Cover illustration

Prometheus' eye

The Cambrian period, (543–503 million years ago) was a time when life exploded onto the planet with diverse phyla, many of which are now extinct. Mollusks, one of the most successful and robust of the phyla, originated in the warm shallow seas of the early Cambrian, and subsequently blossomed into a surprising array of creatures which now haunt the marine and terrestrial environments. Since the Cambrian period, there have been radiations into the shelled bivalve mollusks such as barnacles, clams, oysters, mussels and scallops, as well as other seemingly unrelated creatures such as nudibranchs, chitons, octopus, squid and cuttlefish. Early during this divergence in the late Cambrian period, a shelled mollusk, long since extinct, diverged into cephalopods and gastropods. Although the visual systems of both classes are related, it is the gastropods that have developed a most interesting twist.

The adult *Strombus galeatus*, pictured on the cover and a member of the family Strombidae, is a robust and hearty vegetarian browsing its way through the sea grass of the Costa Rican continental shelf of the eastern Pacific. These heavily armoured marine gastropods have eyes located at the tips of long stalks protruding along the flared edge of the shell. These stalked eyes can be moved independently, and can be almost completely retracted beneath the shell. These eyes are especially intriguing.

Although the eyes of *S. galeatus* have not been studied, the stalked eyes of closely related conchs have good spatial vision, although it is not completely clear why these animals would need such good vision. The adult's eye measures approximately 2.5 mm in diameter, although smaller conchs have smaller eyes, but the eyes continue to grow as the animal, and the stalk, grows. These eyes, resembling those of the box jellyfish (BJO, August 2003) and of cephalopods (octopus, squids and cuttlefish), are camera eyes, like our own. Many strombids have a thin bilayered cornea and a large piscine-style lens. The outer cornea consists of clear epidermal cells overlying the ocular structures in an eye-bulb. The inner cornea consists of an outer basement membrane encircling the eye, and

Figure 1 Eyes of Queen Conch.

an inner layer which undergoes transition to, and becomes, reticular cells beyond what could be called the pupil. The lens is round and piscine-like. Immediately posterior (proximal) to the lens is a cavity filled with fluid, analogous to the vitreous. Proximal to the vitreous is a concave posterior surface lined with reticular cells (Hughes PHI. *Cell Tiss Res* 1976;171:259–71). These reticular cells are the photoreceptors, but there are several differences between them. There are two distinct types of photoreceptor cells, each of them having the photoreceptive element on the distal end of the cell, or on that portion closest to the posterior lens surface. This is an everted retina, as opposed to our inverted retina. Each of these two forms of reticular cells has pigment granules within these same cells that contain the microvillous photopigment. The pigment granules serve as a pigment backing to prevent light penetration. The principal photoreceptive cell has fewer pigment granules and more posterior vesicles. These vesicles or granules within these reticular cells are retinochrome packets which serve much like a tapetum (BJO, July 2004) and function as a repository for retinal or retinaldehyde. This source of retinal replenishes microvillous pigment when needed. This system is unique to the mollusks, but not to the gastropods, as the squid and other cephalopods have a very similar system.

Just what does a slow-moving vegetarian that is an armoured vehicle do with this surprisingly elegant system? The shallow warm continental shelf seas are rich in the algae and sea grass meadows that form the mainstay of the animal's diet, so good vision is not necessary to find food. This environment, however,

would be very bright, with lots of confusing reflexes from the refraction of the waves on sunlight. Good spatial vision would assist in its peregrinations, although this does not seem to be a sufficient answer. Prey avoidance seems likely to require good vision. The strombids are good diggers and, given some warning, can bury themselves in the sand to frustrate predators such as lobster, octopus, marine turtles and some sharks. Nevertheless, it seems clear that good vision is essential to the animal for the most interesting aspect of this eye—its regeneration.

The stalks cannot be completely withdrawn beneath the flared edge of the shell, and perhaps these eyestalks were/are often injured and/or lost. This functional loss may have stimulated an evolutionary adjustment to permit the animal to regenerate an essential sensory mechanism, which is exactly what happens.

If the eyestalk is amputated below the eye, the optic nerve degenerates, but new epidermal cells grow around the nerve towards what would have been the tip, and regenerates a new eye. Embryologically, most invertebrates derive photoreceptors and lenses from the epidermis, and gastropods are no exception. By 8 days after amputation and responding to a stimulus from the cut optic nerve, a ball of cells at the tip of the stalk reveals pigmented cells, proving the beginning of a new eye derived from the epidermis. As the reticular cells (photoreceptor equivalents) are laid down, these cells send growth cones toward the degenerating optic nerve. Eventually, the growth cones unite to travel down the original optic nerve and reassemble correctly in a topographic fashion with the appropriate cerebral ganglion. At first the eye is small, but in a matter of a few weeks these new eyes regenerate to the approximate size of the original eye.

Hence, like Prometheus regenerating his liver, strombids regenerate their eyes.

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