in most species usually have two elongate, parallel rows of small keratinized structures called keradonts in the upper jaw while the lower jaw has three rows of keradonts, surrounded by a horny beak, but the number of rows can be lower or absent, or much higher. Tadpoles are typically herbivorous, feeding mostly on algae, including diatoms filtered from the water through the gills. Some species are carnivorous at the tadpole stage, eating insects, smaller tadpoles, and fish. Cannibalism has been observed among tadpoles. Early developers who gain legs may be eaten by the others, so the late bloomers survive longer. This has been observed in England in the species *Rana temporaria* (common frog).

Tadpoles are highly vulnerable to predation by fish, newts, predatory diving beetles and birds such as kingfishers. Poisonous tadpoles are present in many species, such as Cane Toads. The tadpole stage may be as short as a week, or tadpoles may overwinter and metamorphose the following year in some species, such as the midwife toad (*Alytes obstetricans*) and the common spadefoot (*Pelobates fuscus*). In the Pipidae, with the exception for Hymenochirus, the tadpoles have paired anterior barbels which make them resemble small catfish.

With the exception of the base of the tail, where a few vertebral structures develop to give rise to the urostyle later in life, the tail lacks the completely solid, segmental, skeletal elements of cartilage or bony tissue that are so typical for other vertebrates, although it does contain a notochord

At the end of the tadpole stage, frogs undergo metamorphosis, in which they undergo a transition into the adult form. This metamorphosis last typically only 24 hours and consists of:

Larva of the common frog *Rana temporaria* a day before metamorphisis

Common frog - Metamorphosis stage. Notice the deformed jaws, large eyes and the remains of the gill pouch.

Young frog with tail remains after metamorphosis

Adult leopard frog

- The disappearance of the gill pouch, making the front legs visible.
- The transformation of the jaws into the big jaws of predatory frogs (most tadpoles are scraping of algae or are filter feeders)
- The transformation of the digestive system: the long spiral gut of the larva is being replaced by the typical short gut of a predator.
- An adaptation of the nervous system for stereoscopic vision, locomotion and feeding
- A quick growth and movement of the eyes to higher up the skull and the formation of eyelids.
- Formation of skin glands, thickening of the skin and loss of the lateral line system
- An eardrum is developed to lock the middle ear.

The disappearance of the tail is somewhat later (occurs at higher thyroxin levels) and after the tail has been resorbed the animals are ready to leave the water. The material of the tail is being used for a quick growth of the legs. The disappearing of the larval structures is a regulated process called apoptosis.

Incident of frog cannibalism

After metamorphosis, young adults may leave the water and disperse into terrestrial habitats, or continue to live in the aquatic habitat as adults. Almost all species of frogs are carnivorous as adults, eating invertebrates such as arthropods, annelids and gastropods. A few of the larger species may eat prey such as small mammals, fish and smaller frogs. Some frogs use their sticky tongues to catch fast-moving prey, while others capture their prey and force it into their mouths with their hands. However, there are a very few species of frogs that primarily eat plants. Adult frogs are themselves preyed upon by birds, large fish, snakes, otters, foxes, badgers, coatis, and other animals. Frogs are also eaten by people.

Frogs and toads can live for many years; though little is known about their life span in the wild, captive frogs and toads are recorded living up to 40 years.

Frogs from temperate climates hibernate through the winter, and 4 species are known to freeze during this time, most notably Rana sylvatica.

Reproduction of frogs

Once adult frogs reach maturity, they will assemble at a water source such as a pond or stream to breed. Many frogs return to the bodies of water where they were born, often resulting in annual migrations involving thousands of frogs. In continental Europe, a large proportion of migrating frogs used to die on roads, before special fences and tunnels were built for them.

Male and female Common toad (*Bufo bufo*) in amplexus

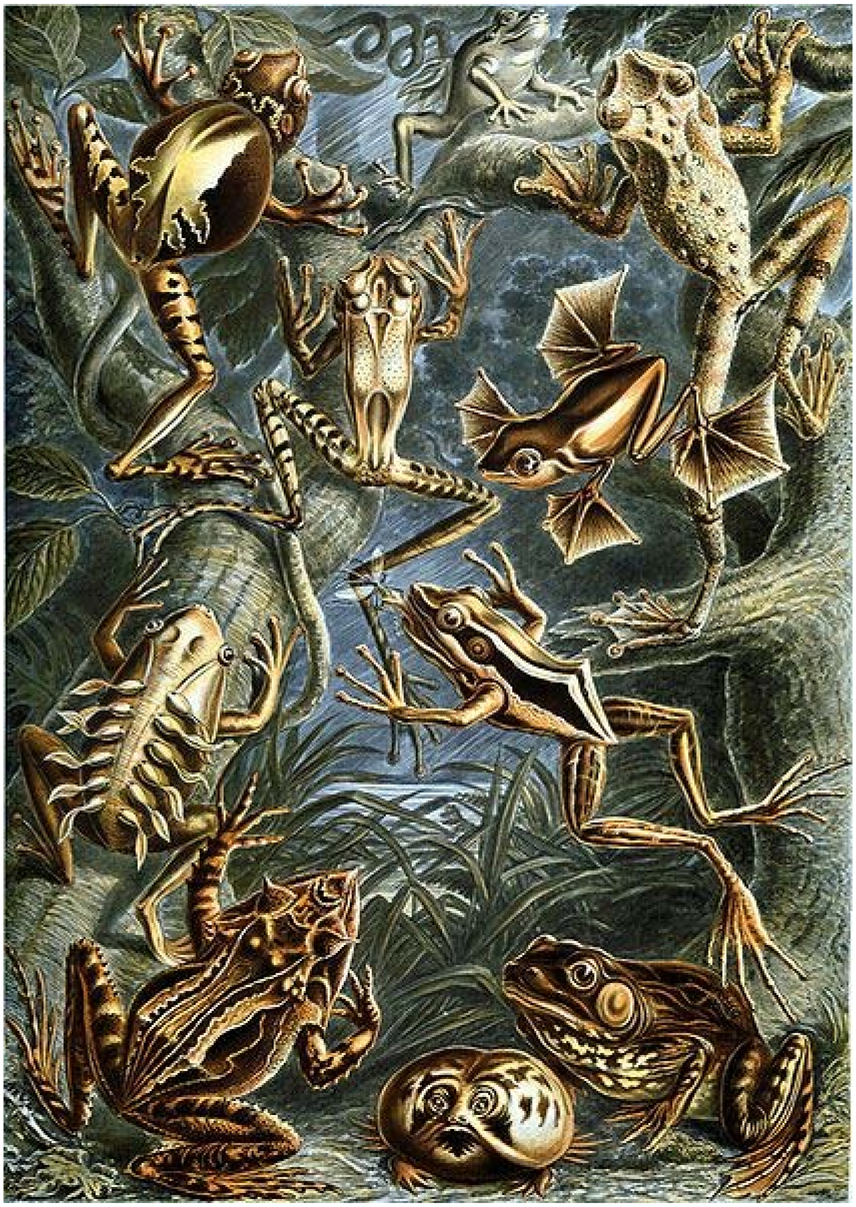
A Male and Female common toad in amplexus. The black strands are eggs released into open water minutes after birth.

Once at the breeding ground, male frogs call to attract a mate, collectively becoming a chorus of frogs. The call is unique to the species, and will attract females of that species. Some species have satellite males who do not call, but intercept females that are approaching a calling male.

The male and female frogs then undergo amplexus. This involves the male mounting the female and gripping her (sometimes with special nuptial pads) tightly. Fertilization is external: the egg and sperm meet outside of the body. The female releases her eggs, which the male frog covers with a sperm solution. The eggs then swell and develop a protective coating. The eggs are typically brown or black, with a clear, gelatin-like covering.

Most temperate species of frogs reproduce between late autumn and early spring. In the UK, most common frog populations produce frogspawn in February, although there is wide variation in timing. Water temperatures at this time of year are relatively low, typically between four and 10 degrees Celsius. Reproducing in these conditions helps the developing tadpoles because dissolved oxygen concentrations in the water are highest at cold temperatures. More importantly, reproducing early in the season ensures that appropriate food is available to the developing frogs at the right time.

Parental care



Colour plate from Ernst Haeckel's 1904 *Kunstformen der Natur*, depicting frog species that include two examples of parental care.

Although care of offspring is poorly understood in frogs, it is estimated that up to 20% of amphibian species may care for their young in one way or another, and there is a great diversity of parental behaviours. Some species of poison dart frog lay eggs on the forest floor and protect them, guarding the eggs from predation and keeping them moist. The frog will urinate on them if they become too dry. After hatching, a parent (the sex depends upon the species) will move them, on its back, to a water-holding bromeliad. The parent then feeds them by laying unfertilized eggs in the bromeliad until the young have metamorphosed. Other frogs carry the eggs and tadpoles on their hind legs or back (e.g. the midwife toads, *Alytes spp.*). Some frogs even protect their offspring inside their own bodies. The male Australian Pouched Frog (*Assa darlingtoni*) has pouches along its side in which the tadpoles reside until metamorphosis. The female Gastric-brooding Frogs (genus *Rheobatrachus*) from Australia, now probably extinct, swallows its tadpoles, which then develop in the stomach. To do this, the Gastric-brooding Frog must stop secreting stomach acid and suppress peristalsis (contractions of the stomach). Darwin's Frog (*Rhinoderma darwinii*) from Chile puts the tadpoles in its vocal sac for development. Some species of frog will leave a 'babysitter' to watch over the frogspawn until it hatches.

The evolution of parental care in frogs is driven primarily by the size of the water body in which they breed. There is an inverse relationship between the level of parental care in a frog species and the degree of parental care they exhibit—frogs that breed in smaller water bodies tend to have more complex parental care behaviors. Water body size shows this strong relationship with parental care because it encompasses several important variables that interact to select for parental care: predation, desiccation, competition, and resource limitation. Because predation of eggs and larvae is high in large water bodies, a number of frog species evolved terrestrial oviposition. Once eggs are deposited on land, the desiccating terrestrial environment demands uniparental care in the form of egg hydration to ensure egg survival. The subsequent need to transport hatched tadpoles to a water source requires an even more intense form of uniparental care. In small water bodies where predators are mostly absent, such as phytotelmata (water-filled leaf axils or small woody cavities), inter-tadpole competition becomes the variable that constrains tadpole survival. Certain frogs species avoid this competition by evolving the use of smaller phytotelmata as tadpole deposition sites. However, while these smaller tadpole rearing sites are free of competition, they also lack nutrients. Because they do not have sufficient nutrients to support a tadpole without parental provisioning behavior, frog species that transitioned from the use of larger to smaller phytotelmata have evolved trophic (unfertilized) egg laying. In this complex form of biparental care, the female provides her offspring with nutritive eggs. While each of these variables select for different behaviors, they correlate with the size of a species' tadpole-rearing site and influence the degree of parental care displayed by a species.

Call

A male *Dendropsophus microcephalus* displaying its vocal sac during its call.

Some frog calls are so loud, they can be heard up to a mile away. The call of a frog is unique to its species. Frogs call by passing air through the larynx in the throat. In most calling frogs, the sound is amplified by one or more vocal sacs, membranes of skin under the throat or on the corner of the mouth that distend during the amplification of the call. The field of neuroethology studies the neurocircuitry that underlies frog audition.

Some frogs lack vocal sacs, such as those from the genera *Heleioporus* and *Neobatrachus*, but these species can still produce a loud call. Their buccal cavity is enlarged and dome-shaped, acting as a resonance chamber that amplifies their call. Species of frog without vocal sacs and that do not have a loud call tend to inhabit areas close to flowing water. The noise of flowing water overpowers any call, so they must communicate by other means.

The main reason for calling is to allow males to attract a mate. Males call either individually or in a group called a chorus. Females of many frog species, for example *Polypedates leucomystax*, produce calls reciprocal to the males', which act as the catalyst for the enhancement of reproductive activity in a breeding colony. A male frog emits a release call when mounted by another male. Tropical species also have a rain call that they make on the basis of humidity cues prior to a rain shower. Many species also have a territorial call that is used to chase away other males. All of these calls are emitted with the mouth of the frog closed.

A distress call, emitted by some frogs when they are in danger, is produced with the mouth open, resulting in a higher-pitched call. The effectiveness of the call is unknown; however, it is suspected the call intrigues the predator until another animal is attracted, distracting them enough for its escape.

Many species of frog have deep calls, or croaks. The English onomatopoeic spelling is "ribbit". The croak of the American bullfrog (*Rana catesbiana*) is sometimes spelt "jug o' rum". Other examples are Ancient Greek *brekekekex koax koax* for probably *Rana ridibunda*, and the description in Rigveda 7:103.6 *gómāyur éko ajámāyur ékaħ* = "one has a voice like a cow's, one has a voice like a goat's".

Distribution and conservation status

The Red-eyed Tree Frog (*Litoria chloris*) is a species of tree frog native to eastern Australia.

The habitat of frogs extends almost worldwide, but they do not occur in Antarctica and are not present on many oceanic islands. The greatest diversity of frogs occurs in the tropical areas of the world, where water is readily available, suiting frogs' requirements due to their skin. Some frogs inhabit arid areas such as deserts, where water may not be easily accessible, and rely on specific adaptations to survive. The Australian genus *Cyclorana* and the American genus *Pternohyla* will bury themselves underground, create a water-impervious cocoon and hibernate during dry periods. Once it rains, they emerge, find a temporary pond and breed. Egg and tadpole development is very fast in comparison to most other frogs so that breeding is complete before the pond dries up. Some frog species are adapted to a cold environment; for instance the wood frog, whose habitat extends north of the Arctic Circle, buries itself in the ground during winter when much of its body freezes.

