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Cephalopods use color change to interact with their own species, with other species, and with their environments.

It sucks!

Cephalopods

Jet-powered Masters of Disguise

Text based on Dr James Wood and Kelsie Jackson's *Cephalopod Lesson Plan*. Adaption edited by Peter Symes

Most cephalopods—the group in which scientists classify octopuses, squid, cuttlefish and nautiluses—can change color faster than a chameleon. They can also change texture and body shape, and if those camouflage techniques don't work, they can still "disappear" in a cloud of ink, which they use as a smoke-screen or decoy.

Cephalopods are also fascinating because they have three hearts that pump blue blood; they're jet powered; and they're found in all the oceans of the world—from the tropics to the poles, from the intertidal to the abyss.

Cephalopods have inspired legends and stories throughout history and are thought to be the most intelligent of the invertebrates. Some can squeeze through the tiniest of cracks. They have eyes and other senses that rival those of humans.

Brainy

The class *Cephalopoda*, which means "head foot", are mollusks and therefore related to bivalves (scallops, oysters, clams), gastropods (snails and slugs), scaphopoda (tusk shells), and polyplacophorans (chitons). Some mollusks, such as bivalves, don't even have a head, much less something large enough to be called a brain! Yet, cephalopods have well-developed senses and large brains. Most mollusks are protected by a hard external shell and many of them are not very mobile. Although the nautilus has an external shell, the trend in cephalopods is to internalize and reduce the shell. The shell in cuttlefish, when present, is internal and is called the cuttlebone, which is sold in many pet shops to supply calcium to birds. Squid also have a reduced internal shell called a pen. Octopuses lack a shell altogether.

Cephalopods are found in all of the world's oceans, from the warm water of the tropics to the near freezing water at the poles. They are found from the wave swept intertidal region to the dark, cold abyss. All species are marine, and with a few exceptions, they do not tolerate even brackish water.

Ancient

Cephalopods are an ancient group that appeared some time in the late Cambrian period several million years before the first primitive fish began swimming in the ocean. Scientists believe that

Cut–away showing the chambers in a nautilus shell

Background resemblance is when the animal changes its color and texture to match as closely as possible that of its background.

the ancestors of modern cephalopods (Subclass *Coleoidea*: octopus, squid, and cuttlefish) diverged from the primitive externally-shelled *Nautiloidea* (Nautilus) very early—perhaps in the Ordovician, some 438 million years ago.

How long ago was this? To put this into perspective, this is before the first mammals appeared, before vertebrates invaded land and even before there were fish in the ocean and upright plants on land! Thus, nautilus is very different from modern cephalopods in terms of morphology and life history.

Cephalopods were once one of the dominant life forms in the world's oceans. Today, there are only about 800 living species of cephalopods. By comparison, there is 30,000 living species of bony fish. However, in terms of productivity, some scientists believe that cephalopods are still giving fish a run for their money.

Many species of cephalopods to grow very fast, reproduce over a short period of time, and then die. With overfishing and climate change, there may be more biomass of cephalopods now than anytime in recent history.

Color change

Cephalopods use their awesome abilities to change their color and appearance primarily for two things: camouflage and communication. The ability of the cephalopods to change color is a trait that has evolved over time due to a greater need to avoid predators and become competitive in an environment shared with vertebrates.

These abilities, and the behaviors associated with them, have become a major contributing factor to the success of the cephalopod family and are great examples of adaptation—physically, through natural selection, and behaviorally.

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The nautilus is similar in general form to other cephalopods, with a prominent head and tentacles. Nautiluses typically have more tentacles than other cephalopods, up to ninety. These tentacles are arranged into two circles and, unlike the tentacles of other cephalopods, they have no suckers, are undifferentiated and retractable.

Camouflage

Camouflage is usually a cephalopod's primary defense against predators. As cephalopods don't have the protection of hard shells like many of their mollusk relatives, they make an easy to digest meal for a hungry predator. Therefore, most cephalopods try to avoid being seen to avoid being eaten. As well as predator avoidance, camouflage can also be used when lying in wait for unsuspecting prey to pass. Interestingly, cephalopods have more than one strategy for camouflage, and these will be discussed here.

Resembling the background

Background resemblance is the most well known form of camouflage. This is when the animal changes its color and texture to match as closely as possible that of its background. Cephalopods use their ***chromatophores*** to change color to match the brightness of the environment they are attempting to blend into, and some can also change texture using muscles in their skin. Many also use different body postures to help with this. They may hold their arms in certain ways or flatten them on the substrate to become what appears to be simply part of the scenery.

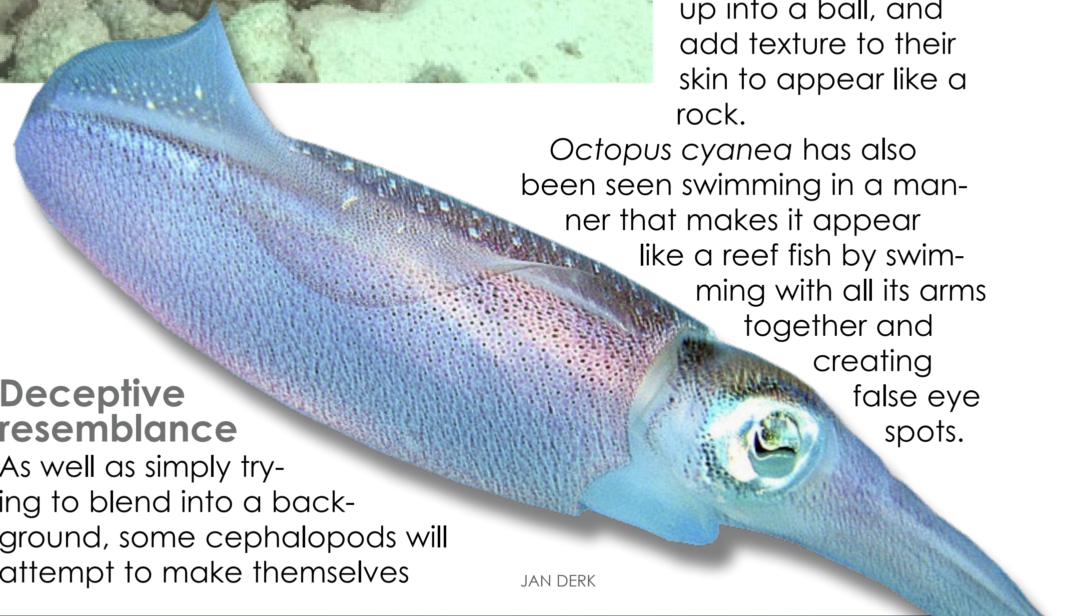
JAMES WOOD

Deceptive resemblance

As well as simply trying to blend into a background, some cephalopods will attempt to make themselves appear like a specific object in their environments. This is termed ***deceptive resemblance***.

