JELLYFISH'S MAW is the four-pointed area visible in the center of this overhead image of *N. punctata*, a species of the genus *Nausithoe*. The creature's eight red gonads also stand out. *Phronima* (upper left corner) was rumored to be an inspiration for the monster in the movie *Alien*; it is actually a nonscary two to three centimeters long. *Cunina* (far right) is a rarely captured hydromedusa, a close relation of the jellyfish.
Ingenious physiological accommodations have evolved to enable a stunning variety of undersea creatures to be remarkably transparent.

Story begins on page 87
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WHOI

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Flamelike, iridescent colors appeared on a hydro-medusa of the genus *Arctapodema* (*large image at left*) when the light from the photographer’s strobe shone on fine muscle striations on the animal’s body. The transparent snail *Pterosoma* (*lower left corner*) has an elongated retina that takes in images line by line, like a television camera. The photograph next to it shows a creature so recently discovered that it has not yet been named. It is a comb jelly, of the phylum Ctenophora, which paddles through the water by moving the comb plates along the edges of its body. The amphipod below, known as *Cystosoma*, resembles a five-centimeter-long crystalline roach. Its exterior shell encloses mostly water, as well as a tiny, needlelike vertical gut that is not visible in this image. This transparent octopus, *Vitreledonella richardi* (*right*), is also rarely captured and little known.
Siphonophores: One’s a Crowd

Some transparent animals use their invisibility for more than passive camouflage. Siphonophores are peculiar relatives of jellyfish—half-individual, half-colony. The best-known example is the Portuguese man-of-war. Most are transparent, but some have colorful stinging organs that mimic the appearance of baby fish, small shrimp and other alluring prey. Animals pursue these organs, unaware of the much larger transparent animal they are attached to, and are quickly killed. Above, a creature of the taxonomic group prayid is shown in a compressed state, only about 10 or 12 centimeters long. The light-colored objects inside it are stinging cells. In hunting mode the animal transforms itself, stretching out to a meter in length, with the stinging cells dangling, netlike, off buoyant organs. Another siphonophore, Forskalea (right), is a close relative of the Portuguese man-of-war; it hunts in much the same way as the prayid does.
In the continual arms race between the eaters and the eaten, some predators have developed a way to counter the camouflage of transparency. In the ocean, water molecules scatter much of the light, creating polarized light, whose light waves oscillate in parallel. People can discern polarized light only if they are wearing Polaroid sunglasses, but many animals, especially crustaceans and squid, can see such light with their unaided eyes. That capability aids their hunting because the tissues of some of the transparent animals they prey on either remove or rotate the polarization of the light that passes through them. Detecting such a change thus enables the predators to sense the presence of their prey. In the photographs of the same *Labidocera* copepod (above), the one at the right shows the creature as it would be seen by eyes that can detect a change in polarization.

Recently Nadav Shashar and his colleagues at the Marine Biological Laboratories in Woods Hole, Mass., have shown that squid use their ability to see polarization to find transparent food and to send secret signals to one another. Shashar, now at the H. Steinitz Marine Biology Laboratory in Eilat, Israel, gave squid a choice of two glass beads to attack. One of the beads affected the polarization of the light; the other did not. He found that the squid preferred to attack the beads that did affect the light’s polarization. Shashar also found that under polarized illumination—the natural state of light in the ocean—the squid were able to detect, at a longer range, creatures that affected polarization.
VENUS’S GIRDLE, a species of comb jelly, drifts in front of diver Neil Swanberg off Bimini, a Bahamian island. The animal, just millimeters thick but up to two meters long, is obviously too big for the specimen jar Swanberg brought along on the dive. Common methods of collecting sea creatures, such as the use of towed nets, leave a mangled mass of tissue (inset, above left) if applied to transparent animals. So within about 30 meters of the surface, divers hand-collect specimens; at greater depths, biologists rely on research submersibles such as the Johnson Sea-Link (inset, above right). The submersible is equipped with jars that can be opened and closed remotely using hydraulics.
Below us yawns the abyss, more than 3,000 meters deep.

Except for the small launch boat I am sitting in and the white mother ship in the distance, there is nothing but sea and sky. Taking a breath from my scuba regulator, I roll over the side of the launch into water so clear and empty that I can see for almost 100 meters. As I descend with three of my colleagues, the blue of the water darkens around us to a medium cobalt that deepens to purple as we face the abyss, more than 3,000 meters deep.

Hundreds of kilometers from land, we are dropping down not to a thriving reef or some storied shipwreck but rather to a point arbitrarily chosen in the open ocean. Below us yawns the abyss, more than 3,000 meters deep. We are in the earth's largest habitat, which occupies more than 99 percent of the planet's livable space. It is a featureless world, where only the gentlest gradations of light and color signal a change in time or space.

For us, the lack of reference is profoundly disorienting. For the animals that live here, it means there is no place to hide.