Golden toad (*Bufo periglenes*) – last seen in 1989

Frog populations have declined dramatically since the 1950s: more than one third of species are believed to be threatened with extinction and more than 120 species are suspected to be extinct since the 1980s. Among these species are the golden toad of Costa Rica and the Gastric-brooding frogs of Australia. Habitat loss is a significant cause of frog population decline, as are pollutants, climate change, the introduction of non-indigenous predators/competitors, and emerging infectious diseases including chytridiomycosis. Many environmental scientists believe that amphibians, including frogs, are excellent biological indicators of broader ecosystem health because of their intermediate position in food webs, permeable skins, and typically biphasic life (aquatic larvae and terrestrial adults). It appears that it is the species with both aquatic eggs and aquatic larvae that are most affected by the decline, while those with direct development are the most resistant.

A Canadian study conducted in 2006, suggested heavy traffic near frog habitats as a large threat to frog populations. In a few cases, captive breeding programs have been attempted to alleviate the pressure on frog populations, and these have proved successful. In 2007, it was reported the application of certain probiotic bacteria could protect amphibians from chytridiomycosis. One current project, The Panama Amphibian Rescue and Conservation Project, has subsequently been developed in order to rescue species at risk of chytridiomycosis in eastern Panama, and to develop field applications of this probiotic cure.

Zoos and aquariums around the world named 2008 the Year of the Frog, to draw attention to the conservation issues.

Evolution

A fossilized frog from the Czech Republic, possibly *Palaeobatrachus gigas*

Until the discovery of the Early Permian *Gerobatrachus hottoni* in 2008, a stem-batrachian with many salamander-like characteristics, the earliest known proto-frog was *Triadobatrachus massinoti*, from the 250 million year old early Triassic of Madagascar. The skull is frog-like, being broad with large eye sockets, but the fossil has features diverging from modern amphibia. These include a different ilium, a longer body with more vertebrae, and separate vertebrae in its tail (whereas in modern frogs, the tail vertebrae are fused, and known as the *urostyle* or *coccyx*). The tibia and fibula bones are unfused and separate, making it probable *Triadobatrachus* was not an efficient leaper.

Another fossil frog, *Prosalirus bitis*, was discovered in 1995. The remains were recovered from Arizona's Kayenta Formation, which dates back to the Early Jurassic epoch, somewhat younger than *Triadobatrachus*. Like *Triadobatrachus*, *Prosalirus* did not have greatly enlarged legs, but had the typical three-pronged pelvic structure. Unlike *Triadobatrachus*, *Prosalirus* had already lost nearly all of its tail and was well adapted for jumping.

The earliest known "true frog" is *Vieraella herbsti*, from the early Jurassic (188–213 million years ago). It is known only from the dorsal and ventral impressions of a single animal and was estimated to be 33 mm (1.3 in) from snout to vent. *Notobatrachus degiustoi* from the middle Jurassic is slightly younger, about 155–170 million years old. It is likely the evolution of modern *Anura* was completed by the Jurassic period. The main evolutionary changes involved the shortening of the body and the loss of the tail.

The earliest full fossil record of a modern frog is of sanyanlichan, which lived 125 million years ago and had all modern frog features, but bore 9 presacral vertebrae instead of the 8 of modern frogs.

Frog fossils have been found on all continents except Antarctica, but biogeographic evidence suggests they inhabited Antarctica when it was warmer.

Uses in agriculture and research

Frogs are raised commercially for several purposes. Frogs are used as a food source; frog legs are a delicacy in China, France, the Philippines, the north of Greece and in many parts of the American South, especially Louisiana. Dead frogs are sometimes used for dissections in high school and university anatomy classes, often after being injected with coloured plastics to enhance the contrast between the organs. This practice has declined in recent years with the increasing concerns about animal welfare.

Frogs have served as important model organisms throughout the history of science. Eighteenth-century biologist Luigi Galvani discovered the link between electricity and the nervous system through studying frogs. The African clawed frog or platanna (*Xenopus laevis*) was first widely used in laboratories in pregnancy assays in the first half of the 20th century. When human chorionic gonadotropin, a hormone found in substantial quantities in the urine of pregnant women, is injected into a female *X. laevis*, it induces them to lay eggs. In 1952, Robert Briggs and Thomas J. King cloned a frog by somatic cell nuclear transfer, the same technique later used to create Dolly the Sheep, their experiment was the first time successful nuclear transplantation had been accomplished in metazoans.

Frogs are used in cloning research and other branches of embryology because frogs are among the closest living relatives of man to lack egg shells characteristic of most other vertebrates, and therefore facilitate observations of early development. Although alternative pregnancy assays have been developed, biologists continue to use *Xenopus* as a model organism in developmental biology because it is easy to raise in captivity and has a large and easily manipulatable embryo. Recently, *X. laevis* is increasingly being displaced by its smaller relative *X. tropicalis*, which reaches its reproductive age in five months rather than one to two years (as in *X. laevis*), facilitating faster studies across generations. The genome sequence of *X. tropicalis* will probably be completed by 2015 at the latest.

Cultural beliefs

Moche Frog 200 A.D. Larco Museum Collection Lima, Peru

Frogs feature prominently in folklore, fairy tales and popular culture. They tend to be portrayed as benign, ugly, clumsy, but with hidden talents. Examples include Michigan J. Frog, *The Frog Prince*, and Kermit the Frog. Michigan J. Frog, featured in the Warner Brothers cartoon *One Froggy Evening*, only performs his singing and dancing routine for his owner. Once another person looks at him, he will return to a frog-like pose. "The Frog Prince" is a fairy tale of a frog who turns into a handsome prince once kissed. Kermit the Frog, on the other hand, is a conscientious and disciplined character of *The Muppet Show* and *Sesame Street*; while openly friendly and greatly talented, he is often portrayed as cringing at the fanciful behavior of more flamboyant characters.

The Moche people of ancient Peru worshipped animals and often depicted frogs in their art. In Panama local legend promised luck to anyone who spotted a golden frog in the wild and some believed that when Panamanian Golden Frogs died, they would turn into a gold talisman, known as a huaca. Today, despite being extinct in the wild, Panamanian Golden Frogs remain an important cultural symbol and can be found on decorative cloth molas made by the Kuna Indians, on T-shirts, as inlaid design on a new overpass in Panama City and even on lottery tickets.

Chapter 8

Seahorse

Seahorses
Temporal range: 23–0 Ma
Lower Miocene to Present

Hippocampus sp.

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Actinopterygii
Subclass:	Neopterygii
Infraclass:	Teleostei
Order:	Syngnathiformes
Family:	Syngnathidae
Subfamily:	Hippocampinae
Genus:	***Hippocampus*** Rafinesque, 1810

Seahorses compose the fish genus ***Hippocampus*** within the family Syngnathidae, in order Syngnathiformes. Syngnathidae also includes the pipefishes. "Hippocampus" comes from the Ancient Greek *hippos* meaning "horse" and *kampos* meaning “sea monster”.

There are nearly 50 species of seahorse. They are mainly found in shallow tropical and temperate waters throughout the world. They prefer to live in sheltered areas such as seagrass beds, coral reefs, or mangroves. Colonies have been found in European waters such as the Thames Estuary. From North America down to South America there are approximately four species, ranging from the very small (dwarf seahorses are only about 2.5 cm (1 in)) to much larger specimens off the Pacific Coast of Central America (the foot-long *H. ingens*). *H. erectus* are larger seahorses that range from Nova Scotia to around Uruguay. Three species live in the Mediterranean Sea: *H. hippocampus* (long snout), *H. brevirostris* (short snout) and *H. fuscus* (immigrated from the Red Sea). These fish form territories, with males staying in about 1 square meter (11 sq ft) of their habitat while females range about one hundred times that area. They bob around in sea grass meadows, mangrove stands, and coral reefs where they adopt murky brown and gray patterns to camouflage themselves among the sea grass. During social moments or in unusual surroundings, seahorses turn bright colors.

Description

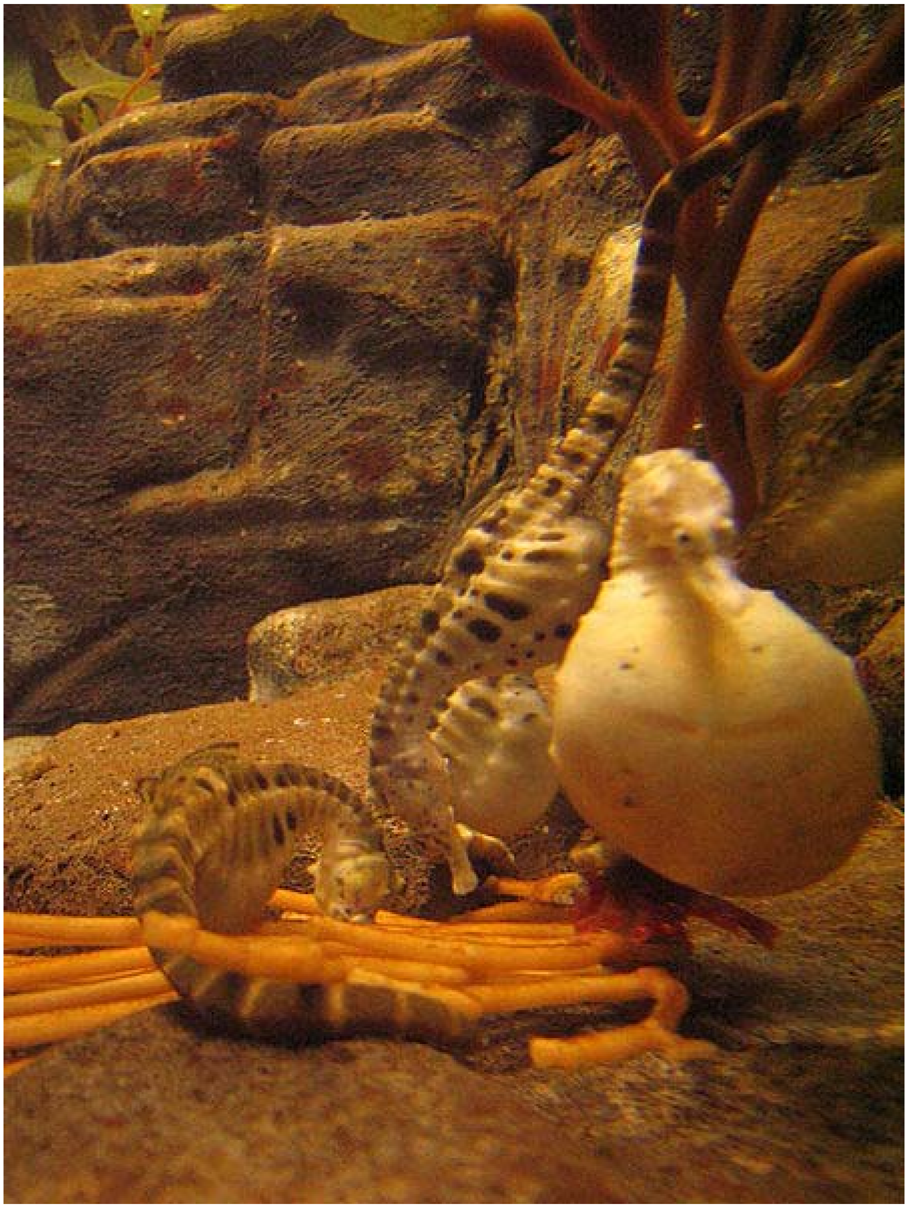
Spiny seahorse *Hippocampus hystrix* from East Timor holding on to soft coral with its prehensile tail

Seahorses are named for their equine profile. Although they are bony fish, they do not have scales, but rather a thin skin stretched over a series of bony plates arranged in rings throughout their body. Each species has a distinct number of rings. Seahorses swim upright, another characteristic that is not shared by their close pipefish relatives, which swim horizontally. Seahorses have a coronet on their head, which is distinct to each individual, much like a human fingerprint. They swim very poorly by using a dorsal fin, which they rapidly flutter and pectoral fins, located behind their eyes, which they use to steer. Seahorses have no caudal fin. Since they are poor swimmers, they are most likely to be found resting, with their prehensile tails wound around a stationary object. They have long snouts, which they use to suck up food, and eyes that can move independently of each other, much like a chameleon. Seahorses eat small shrimp, tiny fish, crustaceans and plankton.

Evolution and fossil record

Anatomical evidence, supported by molecular, physical, and genetic evidence, demonstrates that seahorses are highly modified pipefish. The fossil record of seahorses, however, is very sparse. The best known and best studied fossils are specimens of *H. guttulatus* (though literature more commonly refers to them under the synonym of *H. ramulosus*), from the Marecchia River Formation of Rimini Province, Italy, dating back to the Lower Pliocene, about 3 million years ago. The earliest known seahorse fossils are of two pipefish-like species, *H. sarmaticus* and *H. slovenicus* from the coprolitic horizon of Tunjice Hills, a middle Miocene lagerstätte in Slovenia dating back about 13 million years. Molecular dating finds that pipefish and seahorses separated during the Late Oligocene. This has led to speculation that seahorses evolved in response to large areas of shallow-water, newly created as the result of tectonic events. The shallow water allowed the expansion of seagrass habitats that selected for the camouflage offered by the seahorses' upright posture. These tectonic changes occurred in the Western Pacific Ocean suggesting an origin there with molecular data suggesting two later and separate invasions of the Atlantic Ocean.

Reproduction



Pregnant seahorse, New York Aquarium

The male seahorse is equipped with a brood pouch on the ventral, or front-facing, side. When mating, the female seahorse deposits up to 1,500 eggs in the male's pouch. The male carries the eggs for anywhere from 9 to 45 days until they emerge, expelling fully-developed, miniature seahorses in the water. Once the seahorse babies are released into the water, the male's role is done and he offers no further care.