The Caribbean reef squid, *Sepioteuthis sepioidea*, is often seen floating vertically at the surface of the water with its arms pointing downward to resemble floating sargassum weed. Some octopus may curl all their arms up into a ball, and add texture to their skin to appear like a rock.

Octopus cyanea has also been seen swimming in a manner that makes it appear like a reef fish by swimming with all its arms together and creating false eye spots.



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JAMES WOOD

Deceptive resemblance

Disruptive patterning being displayed by the cuttlefish, *Sepia pharaonis*. The large white band helps to break up the outline of the cuttlefish, making it harder to distinguish it from a complex environment when viewed from above by predators

JAMES WOOD

Disruptive patterning

Disruptive patterning is seen in many creatures as well as cephalopods and serves to break up the outline of the animal to confuse predators. It involves the chromatophores, which are used to create sharply contrasting patterns on the body, often wide stripes or spots. This is best seen in cuttlefish, which employ this technique more readily than other cephalopods.

Countershading

Countershading is used to help a cephalopod blend in when there is no substrate against which to match itself. For instance, squid that spend much of their time in midwater rather than on or near the bottom can be seen easily by predators from below. Photophores and reflector cells on their underside match the light coming in through the water column, to make the squid almost invisible to animals below it. Countershading also makes rounded surfaces appear flat. So, a squid with a darker top surface and shades gradually decreasing to a pale under-surface will be harder to spot when viewed laterally.

Deimatic behavior

Deimatic behavior is often used when camouflage fails, and the cephalopod is still threatened. It involves changing rapidly from the color it was using to blend into its environment, to bold contrasting colors such as white and black. Some species of octopus will change instantly from their mottled appearance to bright white with black around their eyes. Deimatic behavior usually also involves body postures that make the animal appear bigger than it is. If this doesn't work and the animal is still threatened, cephalopods will then usually ink and jet away.

Communication

Cephalopods use color change as well as body postures to communicate, both with members of their own species as well as with members of other species. Many cephalopods have courtship displays in which males attempt to attract females by using chromatic displays (displays using color changes) to show that they are suitable mates. This is well developed in squid and cuttlefish but is less common in octopus in which complex courtship rituals have not yet been seen. Often during courtship, males will not only have to attempt to attract females, but also to fend off other males. As chromatophores are neurally controlled, the animal may be able to produce a pattern on one side of its body to attract a female while producing another pattern on the other side, which it directs at other males.

One side of the body produces a pattern to attract a female while producing another pattern on the other side, which is directed at other males

JAMES WOOD

Fighting between males also exhibits a lot of communication. With squid, time spent in acts of aggression involve mostly displays and very little physical contact. Squid will often show chromatic displays and body postures with increasing intensity until one backs down.

In midwater, light organs and photophores are thought to be used for communication. In the same way as color is used in shallow water, bioluminescence can be used where there is less light to attract a mate, lure prey and dissuade predators.

Predator avoidance may also involve some forms of communication to the predator. As with deimat-

It is hard to know for sure the first benefit that the adaptation of changing appearance had for cephalopods. The fossil record is spotty and does not provide many clues as to behavioral adaptations.

However, most scientists believe the initial benefit of the adaptation of changing appearance was ***crypsis***, the ability to blend in with the environment. This allowed cephalopods to be camouflaged so they could more easily catch their prey. Perhaps even more importantly, camouflage was the first line of defense against predators.

Much of cephalopod evolution is thought to be driven by predator avoidance. The earliest of cephalopods are thought to have used the ability to leave the bottom and swim up into the water column as a way to escape predators.

As both predators and their prey evolved, two major groups of cephalopods—the ammonites and nautilus—became some of the most common marine animals. These two groups relied on their external shell to protect them from predators. The ammonites are extinct, and there are now only six species of nautilus in existence. All the rest of the modern cephalopods, the coleoid cephalopods, have reduced and internalized shells and have the ability to change color, texture and shape to camouflage and avoid detection from predators. ■

JAMES WOOD

A California two-spot octopus, *Octopus bimaculatus*, displays its abilities to camouflage in different environments. This type of camouflage is known as background resemblance, as both octopuses have adopted colors, textures and postures to attempt to blend into the background

JAMES WOOD

Octopuses are, of course, not the only cephalopods to display background resemblance. A cuttlefish, *Sepia pharaonis*, is attempting to match the color and texture of the sand in its laboratory tank. Notice the white tipped papillae closest to the sand that give the appearance of small pebbles that can be seen in other areas of the tank. This ability not only protects the animal from predators, it also assists with hunting as prey can come quite close without realizing there is a hungry cephalopod nearby

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Skin pattern created by cromatophores in this Atlantic Bobtail squid *Sepiola atlantica*

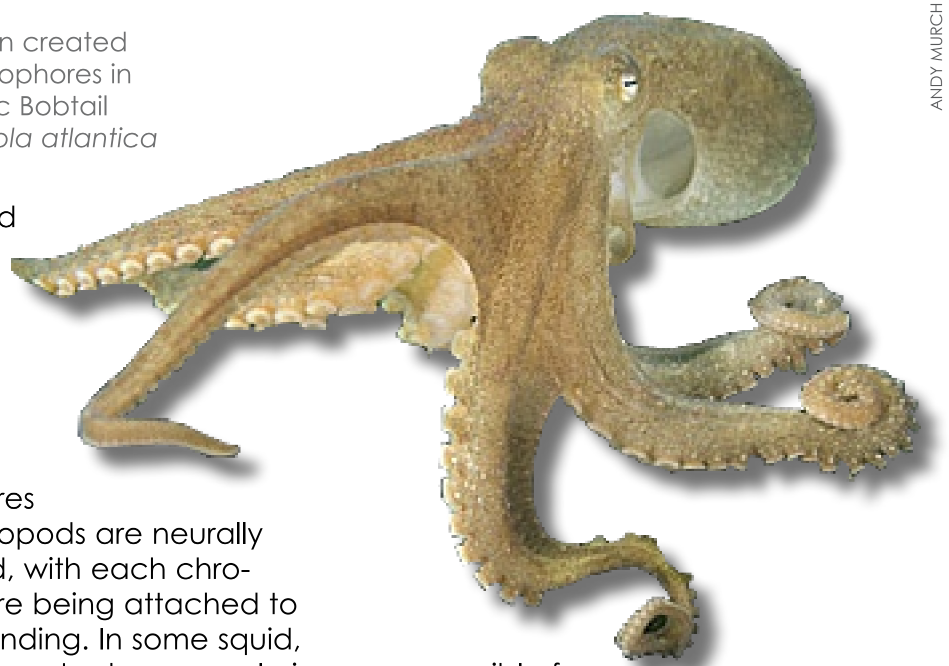
ic behaviors, showing a predator that it has been spotted and attempting to make itself larger and more frightful than it is will at least often make a predator stop and think, giving vital seconds for escape. On the other hand, if the bluff is successful, the predator may back away, thinking that it is not as easy a target as anticipated.

