Vision relies on a series of pigments that filter and absorb light.

Marine animals have a series of **photoreceptor pigments (rhodopsins)** located in a retina. Typical vertebrate retinas contain rods and cones. Rods are more sensitive but do not discriminate wavelengths; cones are less sensitive and vary in their sensitivity to different wavelengths allowing color vision. Invertebrate eyes differ but also have a series of light-sensitive pigments that vary in peak wavelength sensitivity. They use a rhabdomeric system, which is biochemically distinct from the vertebrate system (see Arendt, 2003). An eye structure focuses light on the retina, and the pigment molecule is excited when absorbing the light energy. Sensitivity of the pigments may range from ultraviolet to the red end of the spectrum. A series of photochemical steps ultimately causes phototransduction, which produces a neural signal that is interpreted for the organism by a brain or ganglion (for more information, see Warrant and Nilsson, 2007).

Color vision is widespread among vertebrates and invertebrates.

Although many animals are incapable of discriminating colors, a large number can identify color, which must at least involve discriminating between two wavelengths of light independent of their respective intensities. Individuals use color to discriminate among objects, such as predators, mates, and the general seascape. As might be expected, marine organisms are adapted best for vision in the wavelengths most common in seawater. Many crustacea can discriminate between two basic color types (usually blue and green-yellow), but scallops and others are able to discriminate among three types.

Light is an important cue in behavioral adaptation of marine organisms.

Many mobile intertidal animals use positive and negative responses to light to adjust their optimum position relative to

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Crystal Eyes: Past and Present 5.2

Vision can require astounding degrees of image and color resolution to be effective. Predatory diving seabirds must be able to resolve images rapidly as they approach their prey. Cormorants perform less efficiently in turbid water, because they must resolve the images of swimming prey fish as they scan the bottom before they dive. But in many other cases, shading is a good enough indicator of the approach of a predator, allowing a prey fish to escape without resolving the image of the approaching diving bird. Similar strong variations in image perception occur among the invertebrates. Scallops have a large array of cup-shaped light detectors located on the mantle edges whose perception of approaching shade might be good enough to detect the approach of a predatory crab. But fiddler crabs have a highly concentrated line of ommatidia (arthropod light-capturing units, each with a neuroreceptor) whose main purpose is to detect vertical motion above the horizon, which warns of the approach of a predatory bird. These crabs can also resolve images to detect mates of differing size and color.

How are images resolved with great detail? Humans have an elegant adjustable lens that focuses images on the cornea. It stands to reason that other organisms must have structures that focus an image on a retina or retina-like structure. A challenged human could go to the optometry shop and buy a glass or plastic lens to help increase the focus of an image on the retina when things go a bit wrong. Do animals have such evolved capacities?

Some of the fossil group Trilobita have eyes that usually look superficially like the compound eyes of insects, with a honeycomb pattern of individual units with some sort of clear facet on the surface that gathers light and focuses it at the base of the unit, where a nerve-embedded structure translates a light stimulus into a nervous transmission to the brain or an organized group of nerves known as a ganglion. The orientation of the array of units, or ommatidia (**Box Figure 5.4**), can be used to infer the visual field, even of an extinct trilobite.

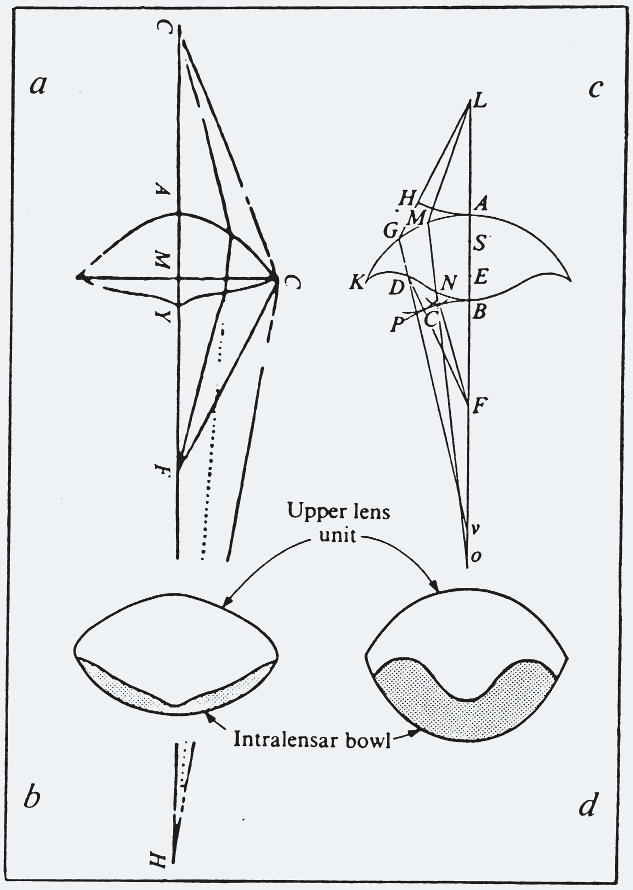
Two genera of trilobites have schizochroal eyes, where the lens is composed of two units, one above the other, of calcite, a crystalline mineral form of calcium carbonate. The upper units have been found in two forms (**Box Figure 5.5**). What is amazing about the two different upper crystalline lens types is that they strongly resemble one of two lenses that were designed by Descartes and Huygens, two major eighteenth-century pioneers in philosophy and the design of telescopes and microscopes. The top units were combined with bowl-shaped lower units that completed the focusing of the image in seawater (see Clarkson and Levi-Setti, 1975).