Courtship

Before breeding, seahorses court for several days. Scientists believe the courtship behavior synchronizes the animals' movements so that the male can receive the eggs when the female is ready to deposit them. During this time they may change color, swim side by side holding tails or grip the same strand of sea grass with their tails and wheel around in unison in what is known as a “pre-dawn dance". They eventually engage in a “true courtship dance" lasting about 8 hours, during which the male pumps water through the egg pouch on his trunk which expands and opens to display its emptiness. When the female’s eggs reach maturity, she and her mate let go of any anchors and snout-to-snout, drift upward out of the seagrass, often spiraling as they rise. The female inserts her ovipositor into the male’s brood pouch and deposits dozens to thousands of eggs. As the female releases her eggs, her body slims while his swells. Both animals then sink back into the seagrass and she swims away.

Gestation

West Australian seahorse, *H. subelongatus*

The male releases his sperm directly into seawater where it fertilizes the eggs, which are then embedded in the pouch wall and become surrounded by a spongy tissue. The male supplies the eggs with prolactin, the same hormone responsible for milk production in pregnant mammals. The pouch provides oxygen as well as a controlled environment incubator. The eggs then hatch in the pouch where the salinity of the water is regulated; this prepares the newborns for life in the sea. Throughout gestation, which in most species requires two to four weeks, his mate visits him daily for “morning greetings”. They interact for about 6 minutes, reminiscent of courtship. The female then swims away until the next morning, and the male returns to vacuuming up food through his snout.

Research published in 2007 indicates the male releases sperm into the surrounding sea water during fertilization, and not directly into the pouch as previously thought.

Birth

White's seahorse, *H. whitei*

The number of young released by the male seahorse averages 100–200 for most species, but may be as low as 5 for the smaller species, or as high as 1,500. When the fry are ready to be born, the male expels them with muscular contractions. He typically gives birth at night and is ready for the next batch of eggs by morning when his mate returns. Like almost all other fish species, seahorses do not nurture their young after birth. Infants are susceptible to predators or ocean currents which wash them away from feeding grounds or into temperatures too extreme for their delicate bodies. Fewer than 0.5% of infants survive to adulthood, explaining why litters are so large. These survival rates are actually fairly high compared to other fish, because of their protected gestation, making the process worth the great cost to the father. The eggs of most other fish are abandoned immediately after fertilization.

Questions surrounding reproductive roles

Reproduction is energetically costly to the male. This brings into question why the sexual role reversal even takes place. In an environment where one partner incurs more energy costs than the other, Bateman's principle suggests that the lesser contributor takes the role of the aggressor. Male seahorses are more aggressive and sometimes “fight” for female attention. According to Amanda Vincent of Project Seahorse, only males tail-wrestle and snap their heads at each other. This discovery prompted further study of energy costs. To estimate the female’s direct contribution, researcher Heather D. Masonjones, associate professor of biology at the University of Tampa, chemically analyzed the energy stored in each egg. To measure the burden on the male, Masonjones measured its oxygen consumption. By the end of incubation, the male consumed almost 33% more oxygen than before mating. The study concluded that the female's energy expenditure while generating eggs is twice that of males during incubation confirming the standard hypothesis.

Why the male seahorse (and other members of Syngnathidae) carries the offspring through gestation is unknown, though some researchers believe it allows for shorter birthing intervals, in turn resulting in more offspring. Given an unlimited number of ready and willing partners, males have the potential to produce 17 percent more offspring than females in a breeding season. Also, females have “time-outs” from the reproductive cycle that are 1.2 times longer than those of males. This seems to be based on mate choice, rather than physiology. When the female’s eggs are ready, she must lay them in a few hours or eject them into the water column. Making eggs is a huge cost to her physically, since they amount to about a third of her body weight. To protect against losing a clutch, the female demands a long courtship. The daily greetings help to cement the bond between the pair.

Monogamy

One common misconception about seahorses is that they mate for life. Many species of seahorses form pair bonds that last through at least the breeding season. Some species show a higher level of mate fidelity than others. However, many species readily switch mates when the opportunity arises. *H. abdominalis* and *H. breviceps* have been shown to breed in groups, showing no continuous mate preference. Many more species mating habits have not been studied, so it is unknown how many species are actually monogamous, or how long those bonds actually last.

Although monogamy within fish is not common, it does appear to exist for some. In this case, the mate guarding hypothesis may be an explanation. This hypothesis states “males remain with a single female because of ecological factors that make male parental care and protection of offspring especially advantageous." Because the rates of survival for newborn seahorses are so low, incubation is essential. Though not proven, males could have taken on this role because of the lengthy period the females require to produce their eggs. If males incubate while females prepare the next clutch (amounting to 1/3 of body weight), they can reduce the interval between clutches.

Feeding habits

Seahorses feed on small crustaceans floating in the water or crawling on the bottom. With excellent camouflage and a lot of patience, seahorses ambush prey that float within striking range. Mysid shrimp and other small crustaceans are favorites, but some seahorses have been observed eating other kinds of invertebrates and even larval fish.

In aquaria

Seahorses (*Hippocampus erectus*) at the New England Aquarium, USA.

While many aquarium hobbyists keep seahorses as pets, seahorses collected from the wild tend to fare poorly in home aquaria. Many eat only live foods such as brine shrimp and are prone to stress, which damages their immune systems and makes them susceptible to disease.

In recent years, however, captive breeding has become more popular. Such seahorses survive better in captivity, and are less likely to carry diseases. They eat frozen mysidacea (crustaceans) that are readily available from aquarium stores, and do not experience the stress of moving out of the wild. Although captive-bred seahorses are more expensive, they take no toll on wild populations.

Seahorses should be kept in an aquarium to themselves, or with compatible tank-mates. Seahorses are slow feeders, and fast, aggressive feeders will leave them without food.

Seahorses can co-exist with many species of shrimp and other bottom-feeding creatures. Gobies also make good tank-mates. Keepers are generally advised to avoid eels, tangs, triggerfish, squid, octopus, and sea anemones.

Animals sold as "freshwater seahorses" are usually the closely related pipefish, of which a few species live in the lower reaches of rivers. The supposed true "freshwater seahorse" called *H. aimei* was not a real species, but a name sometimes used for Barbour's and Hedgehog seahorses. The latter is a species that can be found in brackish waters, but not actually a freshwater fish.

Use in Chinese medicine

Medicinal seahorse.

Seahorses, silkie, and cordyceps after being used to make a broth

Seahorse and scorpion skewers as street food in China

Seahorse populations are thought to have been endangered in recent years by overfishing and habitat destruction. The seahorse is used in traditional Chinese herbology, and as many as 20 million seahorses may be caught each year and sold for this purpose. Medicinal seahorses are not readily bred in captivity as they are susceptible to disease and it is believed that they have different medicinal properties from aquarium seahorses. Seahorses are also used as medicines by the Indonesians, the Central Filipinos, and many other ethnic groups around the world.

Import and export of seahorses has been controlled under CITES since May 15, 2004. However, Indonesia, Japan, Norway, and South Korea have chosen to opt out of the trade rules set by CITES.

The problem may be exacerbated by the growth of pills and capsules as the preferred method of ingesting medication as they are cheaper and more available than traditional, individually tailored prescriptions of raw medicinals but the contents are harder to track. Seahorses once had to be of a certain size and quality before they were accepted by TCM practitioners and consumers. But declining availability of the preferred large, pale and smooth seahorses has been offset by the shift towards prepackaged medicines, which make it possible for TCM merchants to sell previously unused juvenile, spiny and dark-coloured animals. Today almost a third of the seahorses sold in China are prepackaged. This adds to the pressure on the species.

Taxonomy

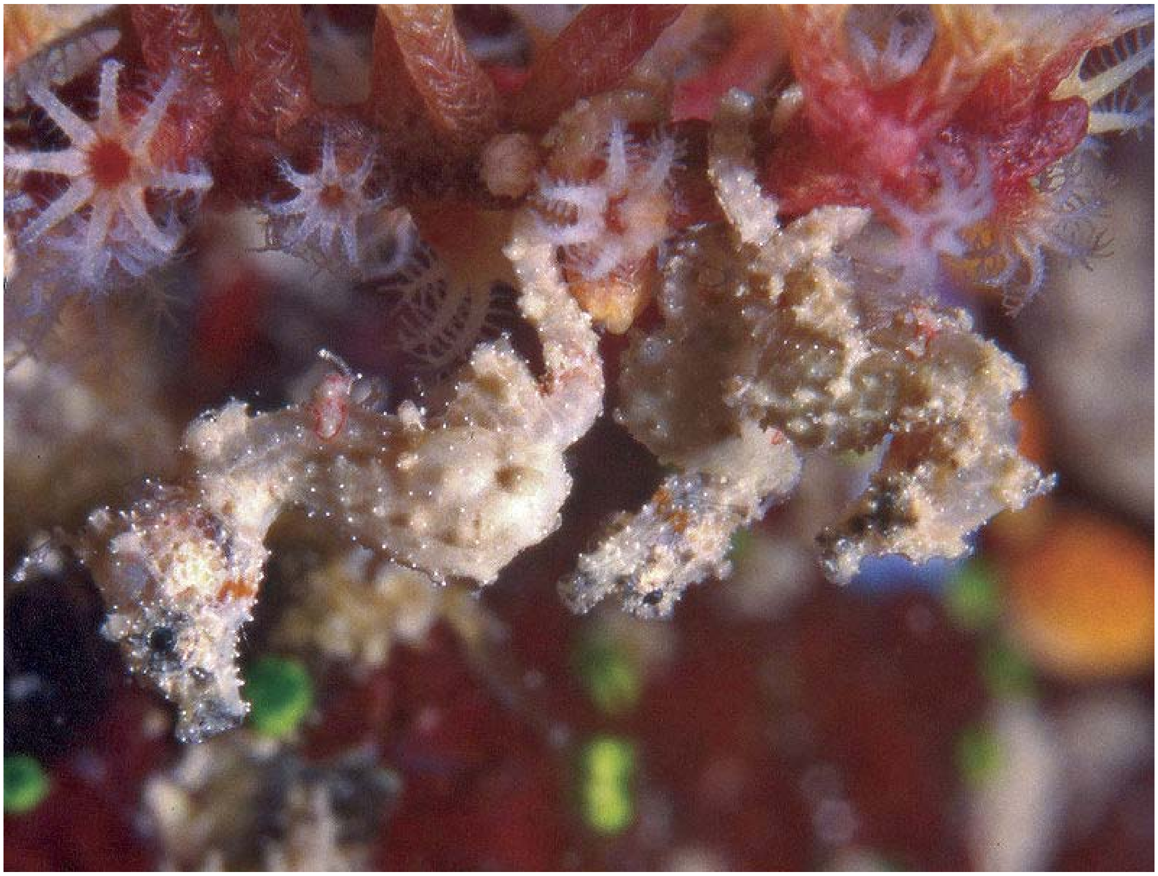
Common seahorse, *Hippocampus kuda*

- Genus *Hippocampus*
  - Big-belly seahorse, *H. abdominalis* Lesson, 1827 (New Zealand and south and east Australia)
  - Winged seahorse, *H. alatus* Kuiter, 2001
  - West African seahorse, *H. algiricus* Kaup, 1856
  - Narrow-bellied seahorse, *H. angustus* Günther, 1870

- Barbour's seahorse, *H. barbouri* Jordan & Richardson, 1908
- Pygmy seahorse, *H. bargibanti* Whitley, 1970 West Pacific area (Indonesia, Philippines, Papua New Guinea, Solomon Islands, etc.)
- False-eyed seahorse, *H. biocellatus* Kuiter, 2001
- Réunion seahorse, *H. borboniensis* Duméril, 1870
- Short-head seahorse or knobby seahorse, *H. breviceps* Peters, 1869 (south and east Australia)
- Giraffe seahorse, *H. camelopardalis* Bianconi, 1854
- Knysna seahorse, *H. capensis* Boulenger, 1900
- *H. colemani* Kuiter, 2003
- Tiger tail seahorse, *H. comes* Cantor, 1850
- Crowned seahorse, *H. coronatus* Temminck & Schlegel, 1850
- Denise's pygmy seahorse, *H. denise* Lourie & Randall, 2003
- Lined seahorse, *H. erectus* Perry, 1810 (east coast of the Americas, between Nova Scotia and Uruguay)
- Fisher's seahorse, *H. fisheri* Jordan & Evermann, 1903
- Sea pony, *H. fuscus* Rüppell, 1838 (Indian Ocean)
- Big-head seahorse, *H. grandiceps* Kuiter, 2001
- Long-snouted seahorse, *H. guttulatus* Cuvier, 1829
- Eastern spiny seahorse, *H. hendriki* Kuiter, 2001
- Short-snouted seahorse, *H. hippocampus* (Linnaeus, 1758) (Mediterranean Sea and Atlantic Ocean)
- Thorny seahorse, *H. histrix* Kaup, 1856 (Indian Ocean, Persian Gulf, Red Sea, and the Far East)
- Pacific seahorse, *H. ingens* Girard, 1858 (Pacific coast of North, Central and South America)
- Jayakar's seahorse, *H. jayakari* Boulenger, 1900
- Collared seahorse, *H. jugumus* Kuiter, 2001
- Great seahorse, *H. kelloggi* Jordan & Snyder, 1901
- Common seahorse, *H. kuda* Bleeker, 1852
- Lichtenstein's seahorse, *H. lichtensteinii* Kaup, 1856
- Bullneck seahorse, *H. minotaur* Gomon, 1997
- Japanese seahorse, *H. mohnikei* Bleeker, 1854
- Monte Bello seahorse, *H. montebelloensis* Kuiter, 2001
- Northern spiny seahorse, *H. multispinus* Kuiter, 2001
- *H. pontohi* Lourie and Kuiter, 2008
- High-crown seahorse, *H. procerus* Kuiter, 2001
- Queensland seahorse, *H. queenslandicus* Horne, 2001
- Longsnout seahorse, *H. reidi* Ginsburg, 1933 (Caribbean coral reefs)
- Satomi's pygmy seahorse, *H. satomiae* Lourie and Kuiter, 2008
- Half-spined seahorse, *H. semispinosus* Kuiter, 2001
- *H. severnsi* Lourie and Kuiter, 2008
- Shiho's seahorse, *H. sindonis* Jordan & Snyder, 1901
- Hedgehog seahorse, *H. spinosissimus* Weber, 1913
- West Australian seahorse, *H. subelongatus* Castelnau, 1873
- Longnose seahorse, *H. trimaculatus* Leach, 1814