Cephalopods have often been referred to as the chameleons of the sea. However, their ability to change color is more impressive than that of the chameleon. Unlike the chameleon, many of the cephalopod's color producing cells are controlled neurally, which allows them to change colors very rapidly.

The patterns and colors seen in cephalopods are produced by different layers of cells stacked together, and it is the combination of certain cells operating at once that allows cephalopods to possess such a large array of patterns and colors.

Chromatophores

The most well known of these cells is the chromatophore. Chromatophores are groups of cells that include an elastic saccule that holds a pigment, as well as 15-25 muscles attached to this saccule. These cells are located directly under the skin of cephalopods. When the muscles contract, they stretch the saccule allowing the pigment inside to cover a larger surface area. When the muscles relax, the saccule shrinks and hides the pigment.

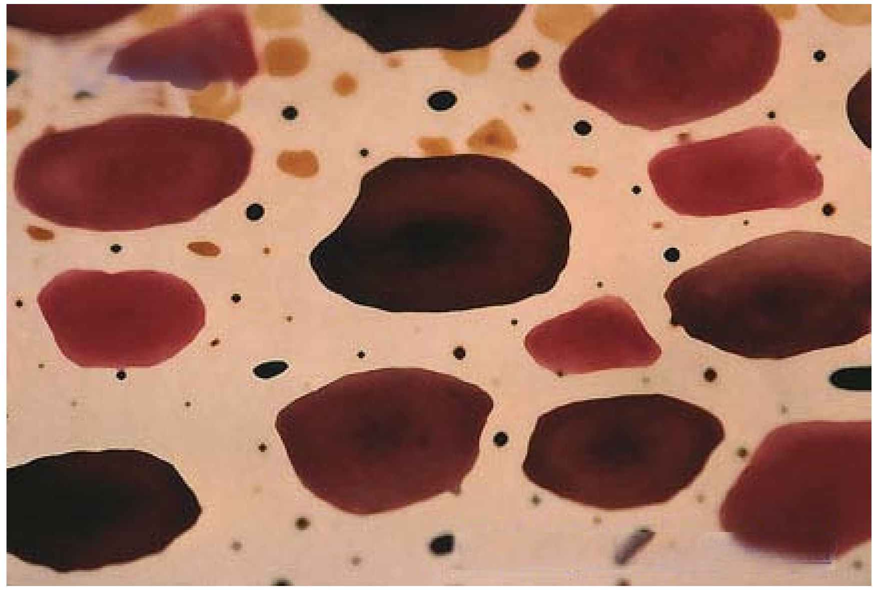


ANDY MURCH

Unlike in other animals, the chromatophores in cephalopods are neurally controlled, with each chromatophore being attached to a nerve ending. In some squid, each chromatophore muscle is innervated by two to six nerves that directly link to the animal's brain.

In this way, the animal can increase the size of one saccule while decreasing the size of another one right next to it. This allows the cephalopods to produce complex patterns, such as the zebra stripes seen in aggressive displays by male cuttlefish.

The speed at which this can be controlled allows the animal to manipulate these patterns in a way that makes them appear to move across the body. In some species of cuttlefish, it has been noted that while hunting, the cuttlefish may produce a series of stripes that move down their bodies and arms. Some scientists have suggested that this could be used to mesmerize prey before striking, but the purpose of this behavior has yet to be proven.



Closeup of cromatophores

The pigments in chromatophores can be black, brown, red, orange or yellow. They are not responsible for producing the blue and green colors seen in some species. Interestingly, many deep water forms possess fewer chromatophores as they are less useful in an environment in little or no light.

Iridophores

Iridophores are found in the next layer under the chromatopphores. Iridophores are layered stacks of platelets that are chitinous in some species and protein based in others. They are responsible for producing the metallic looking greens, blues and golds seen in some species, as well as the silver color around the eyes and ink sac of others. Iridophores work by reflecting light and can be used to conceal organs, as is often the case with the silver coloration around the eyes and ink sacs. Additonally, they assist in concealment and communication.

Previously, it was thought that these colors were permanent and unchanging unlike the colors produced by chromatophores. New studies on some species of squid suggest that the colors may change in response to changing levels of certain hormones. However, these changes are obviously slower than neural-

Chromatophores are located directly under the skin of cephalopods. When the muscles contract, they stretch the saccule allowing the pigment inside to cover a larger surface area. When the muscles relax, the saccule shrinks and hides the pigment.

JON GROSS

ly controlled chromatophore changes. Iridophores can be found in cuttlefish, some squid and some species of octopus.

Leucophores

Leucophores are the last layer of cells. These cells are responsible for the white spots occurring on some species of cuttlefish, squid and octopus. Leucophores are flattened, branched cells that are thought to scatter and reflect incoming light. In this way, the color of the leucophores will reflect the predominant wavelength of light in the environment. In white light, they will be white, while in blue light, they will be blue. It is thought that this adds to the animal's ability to blend into its environment.

Photophores

Cephalopods have one final ability to change color and pattern, the photophores. These produce light by bioluminescence. Photophores are found in most midwater and deep sea cephalopods and are often absent in shallow water species.

Bioluminescence is produced by a chemical reaction similar to that of a chemical light stick. Photophores may produce light constantly or flash light intermittently. The mechanism for this is not yet known, but one theory is that the photophores can be covered up by pigments in the chromatophores when the animal does not wish for them to show.