The use of natural materials and structures to help in the design of engineering schemes for people is known as Biologically Inspired

BOX FIG. 5.4 Side view of a rolled-up specimen of the Devonian trilobite *Phacops rana* showing the large eye with surface parts of individual units, or ommatidia. (From www.fossilmuseum.org)

HOT TOPICS IN MARINE BIOLOGY

Crystal Eyes: Past and Present *continued* 5.2



BOX FIG. 5.5 (a) Aplanatic lens design in air, using two oval lens, designed by Descartes. (b) Lens of the trilobite *Dalmanitina socialis*. (c) Aplanatic lens in air, making use of spherical first surface and a Cartesian second surface, designed by Huygens. (From Clarkson and Levi-Setti, 1975)

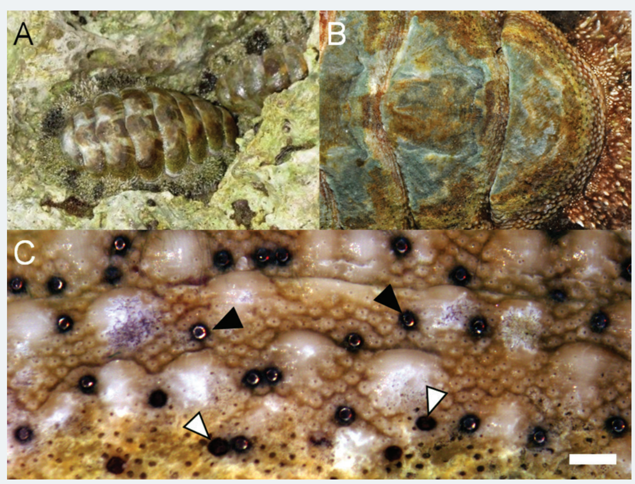
Design. Our example of trilobite lenses, however, puts the whole process backwards. Lenses were invented over 300 years ago by Descartes and Huygens, but the trilobites evolved these lenses hundreds of millions of years ago only to be discovered and compared with those of Descartes and Huygens in 1975. But many living structures today give us insight in the design of new structures and materials for human purposes. For example, in Chapter 6 we mention the bumpy skin of some sharks, which reduces skin friction as the sharks swim through the water. This principle was employed in the design for swimming skin suits for Olympic swimmers, although the outcome was not as beneficial as expected.

So let us consider a remarkable armor found within the shell of the West Indian fuzzy chiton *Acanthopleura granulata* (**Box Figure 5.6**). Many chiton species have hard shells, dotted with tiny eyes. Maybe it's no accident that the chitons superficially resemble trilobites. They both are (were) small epibenthic creatures, which may be very vulnerable to crabs and fish predators. The chitons can clamp to the substratum so the predator cannot pry it off and get to the soft foot beneath. Many trilobites could roll into a ball, and eyes would allow them also to perceive approaching predators before they could be bitten.

Chiton eyes have lenses made of aragonite, another form of calcium carbonate, like the trilobites we mentioned earlier (Speiser et al., 2011). The lenses are translucent and are surrounded by a dark pigment, which makes the eyes show up as dark dots (**Box Figure 5.6**). The eyes are embedded in larger structures known as aesthetes. The lens is either a single crystal or many microcrystals with similar alignment. A thin (~5-mm thick) concavo-convex corneal layer covers the lens and is continuous with the surrounding eye microstructure.

Li and colleagues (2015) showed through experiments that the lenses can form clear images of objects such as fishes. In a previous study, Speiser et al. (2011) demonstrated that chitons could perceive dark objects and appear to have an angular resolution of the objects that is consistent with the perception angle that could be afforded by the aragonite crystal in a single eye lens. This could allow the chiton to distinguish between approaching objects and perhaps distinguish predators. Given the geometry of the lens, a fish at a distance of ca. 2m could be resolved through one lens unit on the chiton's dorsal surface, according to the measurements of Li et al. (2015).

The eyes are lenses embedded in a soft tissue structure, which may be great for detecting approaching mobile predators, but the soft tissue interrupts the otherwise continuous armored dorsal surface of the chiton. The chiton is therefore paying a price in defense for the ability to have windows on the outside world to detect the approach of prey. This overall structure helps us understand that this biologically inspired design suggests that there may be a trade-off when designing armor. In the twelfth century, medieval knights and infantry used a cylindrical helmet, known as a great helm, which had slits for vision. This provided great protection but greatly reduced the field of vision and had poor air circulation. A helmet with more openings for vision weakened the helmet but might have provided quicker response to attackers. Such compromises are the nature of industrial and biological design.



BOX FIG. 5.6 (a) *Acanthopleura granulata* on rocks near Tavernier, Florida. (b) Closeup with anteriormost valve to right; ocelli are small black dots. (c) Chiton eyes: newer, less eroded eyes (black arrowhead); more eroded eyes (white arrowheads). Scale is 200 µm. (From Speiser et al., 2011)