  - White's seahorse, *H. whitei* Bleeker, 1855 (east Australia)
  - Zebra seahorse, *H. zebra* Whitley, 1964
  - Dwarf seahorse, *H. zosterae* Jordan & Gilbert, 1882 (Gulf of Mexico and the Caribbean)

Pygmy seahorses

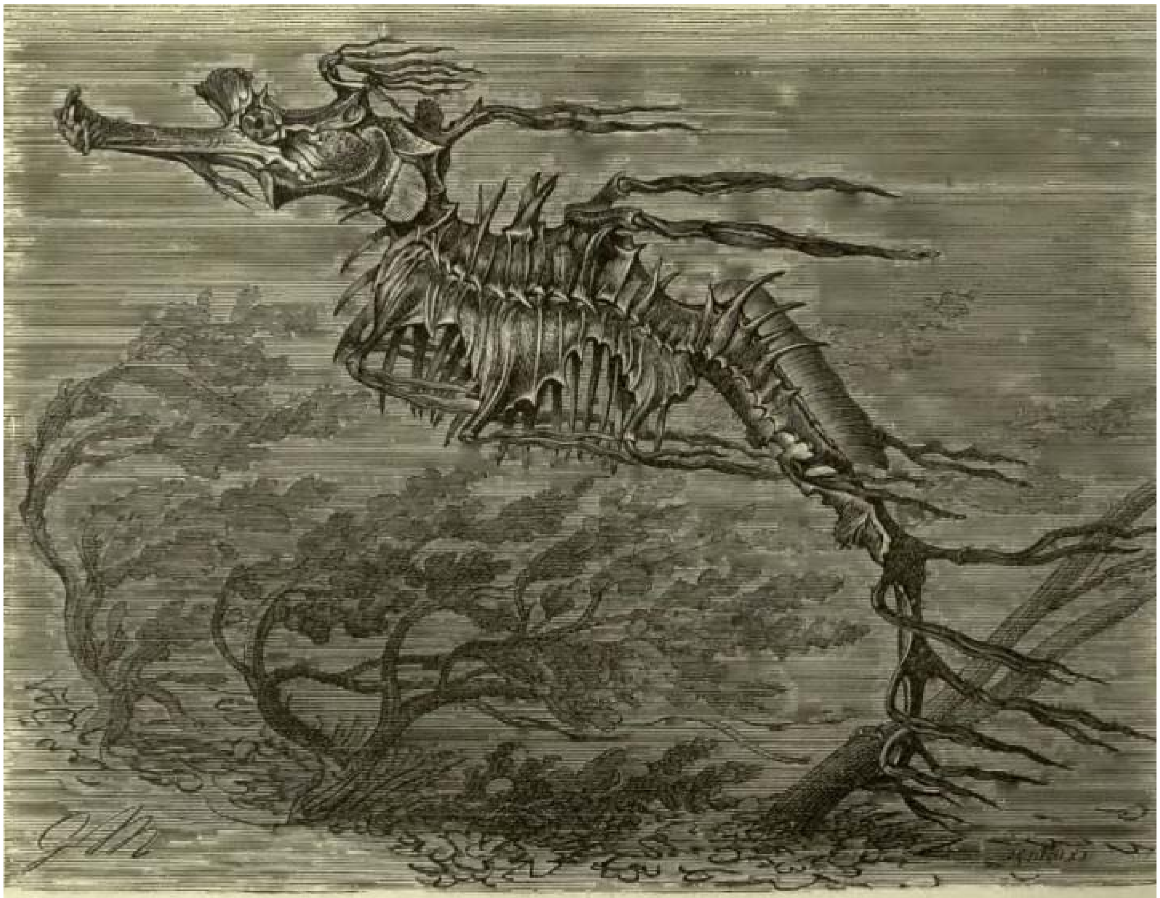


Hippocampus satomiae attached to a coral

Pygmy Seahorses are less than 15 millimeters (0.6 in) tall and 17 millimeters (0.7 in) wide members of the genus. Previously the term was applied exclusively to the species *H. bargibanti* but since 1997, discoveries have made this term obsolete. The species *H. minotaur*, *H. denise*, *H. colemani*, *H. pontohi*, *H. severnsi* and *H. satomiae* have been described. Other species that are believed to be unclassified have also been reported in books, dive magazines and on the Internet. They can be distinguished from other species of seahorse by their 12 trunk rings, low number of tail rings (26–29), the location in which young are brooded in the trunk region of males and their extremely small size. Molecular analysis (of ribosomal RNA) of 32 *Hippocampus* species found that *H. bargibanti* belongs in a separate clade from other members of the genus and therefore that the species diverged from the other species in the "ancient" past.

Most pygmy seahorses are well camouflaged and live in close association with other organisms including colonial hydrozoans (*Lytocarpus* and *Antennellopsis*), coralline algae (*Halimeda*) sea fans (*Muricella*, *Annella*, *Acanthogorgia*). This combined with their small size accounts for why most species have only been noticed in recent years.

Heraldry



FUCUS-LIKE SEA-HORSE ($\frac{2}{3}$ nat. size).

'Fucus like seahorse' from Lydekker's *The Royal Natural History*

A sculpture of a heraldic seahorse that adorned an 18th or 19th century French naval vessel

In heraldry, a seahorse is depicted as a creature with the foreparts of a horse and the hindparts of a fish.

Threats & Future

Most seahorse species are data deficient. This means there is not enough information to make a proper assessment about their risk of extinction. Because seahorse population is unknown, there is a greater risk of losing more seahorses because of the lack of information about how many are dying each year, how many are being born, how many are used for souvenirs, etc. Seahorse habitats are in great danger though. Coral reefs and seagrass beds are deteriorating, meaning seahorses have fewer places to live. Also as stated above, seahorses are used to Chinese Medicine and as souvenirs, which definitely cuts their population down significantly each year.

Chapter 9

Misumena Vatia

Goldenrod Crab Spider

Goldenrod crab spider capturing a wasp

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Arachnida
Order:	Araneae
Family:	Thomisidae
Genus:	*Misumena*
Species:	***M. vatia***

Binomial name

Misumena vatia
(Clerck, 1757)

Synonyms

Araneus vatius
Aranea calycina
Aranea 4-lineata
Aranea kleinii
Aranea osbekii
Aranea hasselquistii
Aranea uddmanni

Aranea scorpiformis
Aranea virginea
Aranea citrea
Aranea citrina
Aranea sulphereoglobosa
Aranea sulphurea
Aranea quinquepuncata
Aranea albonigricans
Aranea calicina
Aranea cretata
Misumena citrea
Thomisus citreus
Thomisus calycinus
Thomisus dauci
Thomisus pratensis
Thomisus spinipes
Thomisus scorpiformis
Thomisus quadrilineatus
Thomisus viridis
Thomisus phrygiatus
Thomisus devius
Thomisus fartus
Thomisus vatius
Pachyptile devia
Thomisus cucurbitinus
Misumena oblonga
Misumena calycina
Misumena occidentalis
Misumenops vatia

Misumena vatia is a species of crab spider with holarctic distribution. In North America, where it is the largest and best-known flower spider, it is called the **goldenrod crab spider** or **flower (crab) spider**, because it is commonly found hunting in goldenrod sprays in the autumn.

Young male, imitating a flower

Young males in the early summer may be quite small and easily overlooked, but females can grow up to 10 mm (excluding legs); males reach 5 mm at most.

These spiders may be yellow or white, depending on the flower in which they are hunting. Especially younger females, which may hunt on a variety of flowers such as daisies and sunflowers, may change color "at will". Older females require large amounts of relatively large prey to produce the best possible clutch of eggs. They are therefore, in North America, most commonly found in goldenrod (*Solidago sp.*), a bright yellow flower which attracts large numbers of insects, especially in autumn. It is often very hard even for a searching human to recognize one of these spiders on a yellow flower.

Reproduction

The much smaller males scamper from flower to flower in search of females and are often seen missing one or more of their legs. This may be due either to near misses by predators such as birds or to fighting with other males.

When a male finds a female, he climbs over her head over her opisthosoma onto her underside, where he inserts his pedipalps to inseminate her.

The young reach a size of about 5mm by autumn and spend the winter on the ground. They molt for the last time in May of the next year.

Color change

These spiders change color by secreting a liquid yellow pigment into the outer cell layer of the body. On a white base, this pigment is transported into lower layers, so that inner glands, filled with white guanine, become visible. If the spider dwells longer on a white plant, the yellow pigment is often excreted. It will then take the spider much longer to change to yellow, because it will have to produce the yellow pigment first. The color change is induced by visual feedback; spiders with painted eyes were found to have lost this ability.

The color change from white to yellow takes between 10 and 25 days, the reverse about six days. The yellow pigments have been identified as kynurenine and 3-hydroxykynurenine

male *M. vatia*

Female *Misumena vatia*, on Achillea millefolium flowers

Misumena vatia

Chapter 10

Pacific Tree Frog

Pacific Tree Frog

Conservation status

Least Concern (IUCN 3.1)

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Amphibia
Order:	Anura
Family:	Hylidae
Genus:	*Pseudacris*
Species:	***P. regilla***

Binomial name

Pseudacris regilla
(Baird & Girard, 1852)

Synonyms

Hyla regilla

A Pacific Tree Frog(green morph)sitting on a sunflower leaf stem, Nanoose Bay British Columbia

The **Pacific Tree Frog** (*Pseudacris regilla*) is a very common species of chorus frog, with a range from the West Coast of the United States (from North California, Oregon, and Washington) to British Columbia in Canada. Living anywhere from sea level up to over 10,000 feet, they are found in shades of greens or browns and even have been known to change between them. They live in many types of habitats and reproduce in aquatic settings. This species is also known as the **Pacific Chorus Frog**. It is also the only frog that goes "ribbit".

Anatomy and morphology

The Pacific Tree Frog is able to grow the length of 5 cm long from snout to urostyle. Male are usually smaller than the female and contain a dark patch of skin on their throat. The dark patch is the vocal sac which stretches out when a male is calling. They can be a number of different colors from green, tan, reddish, gray, brown, cream, or black. Most are found to be a shade of either green or brown, and they can change their color seasonally to better match their environment. They usually have a pale or white color on their bellies. These frogs have many variations of markings on their back and sides that are usually dark and spotty. They can be identified by the black or dark brown eye stripe that goes over the eye from the nose to the shoulder. Their skin is covered in small bumps. They have long legs compared to their bodies and they tend to be slender. Their toes are long and only very slightly webbed. On the end of each toe, there is a round sticky toe pad or disks used for climbing and sticking to surfaces.

Distribution, habitat and ecology

Pacific tree frogs are most common on the pacific coast of California, Oregon and Washington, but they are found anywhere from Baja California all the way up to British Columbia. They are also found eastward to Idaho, Montana, and Nevada. They can also be found upland in ponds, streams, lakes and some times even further away from water. Their habitat consists of a wide variety of climate and vegetation from sea level to high altitudes. The tree frog makes its home in riparian habitat as well as woodlands, grassland, chaparral, pasture land, and even urban areas including back yard ponds. Eggs of the Pacific Tree Frog may be consumed by the Rough-skinned Newt and other amphibians.

Reproduction, development and behavior

The Pacific Tree Frog begins mating in early winter to early spring. Since these frogs are so widespread geographically, it is thought that their breeding season is determined by local conditions. When it is time, the males migrate to the water. They then make a call at the same time, calling "kreck-ek" or ribbiting loudly. This lures the females to the water and they mate. The females lay their eggs in clumps of 10-90 and usually put them on and under vegetation and leaf litter in the pond. Females usually lay their eggs in shallow, calm water that has little action around it. If they survive, embryos will hatch into tadpoles within one to three weeks. The tadpoles feed on periphyton, filamentous algae, diatoms, and pollen in or on the surface of the water. They feed using a beak like structure that helps scrape vegetation off surfaces and suction.

Metamorphosis usually follows about 2 to 2½ months later, but experience raising these tadpoles shows that some may delay metamorphosis, changing up to 5 months after hatching. The survival rate of these delayed metamorphs is lower, and the evolutionary utility of this delayed metamorphosis is uncertain.

During the final stages of transformation when the tadpoles have 4 limbs and a tail, they stop feeding for a short time while their mouths widen and their digestive system adjusts from herbivorous to carnivorous. Then the frogs begin to emerge from the pond, sometimes measuring less than 1 centimetre.

For the most part, Pacific Tree Frogs are nocturnal, but they have been spotted during the day. These frogs spend a lot of time hiding under rotten logs, rocks, long grasses, and leaf litter, where they are very difficult to see unless they move. When they hunt, their toe pads allow them to climb on vegetation and other surfaces where they are to ambush their prey. Much of their diet consists of spiders, beetles, flies, ants, and other insects and arthropods; they can and do eat insects that are almost as large as they are, and will expand their bodies slightly to accommodate these meals.

Pacific Tree Frogs mature quickly, and will most likely be able to mate within the next season after metamorphosis. Predators include snakes, raccoons, herons, egrets, and other small mammals and reptiles. They can get very fat in size.