Some species also have sacs containing resident bacteria that produce bioluminescence such as the tiny squid Euprymna. Midwater squid use photophores to match downwelling light or to attract prey.

It is the use of these cells in combination that allow cephalopods to produce amazing colors and patterns not seen in any other family of animal. However, not all species of cephalopod possess all the cells described above. For instance, photophores may be necessary for animals in deep water environments but are often absent in shallow water forms. Deep sea species may possess few or even no chromatophores as their color changes would not be visible in an environment with no light.

Recent research has suggested that there may be some correlation between the amount of chromatophores (and hence the complexity of patterns available) and the type and complexity of a cephalopod's environment. For instance, midwater species may possess fewer chromatophores. While species living in reef type environments may possess more. However, further research still needs to be conducted in this area.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Octopus burryi showing white spots due to leucophores

Cephalopod vision

Cephalopods are known to have excellent senses, and of these senses, their vision is perhaps the best studied. At first glance, cephalopod eyes look very similar to those of humans, whales and fishes. With the exception of the externally shelled and primitive nautilus, all cephalopods can perceive focused images, just like we can.

Cephalopods are invertebrates and other than being multicellular animals, they are not even closely related to vertebrates such as whales, humans and fish. Cephalopods, and their eyes, evolved independently. Why would animals so distantly related as a fish and a cephalopod have developed an eye that is so similar?

Colorblind

Given the amazing ability of cephalopods to change color perhaps the most surprising difference between vertebrate eyes and those of cephalopods is that most cephalopods are completely color blind. How do we know? We can train octopuses to pick black objects over white objects, white objects over black objects, light grey objects over dark grey objects and vice versa, but we can not train them to differentiate between colorful objects that look the same in grayscale. Also, most cephalopods only have one visual pigment. We have three.

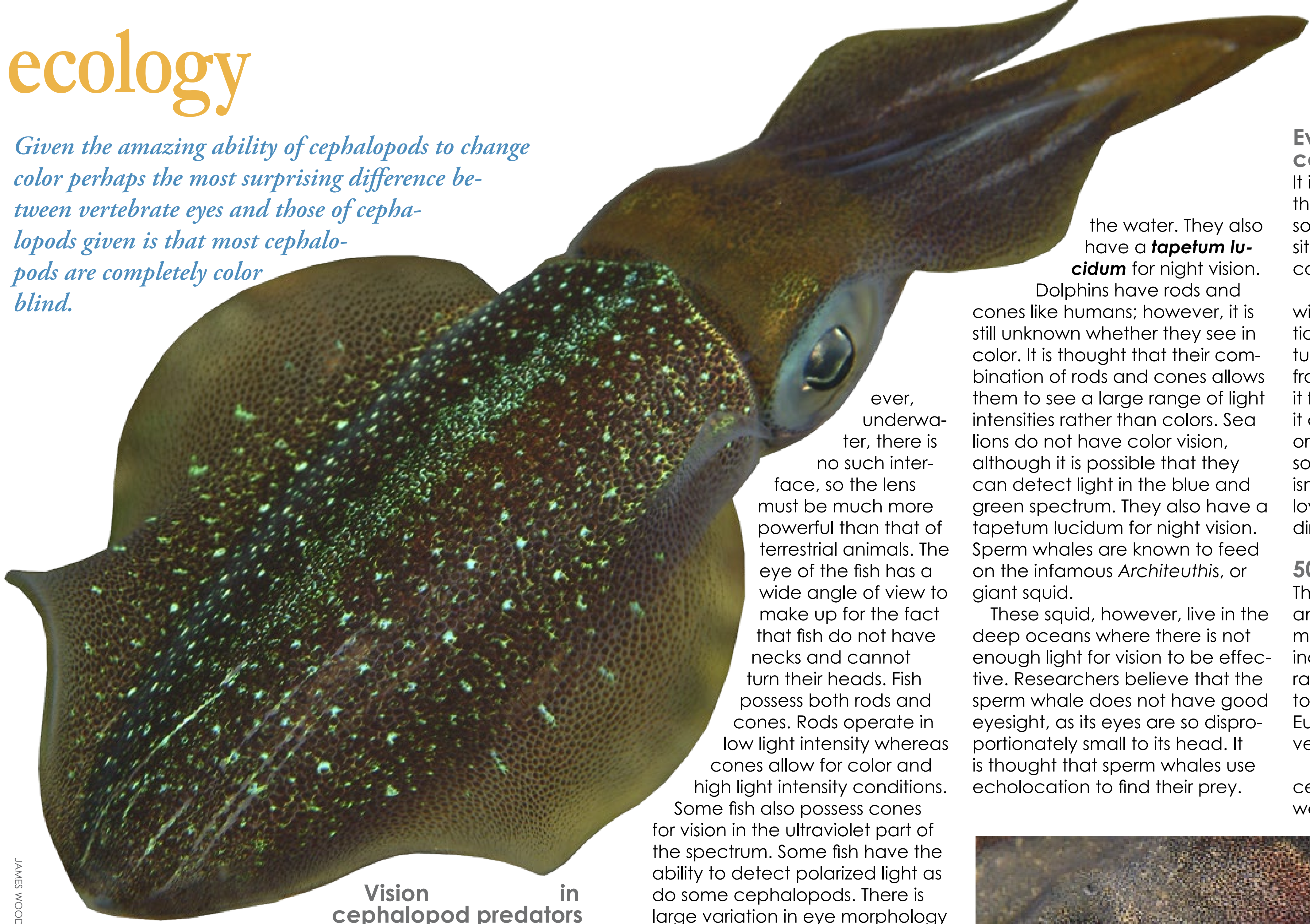
Although many species have not yet been tested, the only cephalopod known so far to have color vision is the firefly squid, *Watasenia scintillans*. This species of midwater squid is bioluminescent and has three visual pigments. All other species tested so far only have one visual pigment.

Polarized light

Although most cephalopods can not see in color, it has been demonstrated that octopuses and cuttlefish can detect differences in polarized light—without wear-

Squids

Given the amazing ability of cephalopods to change color perhaps the most surprising difference between vertebrate eyes and those of cephalopods given is that most cephalopods are completely color blind.



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ing polarized sunglasses. Shashar and Hanlon showed that squids (*Loligo pealei*) and Sepiolids (*Euprymna scolopes*) can exhibit polarized light patterns on their skin. Therefore, cephalopods can not only see differences in polarized light, they can also create patterns using these differences on their bodies. (*See fact file on next page.*)

Vision in cephalopod predators

The predators of cephalopods include fish—such as sharks—birds, marine mammals and other cephalopods. All of these predators have single lens eyes, although often there is some variation between them to make their eyes more suitable to their environment and behavior.