At 18 meters we stop our descent, clip on to a safety line dangling from the launch and begin our search. We do not have to look far: as our eyes adjust, we find we are surrounded by dozens of slow-moving, transparent animals. In this exotic glass menagerie there are a few jellyfish, but most of the creatures are not immediately recognizable. They range from thumb size to bigger than a basketball, and whereas some are revealed by the food in their stomachs or by the occasional color spot or flash of iridescence, others are so clear that they are invisible even centimeters away. We pull glass jars from our net bags and begin collecting.

Gelatinous Life

What most of these creatures have in common are bodies that consist largely of a gelatinous material, which bestows numerous benefits. Because this substance is mostly incompressible water, the animals are protected from the crushing pressure of the deep. It has just enough buoyancy to allow many of them to float like balloons over the abyss. The material is also nonliving and easy to produce, so creatures made of it can live on very little food. When food is abundant, they can grow and reproduce at phenomenal rates, some blooming—in a single week—into colonies of billions of individuals covering thousands of square kilometers.

Perhaps the most important advantage of gelatinous material—and the foundation for its evolutionary success in the undersea realm—is the transparency it can confer: almost all open-ocean animals not otherwise protected by teeth, toxins, speed or small size have some degree of invisibility. In fact, transparency is uncommon only at depths where sunlight never penetrates.

The drawback is that gelatinous animals are delicate and slow. Quite a few of them rely almost completely on invisibility, the ultimate form of camouflage, to elude their predators and to stalk their own prey.

Its importance in the marine environment notwithstanding, transparency is still a largely mysterious characteristic. Thus, my own research has focused on fairly basic questions, such as: How clear can these animals be? And what unusual physiological characteristics enable the creatures to achieve high levels of transparency?

The first step in understanding the ecology of transparency is determining how transparent the animals really are. In that endeavor, the most difficult aspect is capturing them in good condition. They are typically transparent only when alive and healthy and turn opaque very quickly after dying. Catching healthy animals is difficult because they are so fragile; some can be torn apart by the turbulence from the nearby swish of a fish's tail. For that reason, the standard techniques for gathering gelatinous animals depend on scuba divers and submersibles.

Using both techniques, my colleagues and I have collected a wide variety of transparent animals in essentially perfect condition. Then, in a laboratory on the research vessel, I have measured the creatures' transparency across the visible spectrum using a spectrometer based on those that ophthalmologists use to measure the transparency of the human eye.

The animals' transparency varied over a range much greater than would be guessed from a quick visual estimation. The amount of light that passed through their bodies ranged from 20 to 90 percent. Not surprisingly, larger animals with more tissue compensated by having clearer tissue. More shocking was our finding that animals caught at 750 meters were just as transparent as those caught near the surface.

That observation puzzled me; I had expected that those near the surface would be more transparent because the surface world is brighter and harder to hide in. But it turned out that some of the deeper animals were more transparent than was necessary for them to be invisible just centimeters or even millimeters away from their predators' eyes.

To understand how a creature could be so transparent, consider that the visibility of an object depends on its contrast—its brightness compared with that of its surroundings. For a marine creature, the water between the animal and its observer scatters and absorbs the light reflected off the creature. So the farther away an animal is, the less contrast its image has and the harder it is to see. At some distance, depending on the animal's original contrast and how much the water affects the light, the contrast drops below what the observer can see. This distance is known as the sighting distance, and beyond it the animal is invisible (and safe).

Transparency and Structure

Unlike other forms of camouflage, transparency involves the entire body, not just its exterior. That fact presents several fascinating problems that evolution has solved in ingenious ways.

Some solutions can be seen by the naked eye. Some of these creatures are...
flat and thin, because thinner objects pass more light. If a centimeter of transparent snail lets through one ninth of the light, half a centimeter lets through one third. Flatness also makes the animal hard to see edge-on. Some, such as the fish larva called a leptocephalus, have taken this trick to extremes and are like living wafers, just a millimeter or two thick and tens of centimeters long. Certain comb jellies with the romantically evocative common name “Venus’s girdle” are as long and flat as belts. And the young of Caribbean spiny lobsters are about as big as a half-dollar and as flat as paper. About the only way to detect them is to catch a fleeting glimpse of their shadow.

The other obvious changes involve parts that for physical reasons cannot be made transparent. Because retinas have to absorb light to see, at least a part of the eyes is always visible. Three solutions have emerged to this problem. Some organisms have their eyes on the ends of long stalks to distance them as much as possible. Others, such as the crustacean Phronima [see illustration on page 80], have extremely compact retinas and use natural conduits, like fiber optic cables, to channel the light to them. Still others, such as the large crustacean Cystosoma [see illustration on page 83], have huge eyes with very thin, pale retinas just under the cornea.

The stomach is another invariably visible organ. The reason is not the stomach itself, but its contents: partly digested animals or vegetation, which is typically opaque. In some see-through animals, however, the stomach is needle-shaped and always points down, no matter which way the animal is oriented. The arrangement can be effective because many predators search for their prey by looking up for shadows against the light from the ocean surface. Another strategy is to cloak the stomach in reflective tissue. In the open ocean such tissue, like a mirror, is invisible, because the light it reflects is indistinguishable from the light behind it. The same principle, incidentally, explains why so many fish have silvery, mirrorlike scales on the outside of their bodies.