When they sense potential food nearby, they will commonly twitch a toe to attract it within easy reach of their tongue. They can live at least 9 years in captivity on a diet of spiders, moths, and flies.

Evolutionary history

The evolutionary history of these frogs is a very interesting one that is still being debated. Amphibians themselves are thought to have descended from the lobe-finned bony fishes. These fish had an ossified skeleton and emerged from the water as they developed limbs, girdles, and terrestrial characteristics such as lungs and a neck.

It is hard to figure out an exact frog lineage because of the lack of fossil record. The habitat in which these animals lived was moist and decay was quick. This was not helpful in preserving biological clues. The family of Hylidae is somewhat recent, appearing around 50 million years ago. The genus *Hyla* then appeared just after the dinosaurs went extinct. This genus originated in South America and expanded to the north into Mexico and eventually into North America. There was then a rise in sea level and the connection between the northern and southern populations was gone. They have been separate ever since, and have become genetically distinct from one another.

For this reason, the genus *Hyla* has been split into three separate genera: *Aris*, *Limnaoedus*, and *Pseudacris*. This is where the current confusion has taken place. Although the Pacific Tree Frog has carried the scientific name of *Hyla regilla* for many years, the most current consensus among scientists is that they should actually be *Pseudacris regilla*. This is still not agreed upon completely, and in the future we will see what becomes of these names.

Green and brown color morphs

One of the most interesting features of these frogs is their ability to change color from brown to green. Previously, it was thought that there were two different fixed colors that an adult tree frog could be. Now it has been found that some of them are able to change between the two. They can also change from lighter to darker, shift from patterned markings to pure colors and vice versa, and even display combinations of colors, brown/green being the most frequent.

These color changing morphs are triggered not by color change in their environment, but a change in background brightness. This type of environmental change would be caused by seasonal fluctuation. A full change in the dorsal coloration of a color morph can take anywhere from weeks to months, but initial changes can occur in just a few hours. This has been shown to be a very useful cryptic survival feature for these frogs.

Skin color is produced via pigment cells called chromatophores. There are commonly three types of chromatophores found in amphibians: 1. Xanthophores - These contain yellow, orange, or red pigments and are found uppermost on the dermis; 2. Iridophores - These lie below the xanthophores and function by reflecting and scattering white light up through them; in the case of *Pseudacris regilla* and many other North American frogs, iridophores reflect blue light through the yellow pigment cells above to create a green frog; 3. Melanophores - These are the deepest pigment cells and are responsible for the presence of black and brown pigments.

A rare, recessive "blue morph" is known. There was one housed at the Humboldt State University Natural History Museum in Arcata, California; however, this museum is now closed. It has been suggested that this mutation inhibits the xanthophores' ability to produce yellow pigments, thus the normally green frog (possibly of the non-color-changing type) appears blue.

Side view showing a color variant.

Green Morph.

Homing

Research was done on the Pacific Tree Frog to discover if they have homing instincts and what was their main source knowing where their home was. In order to find the answer, these frogs were marked and moved 300 yards away from their pond. Several days later, the researchers did a recapture on the original pond in which 66.3% of the frogs were recaptured indicating that there was some source of homing instinct. This was made apparent again when 24 frogs were placed into a larger pond and 20 of those frogs were returned at their original pond. The frogs' movement patterns, olfactory, auditory, and kinesthetic senses could be explanations for the homing, but not a single factor was able to explain the results indicating that these frogs might be using all or a combination of these factors for homing.

Conservation status

These frogs are the most common frogs on the west coast of North America. Although the Pacific Tree Frog remains abundant, there has been a large decline in amphibian populations. Most populations of tree frogs appear healthy, but there is some evidence of declines. The cause has not been fully understood, but pollution, the introduction of exotic species and habitat loss are very high on the list of factors.

Regional importance

In 2007, the Pacific Chorus Frog was named the state frog of the State of Washington. The Pacific Tree Frog is also a very important species in all of the regions where it is found because it is a keystone species. Many other species such as garter snakes depend upon its abundance as a prey item for their survival.

Chapter 11

Tuatara

Tuatara

Male tuatara

Conservation status

Vulnerable (IUCN 2.3)

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Class:	Reptilia
Order:	Sphenodontia
Family:	Sphenodontidae
Genus:	***Sphenodon*** Gray, 1831

Species

- *Sphenodon guntheri* – (Buller,

1877)
- *Sphenodon punctatus* – (Gray, 1842)
- *Sphenodon diversum* – Colenso, 1885 †

dark red: range (North Island, New Zealand)

The **tuatara** is a reptile endemic to New Zealand which, though it resembles most lizards, is actually part of a distinct lineage, order Sphenodontia. The two species of tuatara are the only surviving members of its order, which flourished around 200 million years ago. Their most recent common ancestor with any other extant group is with the squamates (lizards and snakes). For this reason, tuatara are of great interest in the study of the evolution of lizards and snakes, and for the reconstruction of the appearance and habits of the earliest diapsids (the group that also includes birds, dinosaurs, and crocodiles).

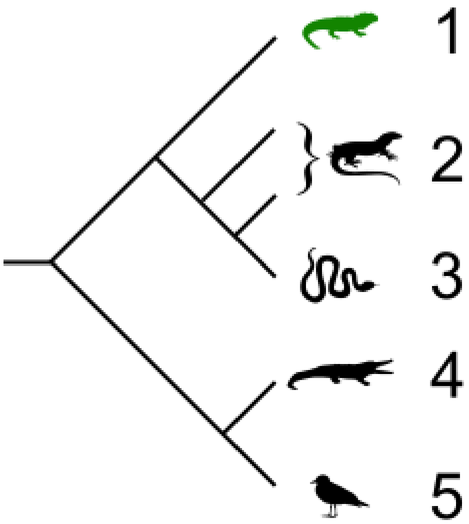
Tuatara are greenish brown, and measure up to 80 cm (31 in) from head to tail-tip and weigh up to 1.3 kilograms (2.9 lb) with a spiny crest along the back, especially pronounced in males. Their dentition, in which two rows of teeth in the upper jaw overlap one row on the lower jaw, is unique among living species. They are further unusual in having a pronounced photo-receptive eye dubbed the "third eye", whose current function is a subject of ongoing research but is thought to be involved in setting circadian and seasonal cycles. They are able to hear although no external ear is present, and have a number of unique features in their skeleton, some of them apparently evolutionarily retained from fish. Although tuatara are sometimes called "living fossils", recent taxonomic and molecular work has shown that they have changed significantly since the Mesozoic era.

The name "tuatara" derives from the Māori language, and means "peaks on the back". As with many other Māori loanwords, the plural form is now generally the same as the singular in formal New Zealand English usage. "Tuataras" remains common in less formal speech, particularly among older speakers. The tuatara has been classified as an endangered species since 1895 (the second species, *S. guntheri*, was not recognised until 1989). Tuatara, like many of New Zealand's native animals, are threatened by habitat loss and introduced predators like the Polynesian Rat *(Rattus exulans)*. They were extinct on the mainland, with the remaining populations confined to 32 offshore islands, until the first mainland release into the heavily fenced and monitored Karori Sanctuary in 2005.

During routine maintenance work at Karori Sanctuary in late 2008, a tuatara nest was uncovered, with a hatchling found the following autumn. This is thought to be the first case of tuatara successfully breeding on the New Zealand mainland in over 200 years, outside of captive rearing facilities.

Taxonomy and evolution

Tuatara, and their sister group Squamata (which includes lizards, snakes and amphisbaenians), belong to the superorder Lepidosauria, the only surviving taxon within Lepidosauromorpha. Squamates and tuatara both show caudal autotomy (loss of the tail-tip when threatened), and have a transverse cloacal slit. The origin of the tuatara probably lies close to the split between the Lepidosauromorpha and the Archosauromorpha. Though tuatara resemble lizards, the similarity is superficial, because the family has several characteristics unique among reptiles. The typical lizard shape is very common for the early amniotes; the oldest known fossil of a reptile, the *Hylonomus*, resembles a modern lizard.



Cladogram showing relationships of extant members of the Sauria. Numbered items are:
1. Tuatara
2. Lizards
3. Snakes
4. Crocodiles
5. Birds
"Lizards" are paraphyletic. Branch lengths do not indicate divergence times.

Tuatara were originally classified as lizards in 1831 when the British Museum received a skull. The genus remained misclassified until 1867, when Albert Günther of the British Museum noted features similar to birds, turtles, and crocodiles. He proposed the order Rhynchocephalia (meaning "beak head") for the tuatara and its fossil relatives. Now, most authors prefer to use the more exclusive order name of Sphenodontia for the tuatara and its closest living relatives.

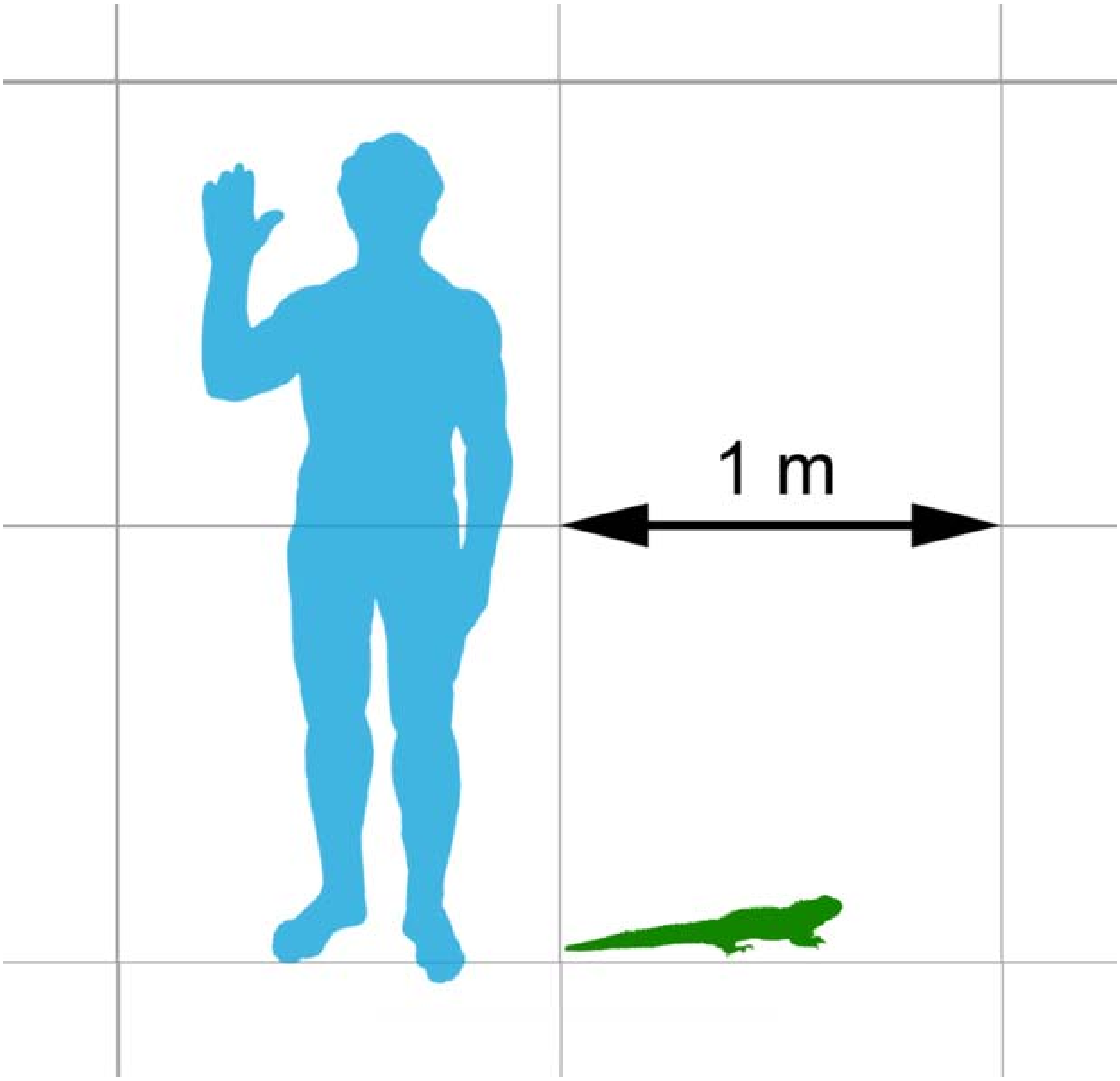
Many disparately related species were subsequently added to the Rhynchocephalia, resulting in what taxonomists call a "wastebasket taxon". Williston proposed the Sphenodontia to include only tuatara and their closest fossil relatives in 1925. *Sphenodon* is derived from the Greek for "wedge" (*σφηνος/sphenos*) and "tooth" (*δόντι/odon(t)*).

Tuatara have been referred to as living fossils, which means their group retains many basal characteristics from around the time of the squamate – rhynchocephalian split (220 MYA). However, taxonomic work on Sphenodontia has shown that this group has undergone a variety of changes throughout the Mesozoic, and a recent molecular study showed that their rate of molecular evolution is faster than of any other animal so far examined. Many of the niches occupied by lizards today were then held by sphenodontians. There was even a successful group of aquatic sphenodontians known as pleurosaurs, which differed markedly from living tuatara. Tuatara show cold weather adaptations that allow them to thrive on the islands of New Zealand; these adaptations may be unique to tuatara since their sphenodontian ancestors lived in the much warmer climates of the Mesozoic.