Fish On land, it is the air-cornea interface of vertebrates that gives most of the ability to focus. However, underwater, there is no such interface, so the lens must be much more powerful than that of terrestrial animals. The eye of the fish has a wide angle of view to make up for the fact that fish do not have necks and cannot turn their heads. Fish possess both rods and cones. Rods operate in low light intensity whereas cones allow for color and high light intensity conditions.

Some fish also possess cones for vision in the ultraviolet part of the spectrum. Some fish have the ability to detect polarized light as do some cephalopods. There is large variation in eye morphology within fish as they inhabit a large number of habitats with varying light regimes, from complex coral reefs to the pitch black of the deep sea.

Marine mammals that feed on cephalopods include dolphins, sea lions, and whales. Dolphins have a few adaptations to their eyes to assist them. For instance, they have muscles that can bend their lenses, so they can focus above the water. They also have a ***tapetum lucidum*** for night vision.

Dolphins have rods and cones like humans; however, it is still unknown whether they see in color. It is thought that their combination of rods and cones allows them to see a large range of light intensities rather than colors. Sea lions do not have color vision, although it is possible that they can detect light in the blue and green spectrum. They also have a tapetum lucidum for night vision. Sperm whales are known to feed on the infamous *Architeuthis*, or giant squid.

These squid, however, live in the deep oceans where there is not enough light for vision to be effective. Researchers believe that the sperm whale does not have good eyesight, as its eyes are so disproportionately small to its head. It is thought that sperm whales use echolocation to find their prey.

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Evolution of cephalopod vision

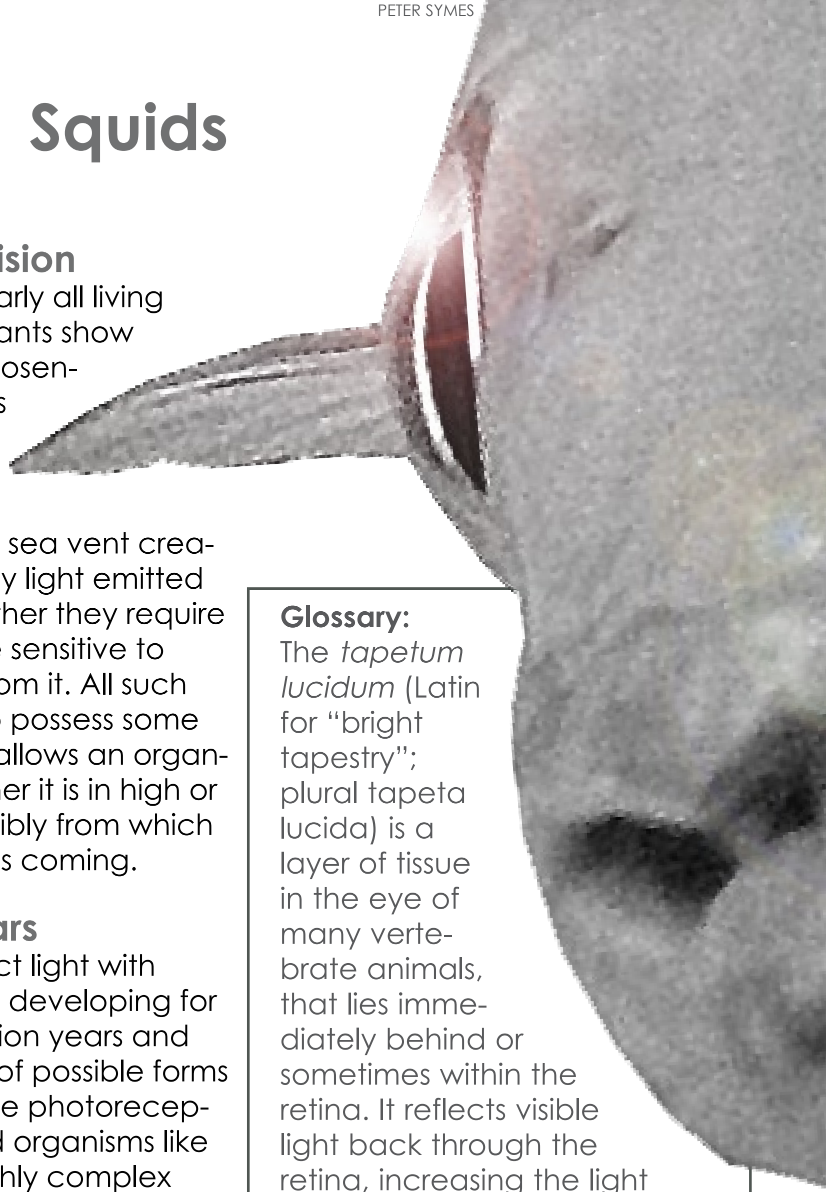
It is known that nearly all living things including plants show some form of photosensitivity. How did this come to be?

Firstly, most life, with the exception of some deep sea vent creatures, is affected by light emitted from the sun, whether they require it for survival or are sensitive to it and must hide from it. All such organisms need to possess some sort of organ that allows an organism to know whether it is in high or low light, and possibly from which direction the light is coming.

500 million years

The ability to detect light with and eye has been developing for more than 500 million years and includes a variety of possible forms ranging from simple photoreceptors in single celled organisms like Euglena to the highly complex vertebrate eye.