Skin is the third troublesome organ because it always reflects at least some light. Some animals get by with simple body shapes that reduce the amount of skin and the complexity of the reflections. Less commonly but more intriguingly, some creatures have a microscopically bumpy texture on the surface of their bodies, which minimizes reflectivity in a way that is at once fascinating and subtle.

This strategy was the subject of a recent paper by Andrew Parker of the Australian Museum in Sydney. It depends on the refractive index of the material, which indicates how fast light travels through a material. Light travels more slowly in a material with a high refractive index than in one with a low index.

If a surface has a large number of bumps that are smaller than half the wavelength of the light falling on them, the whole surface acts like a uniform substance with a refractive index that is the average of the bumps and the surrounding medium (water, for our purposes). Because the bumps are larger at the bottom than at the top, however, the refractive index at the bottom is closer to that of the material—which is typically higher than that of water. For the same reason, the index is lower near the top of the bumps.

Thus, there is a gentle, rather than abrupt, increase in refractive index from the surrounding water to the body of the animal. That gentle transition reduces reflection; in fact, it works so well that lens designers are now using the principle to improve lens coatings in high-performance optics. It is also reportedly employed by Northrop Grumman in its B-2 stealth bomber to minimize the radar reflections from the aircraft’s surface.

Requirements for Invisibility

Keeping reflections to a minimum is necessary but not sufficient for invisibility. Light must also pass unimpeded through the body, which requires that the beams are neither scattered nor absorbed as they travel through. Either

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**Why the Cornea Is Clear**

Fourier analysis, which determines the predominant frequencies in a collection of waves or other repeating phenomena, has turned out to be extremely useful in analyzing transparency not only in gelatinous animals but also in the human cornea. Like the animals’ bodies, the cornea and the surrounding white of the eye consist of periodic or semiregular arrangements of fibrous proteins. When these fibers are neatly ordered and spaced out with a “wavelength” less than half that of the shortest wavelength of visible light, the tissue approaches perfect transparency. The reason is that light passing directly through the tissue constructively reinforces itself, whereas light scattering off to the sides is eliminated by destructive interference.

This graph shows data I collected for both the cornea and the white of the eye (the sclera). In both cases, the fibers of the tissue exist in a variety of repeating patterns, each with a different wavelength. These wavelengths are plotted on the X axis. The predominance of a tissue with a certain wavelength is indicated by its corresponding value on the Y axis. In the cornea, for example, fibers repeating in a pattern with a wavelength of about 50 nanometers predominate. That value is well below 200 nanometers, which is about half the wavelength of violet light, the shortest the human eye can see. In contrast, the sclera has peaks above 200 nanometers, rendering it opaque.

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—S.J.

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phenomenon would render the body more visible, but of the two, scattering is the more significant barrier to animal transparency because very few organic molecules absorb light.

Scattering is caused by variations in refractive index. As light passes from one material to another, a change in refractive index alters the light's speed. In addition, unless the light beam enters the new material perfectly perpendicularly, the direction of the beam changes.

Animal tissue normally has many variations in refractive index because of the diverse components required for life (cells, fibers, nuclei, nerves and so on). Even gelatinous animals, which contain a relatively large amount of water, have refractive index variations. The relation between refractive index variation and light scattering is extraordinarily complicated, and we do not know the details about the refractive index distribution inside living tissue.

Nevertheless, using simplified models and the assumption that tissue needs certain volumes of different components to survive, I examined how the size, shape and refractive index of these components affect the total amount of light scattering. Developers of house paints use similar methods to maximize the light scattering and therefore the hiding power of their paints.

The most important factors were the distribution and size of the components. If a cell requires a certain volume of fat to survive but must scatter as little light as possible, the best strategy is to divide the fat into a large number of very small droplets. A slightly worse strategy is to divide it into a few large droplets, and the worst strategy by many orders of magnitude is to divide the fat into drops about the size of the wavelength of light. The refractive index of the fat is less important; the shape of the droplets is least important. These factors provide a guide to what to look for in the microscopic anatomy of transparent animals.

Refractive index variations do not always cause scattering, however. If the sizes of the refractive index variations are all smaller than half the wavelength of light, the scattered light from all the variations is eliminated by destructive interference. In destructive interference, light waves overlap in such a way that they cancel one another out.

For instance, the white and the cornea of the eye are both made of dense layers of collagen fibers, but because the fibers of the cornea are smaller and more tightly packed, the refractive index variations are all smaller than half the wavelength of light [see box on opposite page]. Therefore, there is strong destructive interference, and the organ is transparent. Without this interference, the cornea would be completely opaque. Cataracts arise when, in old age, this uniform packing of fibers becomes disturbed, throwing off their destructive interference.

Transparency is an extraordinary example of evolution in response to difficult circumstances. Through clever modifications of their bodies and cells, these delicate animals have found a way to survive in an exposed and dangerous environment. As is so often true, their naturally evolved methods rival the latest technological breakthroughs—in this case, in fiber optics, antireflection optical coatings and house paints. Their study is relevant to cataract research and to the expanding field of diagnosis and treatment of skin diseases with light. These animals, so common and yet so mysterious, have surprising things to teach us.