Species

There are two extant species: *Sphenodon punctatus* and the much rarer *Sphenodon guntheri*, or Brothers Island tuatara, which is confined to North Brother Island in Cook Strait. The species name *punctatus* is Latin for "spotted", and *guntheri* refers to Albert Günther. *S. punctatus* was named when only one species was known, and its name is misleading, since both species can have spots. The Brother's Island tuatara (*S. guntheri*) has olive brown skin with yellowish patches, while the colour of the other species, (*S. punctatus*), ranges from olive green through grey to dark pink or brick red, often mottled, and always with white spots. In addition, *S. guntheri* is considerably smaller. A third, extinct species of *Sphenodon* was identified in November 1885 by William Colenso, who was sent an incomplete sub-fossil specimen from a local coal mine. Colenso named the new species *S. diversum*. *Sphenodon punctatus* is further divided into two subspecies: the Cook Strait tuatara (unnamed subspecies), which lives on other islands in and near Cook Strait, and the northern tuatara (*Sphenodon punctatus punctatus*), which lives on the Bay of Plenty, and some islands further north. A 2009 paper reexamined the genetic bases used to distinguish the two species of tuatara, and concluded that they only represent geographic variants, and only one species should be recognized.

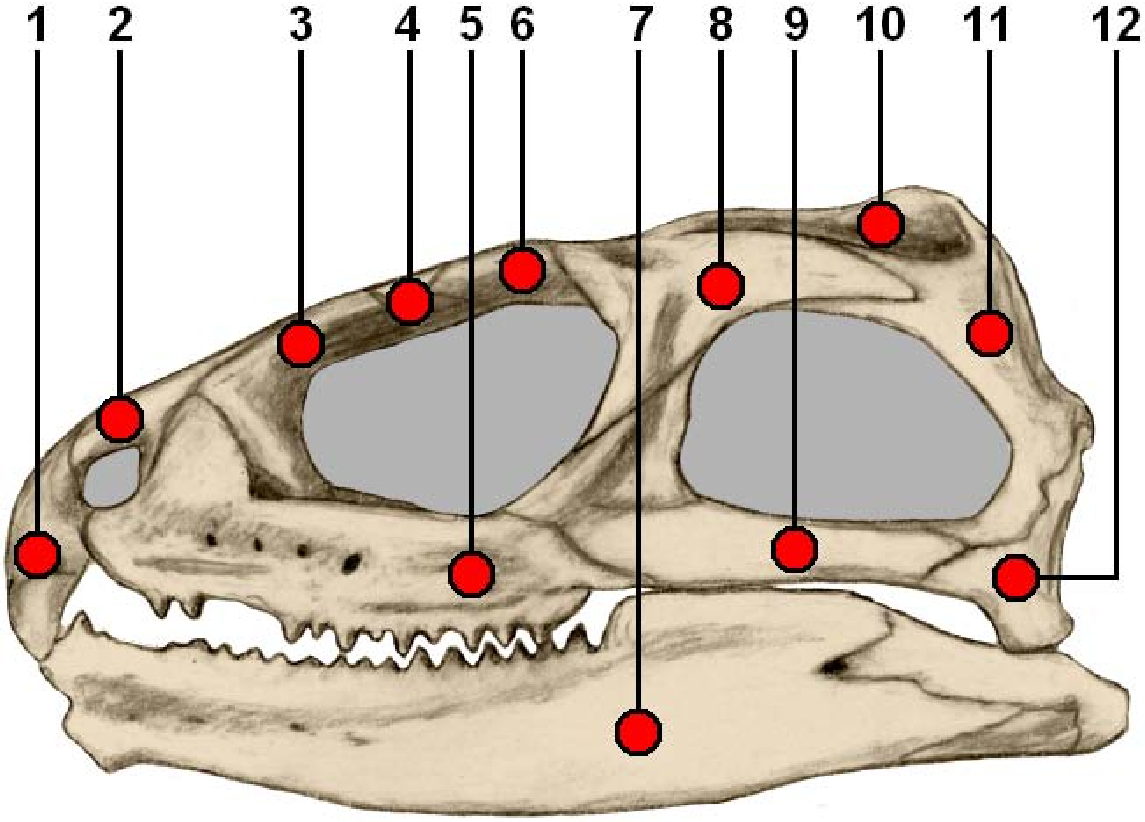
Description



Size comparison of male *S. punctatus* and human.

The tuatara is considered the most unspecialised living amniote; the brain and mode of locomotion resemble that of amphibians and the heart is more primitive than that of any other reptile. Their lungs have a single chamber and lack bronchi. Both species are sexually dimorphic, males being larger. Adult *S. punctatus* males measure 61 cm (24 in) in length and females 45 cm (18 in). The San Diego Zoo even cites a length of up to 80 cm (31 in). Males weigh up to 1 kg (2.2 lb), and females up to 0.5 kg (1.1 lb). Brother's Island tuatara are slightly smaller, weighing up to 660 g (1.3 lb).

The tuatara's greenish brown colour matches its environment, and can change over its lifetime. Tuatara shed their skin at least once per year as adults, and three or four times a year as juveniles. Tuatara sexes differ in more than size. The spiny crest on a tuatara's back, made of triangular soft folds of skin, is larger in males, and can be stiffened for display. The male abdomen is narrower than the female's.



Skull of a tuatara, showing the complete temporal arches, and individual bones:
1 = premaxilla
2 = nasal
3 = prefrontal
4 = frontal
5 = maxilla
6 = postfrontal
7 = dentary
8 = postorbital
9 = jugal
10 = parietal
11 = squamosal
12 = quadrate

Skull

In the course of evolution, the skull has been modified in most diapsids from the original version evident in the fossil record. However, all the original features are preserved in that of the tuatara; it has two openings (*temporal fenestra*) on each side of the skull, with complete arches. In addition, the upper jaw is firmly attached to the skull. This makes for a very rigid, inflexible construction. Testudines (turtle and tortoise) skulls with their single temporal fenestra are widely considered to be the most primitive among amniotes, though there is evidence they may have lost the temporal holes rather than never having had them.

The tip of the upper jaw is beak-like and separated from the remainder of the jaw by a notch. There is a single row of teeth in the lower jaw and a double row in the upper, with the bottom row fitting perfectly between the two upper rows when the mouth is closed. This specific tooth arrangement is not seen in any other reptile; although most snakes have a double row of teeth in their upper jaw, their arrangement and function is different from the tuatara's. The jaws, joined by ligament, chew with backwards and forwards movements combined with a shearing up and down action. The force of the bite is suitable for shearing chitin and bone. The tuatara's teeth are not replaced, since they are not separate structures like real teeth, but sharp projections of the jaw bone. As their teeth wear down, older tuatara have to switch to softer prey such as earthworms, larvae, and slugs, and eventually have to chew their food between smooth jaw bones. The brain of *Sphenodon* fills only half of the volume of its endocranium. This proportion has been used by paleontologists trying to estimate the volume of dinosaur brains based on fossils. The use of tuataras as a model animal for dinosaur brain volume has been criticized because since bird brains occupy a greater portion of their skulls and dinosaurs are their ancestors at least some dinosaurs must have volumes intermediate between the two.

Sensory organs

The eyes can focus independently, and are specialized with a duplex retina that contains two types of visual cells for both day and night vision, and a tapetum lucidum which reflects on to the retina to enhance vision in the dark. There is also a third eyelid on each eye, the nictitating membrane.

The tuatara has a third eye on the top of its head called the parietal eye. It has its own lens, cornea, retina with rod-like structures, and degenerated nerve connection to the brain, suggesting it evolved from a real eye. The parietal eye is only visible in hatchlings, which have a translucent patch at the top centre of the skull. After four to six months it becomes covered with opaque scales and pigment. Its purpose is unknown, but it may be useful in absorbing ultraviolet rays to manufacture vitamin D, as well as to determine light/dark cycles, and help with thermoregulation. Of all extant tetrapods, the parietal eye is most pronounced in the tuatara. The parietal eye is part of the pineal complex, another part of which is the pineal gland, which in tuatara secretes melatonin at night. It has been shown that some salamanders use their pineal body to perceive polarised light, and thus determine the position of the sun, even under cloud cover, aiding navigation.

Together with turtles, the tuatara has the most primitive hearing organs among the amniotes. There is no eardrum and no earhole, and the middle ear cavity is filled with loose tissue, mostly adipose (fatty) tissue. The stapes comes into contact with the quadrate (which is immovable) as well as the hyoid and squamosal. The hair cells are unspecialized, innervated by both afferent and efferent nerve fibres, and respond only to low frequencies. Even though the hearing organs are poorly developed and primitive with no visible external ears, they can still show a frequency response from 100–800 Hz, with peak sensitivity of 40 dB at 200 Hz.

Spine and ribs

The tuatara spine is made up of hour-glass shaped amphicoelous vertebrae, concave both before and behind. This is the usual condition of fish vertebrae and some amphibians, but is unique to tuatara within the amniotes.

The tuatara has gastralia, rib-like bones also called gastric or abdominal ribs, the presumed ancestral trait of diapsids. They are found in some lizards, where they are mostly made of cartilage, as well as crocodiles and the tuatara, and are not attached to the spine or thoracic ribs. The true ribs are small projections, with small, hooked bones, called uncinate processes, found on the rear of each rib. This feature is also present in birds. The tuatara is the only living tetrapod with well developed gastralia and uncinate processes.

In the early tetrapods, the gastralia and ribs with uncinate processes, together with bony elements such as bony plates in the skin (osteoderms) and clavicles (collar bone), would have formed a sort of exo-skeleton around the body, protecting the belly and helped to hold in the guts and inner organs. These anatomical details most likely evolved from structures involved in locomotion even before the vertebrates ventured onto land. The gastralia may have been involved in the breathing process in early amphibians and reptiles. The pelvis and shoulder girdles are arranged differently to those of lizards, as is the case with other parts of the internal anatomy and its scales.

Tail and back

The spiny plates on the back and tail of the tuatara resemble those of a crocodile more than a lizard, but has the latter reptile's ability to break off its tail when caught by a predator, and then regenerate it. The tail and back are covered with spiny plates that, too, resemble modern crocodiles more than they do those of a lizard.

Behaviour

Adult tuatara are terrestrial and nocturnal reptiles, though they will often bask in the sun to warm their bodies. Hatchlings hide under logs and stones, and are diurnal, likely because adults are cannibalistic. Tuatara thrive in temperatures much lower than those tolerated by most reptiles, and hibernate during winter. They remain active at temperatures as low as 5 °C (41 °F), while temperatures over 28 °C (82 °F) are generally fatal. The optimal body temperature for the tuatara is from 16 to 21 °C (61 to 70 °F), the lowest of any reptile. The body temperature of tuatara is lower than that of other reptiles ranging from 5.2–11.2 °C (41–52 °F) over a day, whereas most reptiles have body temperatures around 20 °C (68 °F). The low body temperature results in a slower metabolism.

Burrowing seabirds such as petrels, prions, and shearwaters share the tuatara's island habitat during the bird's nesting season. The tuatara use the bird's burrows for shelter when available, or dig their own. The seabirds' guano helps to maintain invertebrate populations that tuatara predominantly prey on; including beetles, crickets, and spiders. Their diet also consists of frogs, lizards, and bird's eggs and chicks. The eggs and young of seabirds that are seasonally available as food for tuatara may provide beneficial fatty acids. Tuatara of both sexes defend territories, and will threaten and eventually bite intruders. The bite can cause serious injury. Tuatara will bite when approached, and will not let go easily.

Reproduction

A male tuatara named Henry, living at the Southland Museum and Art Gallery, is still reproductively active at 111 years of age.

Tuatara reproduce very slowly, taking ten to twenty years to reach sexual maturity. Mating occurs in midsummer; females mate and lay eggs once every four years. During courtship, a male makes his skin darker, raises his crests, and parades toward the female. He slowly walks in circles around the female with stiffened legs. The female will either submit, and allow the male to mount her, or retreat to her burrow. Males do not have a penis; they reproduce by the male lifting the tail of the female and placing his vent over hers. The sperm is then transferred into the female, much like the mating process in birds.

Tuatara juvenile (*Sphenodon punctatus*)

Tuatara eggs have a soft, parchment-like shell. It takes the females between one and three years to provide eggs with yolk, and up to seven months to form the shell. It then takes between 12 and 15 months from copulation to hatching. This means reproduction occurs at two- to five-year intervals, the slowest in any reptile. Wild tuatara are known to be still reproducing at about 60 years of age—"Henry", a 111-year-old tuatara at Southland Museum in Invercargill, New Zealand, became a father (possibly for the first time) on 23 January 2009.

The sex of a hatchling depends on the temperature of the egg, with warmer eggs tending to produce male tuatara, and cooler eggs producing females. Eggs incubated at 21 °C (70 °F) have an equal chance of being male or female. However, at 22 °C (72 °F), 80% are likely to be males, and at 20 °C (68 °F), 80% are likely to be females; at 18 °C (64 °F) all hatchlings will be females. There is some evidence that sex determination in tuatara is determined by both genetic and environmental factors.

Tuatara probably have the slowest growth rates of any reptile, continuing to grow larger for the first 35 years of their lives. The average lifespan is about 60 years, but they can live to be well over 100 years old. Some experts believe that captive tuatara could live as long as 200 years.

Conservation

Current distribution of tuatara (in black). Circles represent the North Island tuatara, squares the Brothers Island tuatara. Symbols may represent up to seven islands.

Distribution and threats

Tuatara were long confined to 32 offshore islands free of mammals. The islands are difficult to get to, and are colonised by few animal species, indicating that some animals absent from these islands may have caused tuatara to disappear from the mainland. However, kiore (Polynesian rats) had recently established on several of the islands, and tuatara were persisting, but not breeding, on these islands. Additionally, tuatara were much rarer on the rat-inhabited islands.

The recent discovery of a tuatara hatchling on the New Zealand mainland indicates that attempts to reestablish a breeding population on the mainland have had some success. The total population of tuatara of all species and subspecies is estimated to be greater than 60,000, but less than 100,000.