The first “eye” seen in single-celled organisms and flatworms were simple photoreceptors that



PETER SYMES

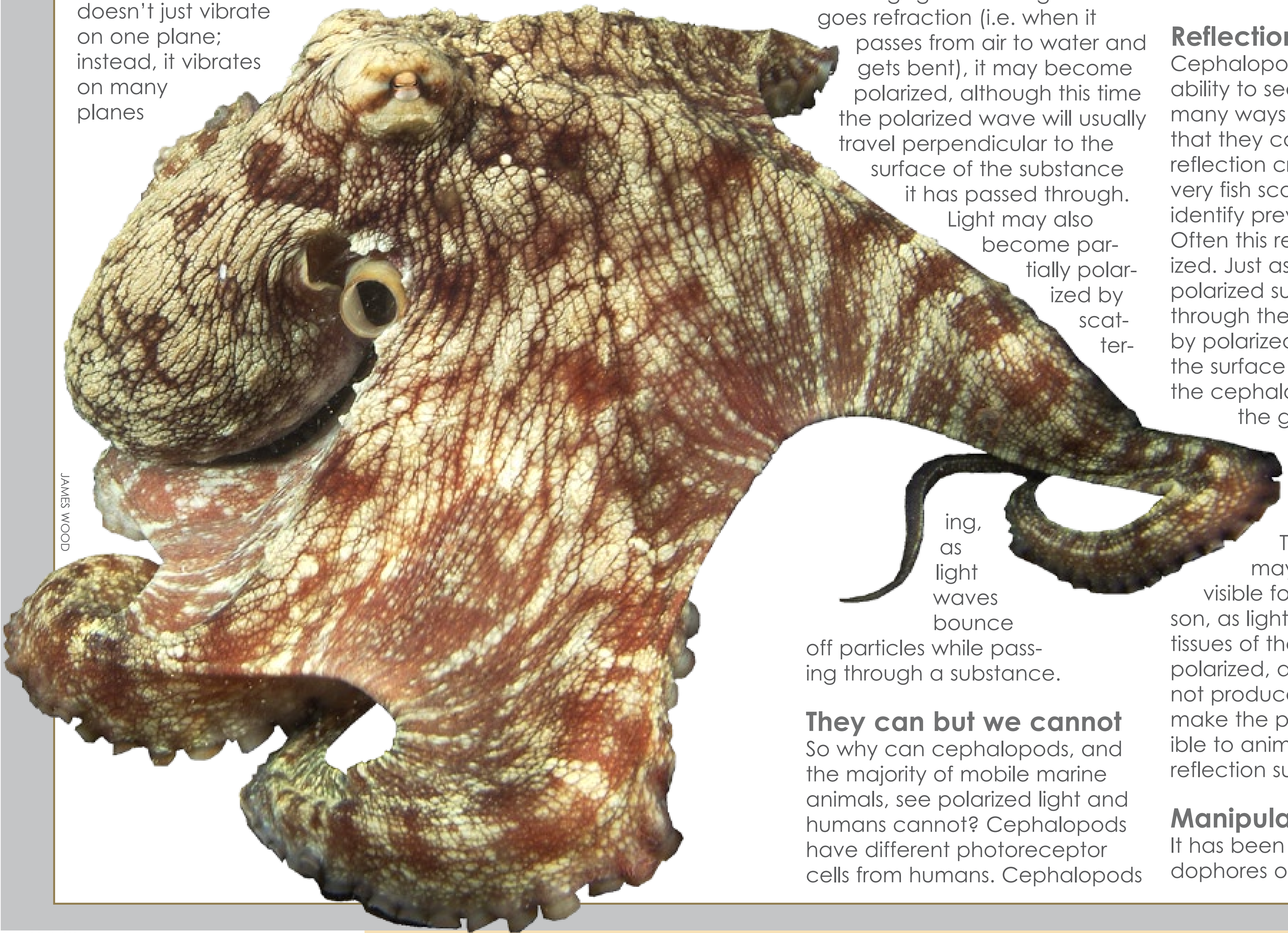
Glossary:
The *tapetum lucidum* (Latin for “bright tapestry”; plural tapeta lucida) is a layer of tissue in the eye of many vertebrate animals, that lies immediately behind or sometimes within the retina. It reflects visible light back through the retina, increasing the light available to the photoreceptors. This improves vision in low-light conditions, but can cause the perceived image to be blurry from the interference of the reflected light. The tapetum lucidum contributes to the superior night vision of some animals. Many of these animals are nocturnal, especially carnivores that hunt their prey at night, while others are deep sea animals. Although strepsirrhine primates have a tapetum lucidum, humans and other haplorhine primates do not. ■

Seeing Polarized Light

It has been shown through scientific experiments that squid, octopus and cuttlefish are able to detect polarized light as well as create signals using polarized light on their skin.

What the difference?

What is polarized light and how is it different from unpolarized light? Light is a form of electromagnetic radiation that travels as a wave. The wave doesn't just vibrate on one plane; instead, it vibrates on many planes and in many directions at once while still traveling in the same general direction. Looking head on at a light wave, the assumption is that the wave is a straight vertical line as it moves toward the viewer. But, in actual fact, the wave moves vertically, horizontally, and diagonally all at the same time. This is how unpolarized light from the sun behaves, it is disorganized. Polarized light, on the other hand, only vibrates on one plane. The wave of polarized light, traveling toward the viewer appears as only one vertical or horizontal line



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How does it happen?

Polarization can happen in a number of ways. Firstly, when light hits an object, it can become polarized if it is reflected, refracted or scattered of off certain surfaces. Light may reflect off a non-metallic object or substance (like water) and become polarized. Polarized light that has experienced reflection will travel parallel to the surface of the object, which in the case of bodies of water, creates glare.

The amount of polarization will depend on the angle of the incoming light. When light undergoes refraction (i.e. when it passes from air to water and gets bent), it may become polarized, although this time the polarized wave will usually travel perpendicular to the surface of the substance it has passed through. Light may also become partially polarized by scattering, as light waves bounce off particles while passing through a substance.

They can but we cannot

So why can cephalopods, and the majority of mobile marine animals, see polarized light and humans cannot? Cephalopods have different photoreceptor cells from humans. Cephalopods have photoreceptor cells that contain microvilli. The microvilli of each receptor cell are lined up parallel to each other. Microvilli contain the visual pigment rhodopsin, which is also orientated parallel in the microvilli. Receptor cells are aligned at right angles to each other, and hence the microvilli of one receptor cell will be at right angles to that of the next receptor cell. The rhodopsin assist in seeing the polarized light. Because the microvilli are arranged at right angles to one another, the animal is able to distinguish between different planes that the light is traveling on.

Reflections

Cephalopods can use their ability to see polarized light in many ways. Firstly, it is thought that they can see though the reflection created by silvery fish scales to better identify prey and predators Often this reflection is polarized. Just as humans put on polarized sunglasses to see through the glare created by polarized reflection off the surface of the ocean, the cephalopod can cut out the glare of polarized light produced by reflection off fish scales to better distinguish prey. Translucent prey may also be more visible for the same reason, as light reflecting off the tissues of the prey may be polarized, and while it may not produce glare, it would make the prey animal more visible to animals that can see this reflection such as cephalopods.

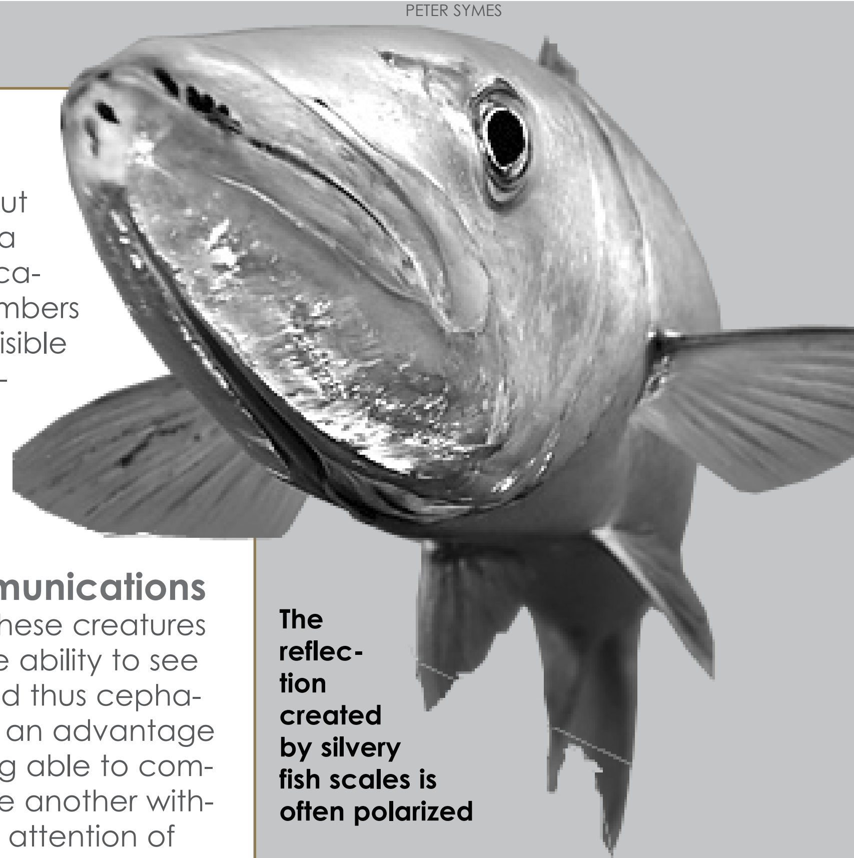
Manipulating polarisations

It has been shown that the iridophores on cuttlefish reflect polarized light in a way that they can intensify or shut off. This could be a form of communication between members of a species not visible to some other animals, especially predators such as sharks, seals and cetaceans.

Cuttlefish reflect polarized light in a way that they can intensify or shut off

Invisible communications

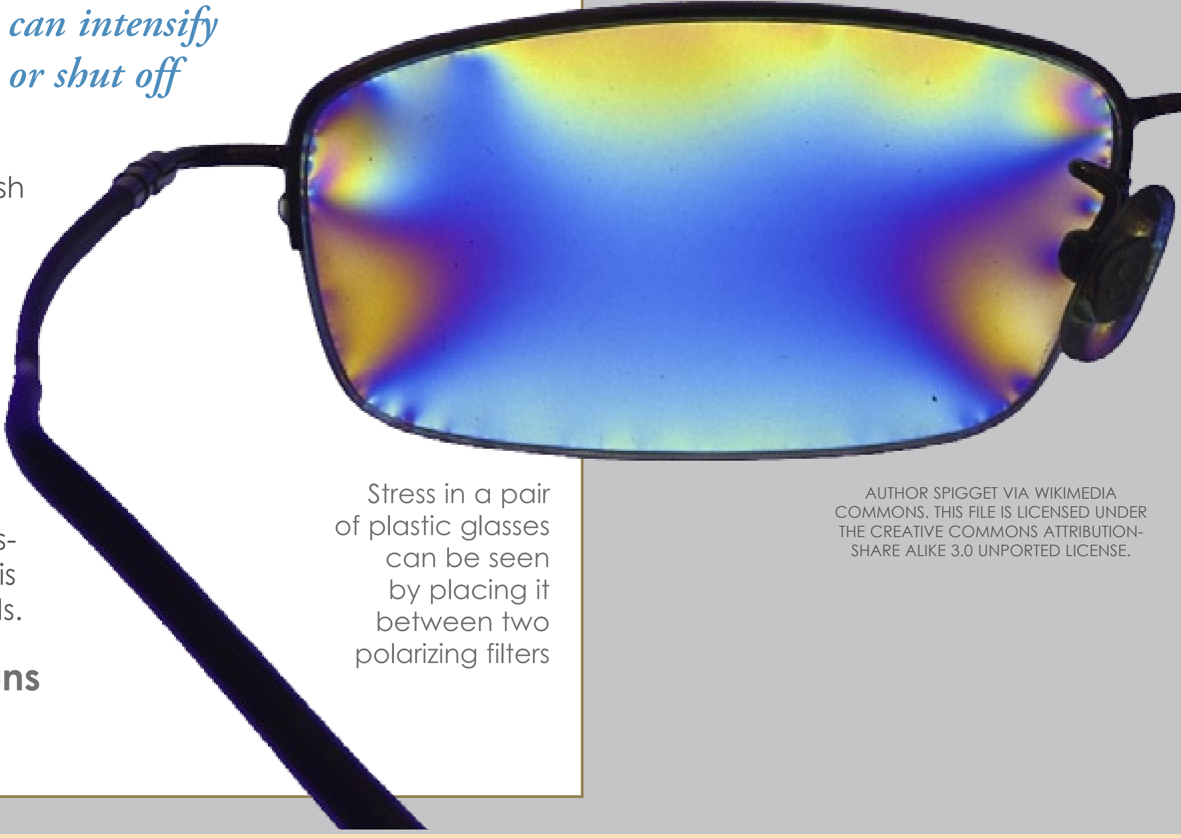
It is thought that these creatures do not possess the ability to see polarized light, and thus cephalopods may have an advantage over them in being able to communicate with one another without attracting the attention of predators. It is also thought that cephalopods and other marine animals that can detect differences in polarized light may use their abilities to detect polarization to assist them in navigation. ■



PETER SYMES

The reflection created by silvery fish scales is often polarized

Unpolarized light is disorganized. Polarized light, on the other hand, only vibrates on one plane.