Eradication of rats

Tuatara were removed from Stanley, Red Mercury and Cuvier Islands in 1990 and 1991, and maintained in captivity to allow Polynesian rats to be eradicated on those islands. All three populations bred in captivity, and after successful eradication of the rats, all individuals including the new juveniles were returned to their islands of origin. In the 1991/92 season, Little Barrier Island was found to hold only eight tuatara, which were taken into *in situ* captivity, where females produced 42 eggs, which were incubated at Victoria University. The resulting offspring were subsequently held in an enclosure on the island, then released into the wild in 2006 after rats were eradicated there.

In the Hen and Chicken Islands, Pacific rats were eradicated on Whatupuke in 1993, Lady Alice Island in 1994, and Coppermine Island in 1997. Following this program, juveniles have once again been seen on the latter three islands. In contrast, rats persist on Hen Island of the same group, and no juvenile tuatara had been seen there as of 2001. In the Alderman Islands, Middle Chain Island holds no tuatara, but it is considered possible for rats to swim between Middle Chain and other islands that do hold tuatara, and the rats were eradicated in 1992 to prevent this. Another rodent eradication was carried out on the Rangitoto Islands east of D’Urville Island, to prepare for the release of 432 Cook Strait tuatara juveniles in 2004, which were being raised at Victoria University as of 2001.

Tuatara at the Karori Sanctuary are given coloured markings on the head for identification.

Brothers Island tuatara

Sphenodon guntheri is present naturally on one small island with a population of approximately 400. In 1995, 50 juvenile and 18 adult Brothers Island tuatara were moved to Titi Island in Cook Strait, and their establishment monitored. Two years later, more than half of the animals had been re-sighted and all but one had gained weight. In 1998, 34 juveniles from captive breeding and 20 wild caught adults were similarly transferred to Matiu/Somes Island, a more publicly accessible location within Wellington Harbour. The captive juveniles were from induced layings from wild females.

In late October 2007, it was announced that 50 tuatara collected as eggs from North Brother Island and hatched at Victoria University were being released onto Long Island in the outer Marlborough Sounds. The animals had been cared for at Wellington Zoo for the last five years and have been kept in secret in a specially built enclosure at the zoo, off display.

Northern tuatara

Sphenodon punctatus naturally occurs on 29 islands and its population is estimated to be over 60,000 individuals. In 1996, 32 adult northern tuatara were moved from Moutoki Island to Moutohora. The carrying capacity of Moutohora is estimated at 8500 individuals, and the island could allow public viewing of wild tuatara. In 2003, sixty northern tuatara were introduced to Tiritiri Matangi Island from Middle Island in the Mercury group. They are occasionally seen sunbathing by visitors to the island.

A mainland release of *S. punctatus* occurred in 2005 in the heavily fenced and monitored Karori Sanctuary. The second mainland release took place in October 2007, when a further 130 were transferred from Stephens Island to the Karori Sanctuary. In early 2009 the first recorded wild-born offspring were observed.

Captive breeding

There are several tuatara breeding programmes within New Zealand. Southland Museum and Art Gallery in Invercargill, was the first to have a tuatara breeding programme; they breed *Sphenodon punctatus*. Hamilton Zoo and Wellington Zoo also breed tuatara for release into the wild. The Victoria University of Wellington maintains a research programme into the captive breeding of tuatara, and the Pukaha Mount Bruce Wildlife Centre keeps a pair and a juvenile. The WildNZ Trust has a tuatara breeding enclosure at Ruawai. On 28 January 2009, the 11th of 11 eggs belonging to tuataras Henry and Mildred hatched. This rare occurrence came after Henry had surgery to remove a cancerous tumor that was inhibiting both his ability and desire to breed.

Cultural significance

Tuatara feature in a number of indigenous legends, and are held as *ariki* (God forms). Tuatara are regarded as the messengers of Whiro, the god of death and disaster, and Māori women are forbidden to eat them. Tuatara also indicate *tapu* (the borders of what is sacred and restricted), beyond which there is *mana*, meaning there could be serious consequences if that boundary is crossed. Māori women would sometimes tattoo images of lizards, some of which may represent tuatara, near their genitals. Today, tuatara are regarded as a *taonga* (special treasure).

The tuatara was featured on one side of the New Zealand 5 cent coin, which was phased out in October 2006. *Tuatara* was also the name of the Journal of the Biological Society of Victoria University College and subsequently Victoria University of Wellington, published from 1947 until 1993. It has now been digitised by the New Zealand Electronic Text Centre, also at Victoria.

Chapter 12

Octopus

Octopus

The Common Octopus, *Octopus vulgaris*.

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Superorder:	Octopodiformes
Order:	**Octopoda** Leach, 1818

Suborders

- Cirrina
- Incirrina

Synonyms

- Octopoida
  Leach, 1817

The **octopus** is a cephalopod mollusc of the order **Octopoda**. Octopuses have two eyes and four pairs of arms, and like other cephalopods they are bilaterally symmetric. An octopus has a hard beak, with its mouth at the center point of the arms. Octopuses have no internal or external skeleton (although some species have a vestigial remnant of a shell inside their mantle), allowing them to squeeze through tight places. Octopuses are among the most intelligent and behaviorally flexible of all invertebrates.

The octopus inhabits many diverse regions of the ocean, including coral reefs, pelagic waters, and the ocean floor. They have numerous strategies for defending themselves against predators, including the expulsion of ink, the use of camouflage and deimatic displays, their ability to jet quickly through the water, and their ability to hide. An octopus trails its eight arms behind it as it swims. All octopuses are venomous, but only one group, the blue-ringed octopuses, is known to be deadly to humans.

There are around 300 recognized octopus species, which is over one-third of the total number of known cephalopod species. The term *octopus* may also be used to refer only to those creatures in the genus *Octopus*.

Biology

A Common Octopus (*Octopus vulgaris*)

Octopuses are characterized by their eight arms, usually bearing suction cups. The arms of octopuses are often distinguished from the pair of feeding tentacles found in squid and cuttlefish. Both types of limbs are muscular hydrostats. Unlike most other cephalopods, the majority of octopuses – those in the suborder most commonly known, Incirrina – have almost entirely soft bodies with no internal skeleton. They have neither a protective outer shell like the nautilus, nor any vestige of an internal shell or bones, like cuttlefish or squid. A beak, similar in shape to a parrot's beak, is the only hard part of their body. This enables them to squeeze through very narrow slits between underwater rocks, which is very helpful when they are fleeing from morays or other predatory fish. The octopuses in the less familiar Cirrina suborder have two fins and an internal shell, generally reducing their ability to squeeze into small spaces. These cirrate species are often free-swimming and live in deep-water habitats, while incirrate octopus species are found in reefs and other shallower seafloor habitats.

An octopus moving between tide pools during low tide

Octopuses have a relatively short life expectancy, and some species live for as little as six months. Larger species, such as the North Pacific Giant Octopus, may live for up to five years under suitable circumstances. However, reproduction is a cause of death: males can only live for a few months after mating, and females die shortly after their eggs hatch. They neglect to eat during the (roughly) one month period spent taking care of their unhatched eggs, but they do not die of starvation. Endocrine secretions from the two optic glands are the cause of genetically programmed death (and if these glands are surgically removed, the octopus may live many months beyond reproduction, until she finally starves).

Grimpoteuthis discoveryi, a finned octopus of the suborder Cirrina

Octopuses have three hearts. Two branchial hearts pump blood through each of the two gills, while the third pumps blood through the body. Octopus blood contains the copper-rich protein hemocyanin for transporting oxygen. Although less efficient under normal conditions than the iron-rich hemoglobin of vertebrates, in cold conditions with low oxygen pressure, hemocyanin oxygen transportation is more efficient than hemoglobin oxygen transportation. The hemocyanin is dissolved in the plasma instead of being carried within red blood cells and gives the blood a bluish color. Octopuses draw water into their mantle cavity where it passes through its gills. As mollusks, octopuses have gills that are finely divided and vascularized outgrowths of either the outer or the inner body surface.

Intelligence

Octopuses are highly intelligent, likely more so than any other order of invertebrates. The exact extent of their intelligence and learning capability is much debated among biologists, but maze and problem-solving experiments have shown that they show evidence of a memory system that can store both short- and long-term memory. It is not known precisely what contribution learning makes to adult octopus behavior. Young octopuses learn almost no behaviors from their parents, with whom they have very little contact.

An octopus opening a container with a screw cap

An octopus has a highly complex nervous system, only part of which is localized in its brain. Two-thirds of an octopus's neurons are found in the nerve cords of its arms, which have limited functional autonomy. Octopus arms show a variety of complex reflex actions that persist even when they have no input from the brain. Unlike vertebrates, the complex motor skills of octopuses are not organized in their brain using an internal somatotopic map of its body, as is the motor system in vertebrates Some octopuses, such as the mimic octopus, will move their arms in ways that emulate the shape and movements of other sea creatures.

In laboratory experiments, octopuses can be readily trained to distinguish between different shapes and patterns. They have been reported to practice observational learning, although the validity of these findings is widely contested on a number of grounds. Octopuses have also been observed in what some have described as play: repeatedly releasing bottles or toys into a circular current in their aquariums and then catching them. Octopuses often break out of their aquariums and sometimes into others in search of food. They have even boarded fishing boats and opened holds to eat crabs.

In some countries, octopuses are on the list of experimental animals on which surgery may not be performed without anesthesia. In the UK, cephalopods such as octopuses are regarded as *honorary vertebrates* under the Animals (Scientific Procedures) Act 1986 and other cruelty to animals legislation, extending to them protections not normally afforded to invertebrates.

The octopus is the only invertebrate which has been shown to use tools. At least four specimens of the Veined Octopus (*Amphioctopus marginatus*) have been witnessed retrieving discarded coconut shells, manipulating them, and then reassembling them to use as shelter. This discovery was documented in the journal *Current Biology* and has also been caught on video.

Defense

Greater Blue-ringed Octopus (*Hapalochlaena lunulata*)

An octopus's main (primary) defense is to hide, either not to be seen at all, or not to be detected as an octopus. Octopuses have several secondary defenses (defenses they use once they have been seen by a predator). The most common secondary defense is fast escape. Other defenses include the use of ink sacs, camouflage, and autotomising limbs.

Most octopuses can eject a thick blackish ink in a large cloud to aid in escaping from predators. The main coloring agent of the ink is melanin, which is the same chemical that gives humans their hair and skin color. This ink cloud is thought to reduce the efficiency of olfactory organs, which would aid an octopus's evasion from predators that employ smell for hunting, such as sharks. Ink clouds of some species might serve as pseudomorphs, or decoys that the predator attacks instead.

Amphioctopus marginatus travels with shells it has collected for protection

An octopus's camouflage is aided by certain specialized skin cells which can change the apparent color, opacity, and reflectiveness of the epidermis. Chromatophores contain yellow, orange, red, brown, or black pigments; most species have three of these colors, while some have two or four. Other color-changing cells are reflective iridophores, and leucophores (white). This color-changing ability can also be used to communicate with or warn other octopuses. The very venomous blue-ringed octopus becomes bright yellow with blue rings when it is provoked. Octopuses can use muscles in the skin to change the texture of their mantle to achieve a greater camouflage. In some species the mantle can take on the spiky appearance of seaweed, or the scraggly, bumpy texture of a rock, among other disguises. However in some species skin anatomy is limited to relatively patternless shades of one color, and limited skin texture. It is thought that octopuses that are day-active and/or live in complex habitats such as coral reefs have evolved more complex skin than their nocturnal and/or sand-dwelling relatives.

When under attack, some octopuses can perform arm autotomy, in a similar manner to the way skinks and other lizards detach their tails. The crawling arm serves as a distraction to would-be predators.

A few species, such as the Mimic Octopus, have a fourth defense mechanism. They can combine their highly flexible bodies with their color changing ability to accurately mimic other, more dangerous animals such as lionfish, sea snakes, and eels.

Reproduction

When octopuses reproduce, males use a specialized arm called a hectocotylus to insert spermatophores (packets of sperm) into the female's mantle cavity. The hectocotylus in benthic octopuses is usually the third right arm. Males die within a few months of mating. In some species, the female octopus can keep the sperm alive inside her for weeks until her eggs are mature. After they have been fertilized, the female lays about 200,000 eggs (this figure dramatically varies between families, genera, species and also individuals). The female hangs these eggs in strings from the ceiling of her lair, or individually attaches them to the substrate depending on the species. The female cares for the eggs, guarding them against predators, and gently blowing currents of water over them so that they get enough oxygen. The female does not hunt during the roughly one-month period spent taking care of the unhatched eggs and may ingest some of her own arms for sustenance. At around the time the eggs hatch, the mother leaves the lair and is too weak to defend herself from predators like cod, often succumbing to their attacks. The young larval octopuses spend a period of time drifting in clouds of plankton, where they feed on copepods, larval crabs and larval starfish until they are ready to descend to the ocean bottom, where the cycle repeats. This is a dangerous time for the larval octopuses; in the plankton cloud they are vulnerable to plankton eaters. In some deeper dwelling species, the young do not go through this period.

Sensation

Eye of *Octopus vulgaris*

Octopuses have keen eyesight. Octopuses, like other cephalopods, can distinguish the polarization of light. Color vision appears to vary from species to species, being present in *Octopus aegina* but absent in *Octopus vulgaris*. Attached to the brain are two special organs, called statocysts, that allow the octopus to sense the orientation of its body relative to horizontal. An autonomic response keeps the octopus's eyes oriented so that the pupil slit is always horizontal.