Stress in a pair of plastic glasses can be seen by placing it between two polarizing filters

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The ability to detect light with and eye has been developing for more than 500 million years and includes a variety of possible forms ranging from simple photoreceptors in single celled organisms to the highly complex vertebrate eye.

JAMES WOOD

The pinhole eye of a Nautilus is incapable of focusing on objects at different distances. Instead, the size of the image produced will change in relation to the distance away from the object.

could ascertain only the amount of light in the environment. The more advanced form of this was cup-shaped, which allowed the animal to discern from which direction the light was coming. However, this sort of eye did not allow the organisms to see as we think of it. Thus, the pinhole eye developed.

Pinhole eye

The pinhole eye is found in the Nautilus and consists of a small opening into a chamber, which allows a very small amount of light through. Light will pass through the pinhole after bouncing off different points of an object, and in this way basic shapes can be interpreted, not in any detail however. The hole is so tiny only a small amount of light can get in which makes the image faint. If the hole were larger, the image would be distorted. This type of eye is incapable of focusing on objects at different distances. Instead, the size of the image produced will change in relation to the distance away from the object.

The compound eye was the first true image-forming eye, which was thought to have formed some time during the Cambrian period, about 500 million years ago. The compound eye is common in insects and arthropods and consists of many ommatidia. Each ommatidia consists of a lens, crystalline cells, pigment cells and visual cells. The number of ommatidia will vary between species but may be up to 1000 per eye. Each ommatidia passes information on to the brain. This forms an image that is made of up dots, as if looking very close at a digital photo. A higher number of ommatidia mean more dots which make the image clearer. This type of eye is only useful over short distances. However, it is excellent for movement detection.

For an animal to be able to focus on objects at different distances or even to produce a clear image of its surroundings at all, its eyes needed to develop lenses. It is thought that early cup-shaped eyes, like those of flatworms, contained a substance that protected them from seawater. If this substance were to bulge, it would form a pseudo lens that would help to make an image form more precisely, and this may be favored by the process of natural selection. Although the compound eye is full of lenses, the only way to make the image sharper with this design was to add more ommatidia. Of course, this means the eye would have to increase in size and can only do this to a point before it is too large for the animal. Thus, more complex lens eyes formed in both vertebrates and in cephalopods. Although both of these designs have many differences, there are also many similarities.

Cephalopod vs. Vertebrate Vision

As already stated, both cephalopods and vertebrates have very complex image-forming eyes with lenses. Both cephalopods and vertebrates have single lens eyes. They work by allowing light to enter through the pupil and be focused by the lens onto the photoreceptor cells of the retina. However, between the two groups of animals, there are differences in the shape of the pupil, the way the lens changes focus for distance, the type of receptor cells that receive the light as well as some more subtle differences.

JAMES WOOD

Squids

In vertebrates the pupil is round, and it changes in diameter depending on the amount of light in the environment. This is important because too much light will distort the image, and too little light will be interpreted as a very faint image. The cephalopod pupil is square and adjusts for the level of light by changing from a square to a narrow rectangle.

The way in which the two groups use the lens to focus differs. Vertebrates use muscles around the eye to change the shape of the lens, while cephalopods are able to manipulate their lens in or out to focus at different distances.

The receptor cells of vertebrate eyes are rods and cones. The cones are used for vision in high light environments, while the rods are used in low light. The time of day the animal needs its vision to be most effective will dictate the ratio of rods to cones. Cephalopods, however, have receptor cells called rhabdomeres similar to those of other mollusks. These contain microvilli, which allow the animal to see polarized and unpolarized light (see page on polarization vision).

Lastly, the way in which light is directed at the retina differs between the two groups. Cephalopod retinas receive incoming light directly, while vertebrate retinas receive light that is bounced back from the back of the eye.

Evolution

The evolution of cephalopods is thought to be due to an evolutionary “arms race”. Over the course of cephalopod history, they have moved from the sea floor, lost their shells, developed abilities to change color, shape and texture as well as the ability to communicate in complex ways. It was their capacity to adapt to changing pressures that ensured their survival as a family. Those that did not adapt mostly became extinct.

The first cephalopods appeared 500 mya, before bony fish existed. These first cephalopods had a hard external shell like many other mollusks but were able to leave the ocean bottom and swim to escape predators. When a predator came along, all the cephalopod had to do was let go of the bottom and float away like a hot air balloon. One of the first advances may have been the creation of multiple chambers connected by a ***siphuncle***; this allowed these early cephalopods to slowly change their buoyancy.

Other early advances were likely to have been the ability to swim slowly to control direction. Two groups of cephalopods, the Nautiloids and Ammonids (570 mya), depended on their external shell and ability to swim to protect them from predators. Both of these sub-classes of cephalopods do not have many of the traits of their modern relatives, such as the ability to change color, to produce sharp images with a lens-based eye, or the ability to swim fast.

It is hard to say why the Ammonites and all but six species of Nautilus have become extinct. These cephalopods had a wide variety of external shells, some coiled, some long and straight, some with spines. These shells provided good protection from predators but inhibited the animals’ mobility.

Predation pressure has long been thought to be one of the major forces driving cephalopod evolution. Perhaps as species of bony fish, many of which swim much faster than an externally shelled cephalopod, appeared in the early oceans, armor just wasn’t enough, and of those species that depended on armor, almost all have become extinct.

Differently strategy

Modern cephalopods have evolved a different strategy. Instead of a heavy protective external shell, they have reduced and internalized this armor. The loss of the heavy armor frees them from the weight of carrying it around and the energy needed to produce it. Most modern cephalopods are active predators. Instead of heavy armor, they rely on speed and visual tricks to avoid being eaten. Some scientists have suggested that these adaptations were in response to pressure from predators. Indeed, many of the tricks such as the ability to change color, shape and texture as well as the ability to produce a visual ink decoy seem to be aimed directly at their predators. ■

Squid fossil hundreds of millions years old

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Ammonoids first appeared in the Late Silurian to Early Devonian (circa 400 million years ago)

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Glossary:
The siphuncle is a strand of tissue passing longitudinally through the shell of a cephalopod mollusk. Only cephalopods with chambered shells have siphuncles, such as the extinct ammonites and belemnites, and the living nautiluses, cuttlefish, and Spirula. In the case of the cuttlefish, the siphuncle is indistinct and connects all the small chambers of that animal’s highly modified shell; in the other cephalopods it is thread-like and passes through small openings in the walls dividing the chambers. ■