Octopuses also have an excellent sense of touch. An octopus's suction cups are equipped with chemoreceptors so that the octopus can taste what it is touching. The arms contain tension sensors so that the octopus knows whether its arms are stretched out. However, the octopus has a very poor proprioceptive sense. The tension receptors are not sufficient for the octopus brain to determine the position of the octopus's body or arms. (It is not clear that the octopus brain would be capable of processing the large amount of information that this would require; the flexibility of an octopus's arms is much greater than that of the limbs of vertebrates, which devote large areas of cerebral cortex to the processing of proprioceptive inputs.) As a result, the octopus does not possess stereognosis; that is, it does not form a mental image of the overall shape of the object it is handling. It can detect local texture variations, but cannot integrate the information into a larger picture.

The neurological autonomy of the arms means that the octopus has great difficulty learning about the detailed effects of its motions. The brain may issue a high-level command to the arms, but the nerve cords in the arms execute the details. There is no neurological path for the brain to receive feedback about just how its command was executed by the arms; the only way it knows just what motions were made is by observing the arms visually.

Octopuses appear to have limited hearing.

Octopuses swim headfirst, with arms trailing behind

Locomotion

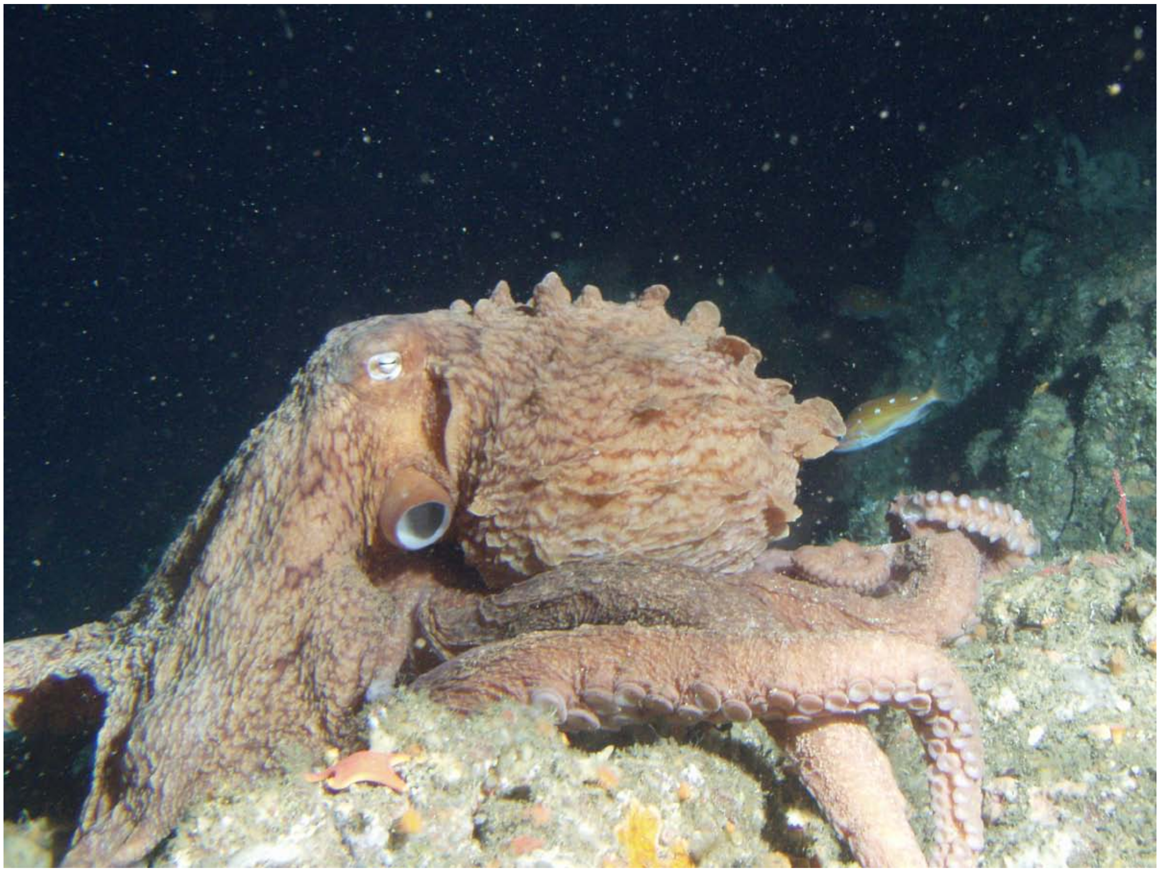
An octopus in its natural habitat

Octopuses move about by crawling or swimming. Their main means of slow travel is crawling, with some swimming. Jet propulsion is their fastest means of locomotion, followed by swimming and walking.

They crawl by walking on their arms, usually on many at once, on both solid and soft surfaces, while supported in water. In 2005 it was reported that some octopuses (*Adopus aculeatus* and *Amphioctopus marginatus* under current taxonomy) can walk on two arms, while at the same time resembling plant matter. This form of locomotion allows these octopuses to move quickly away from a potential predator while possibly not triggering that predator's search image for octopus (food).

Octopuses swim by expelling a jet of water from a contractile mantle, and aiming it via a muscular siphon.

Size



An adult North Pacific Giant Octopus, *Enteroctopus dofleini*

The North Pacific Giant Octopus, *Enteroctopus dofleini*, is often cited as the largest octopus species. Adults usually weigh around 15 kg (33 lb), with an arm span of up to 4.3 m (14 ft). The largest specimen of this species to be scientifically documented was an animal with a live mass of 71 kg (156.5 lb). The alternative contender is the Seven-arm Octopus, *Haliphron atlanticus*, based on a 61 kg (134 lb) carcass estimated to have a live mass of 75 kg (165 lb). However, there are a number of questionable size records that would suggest *E. dofleini* is the largest of all octopus species by a considerable margin; one such record is of a specimen weighing 272 kg (600 lb) and having an arm span of 9 m (30 ft).

Terminology

The term octopus with plural forms: Currently, *octopuses* is the most common form in both the US and the UK; *octopodes* is rare, and *octopi* is often objectionable.

The plural form *octopi* is often described as a hypercorrection. The *Oxford English Dictionary* (2008 Draft Revision) lists *octopuses*, *octopi* and *octopodes* (in that order); it labels *octopodes* "rare", although the correct Greek plural form, and notes that *octopi* derives from the "apprehension" that *octōpūs* is a second declension Latin noun, though it is not. It is a Latinization of Greek third-declension masculine *oktṓpous* (ὀκτώπους, 'eight-foot'), plural *oktṓpodes* (ὀκτώποδες). If the word were native to Latin, it would be *octōpēs*, plural *octōpedes*, after the pattern of *pēs* ('foot'), plural *pedēs*, analogous to "centipede". The actual Latin word for octopus and other similar species is *polypus*, from Greek *polýpous* (πολύπους, 'many-foot'); usually the inaccurate plural *polypī* is used instead of *polypodēs*.

In modern Greek, the word is *khtapódi* (χταπόδι), plural *khtapódia* (χταπόδια), from Medieval *oktapódion* (ὀκταπόδιον), equivalent to Classical *oktápous* (ὀκτάπους), variant of *oktṓpous*.

Chambers 21st Century Dictionary and the *Compact Oxford Dictionary* list only *octopuses*, although the latter notes that *octopodes* is "still occasionally used"; the British National Corpus has 29 instances of *octopuses*, 11 of *octopi* and 4 of *octopodes*. *Merriam-Webster 11th Collegiate Dictionary* lists *octopuses* and *octopi*, in that order; *Webster's New World College Dictionary* lists *octopuses*, *octopi* and *octopodes* (in that order).

Fowler's Modern English Usage states that "the only acceptable plural in English is *octopuses,*" and that *octopi* is misconceived and *octopodes* pedantic.

The term *octopod* (plural *octopods* or *octopodes*) is taken from the taxonomic order Octopoda but has no classical equivalent. The collective form *octopus* is usually reserved for animals consumed for food.

In mythology

The Hawaiian creation myth relates that the present cosmos is only the last of a series, having arisen in stages from the wreck of the previous universe. In this account, the octopus is the lone survivor of the previous, alien universe.

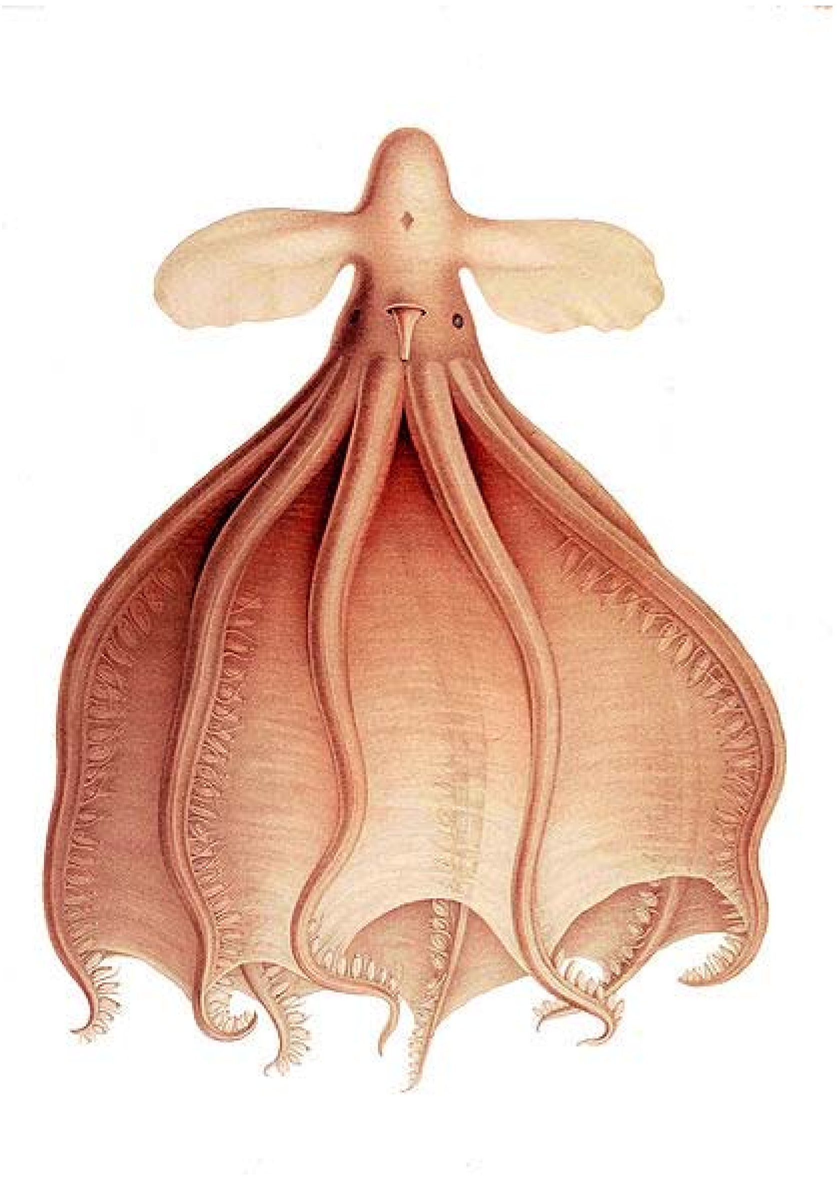
In literature

The octopus has a significant role in Victor Hugo's book *Travailleurs de la mer* (*Toilers of the Sea*).

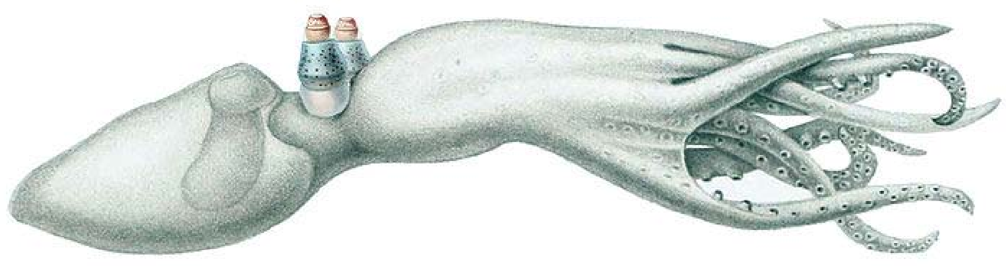
As a metaphor

Due to having numerous tentacles that emanate from a common center, the octopus is often used as a metaphor for a group or organziation which is perceived as being powerful, manipulative or bent on domination. Use of this terminology is invariably negative and employed by the opponents of the groups or institutions so described.

Classification



Cirrothauma murrayi



Amphitretus pelagicus

Class CEPHALOPODA

- Subclass Nautiloidea: nautilus
- Subclass Coleoidea
  - Superorder Decapodiformes: squid, cuttlefish
  - Superorder Octopodiformes
    - Family †Trachyteuthididae (*incertae sedis*)
    - Order Vampyromorphida: Vampire Squid
    - **Order Octopoda**
      - Genus †*Keuppia* (*incertae sedis*)
      - Genus †*Palaeoctopus* (*incertae sedis*)
      - Genus †*Paleocirroteuthis* (*incertae sedis*)
      - Genus †*Pohlsepia* (*incertae sedis*)
      - Genus †*Proteroctopus* (*incertae sedis*)
      - Genus †*Styletoctopus* (*incertae sedis*)
      - Suborder Cirrina: finned deep-sea octopus
        - Family Opisthoteuthidae: umbrella octopus
        - Family Cirroteuthidae
        - Family Stauroteuthidae

Suborder Incirrina

- Family Amphitretidae: telescope octopus
- Family Bolitaenidae: gelatinous octopus
- Family Octopodidae: benthic octopus
- Family Vitreledonellidae: Glass Octopus
- Superfamily Argonautoida
  - Family Alloposidae: Seven-arm Octopus
  - Family Argonautidae: argonauts
  - Family Ocythoidae: Tuberculate Pelagic Octopus
  - Family Tremoctopodidae: blanket octopus