Cover illustration

Can you keep a secret?

Worms seem taciturn and pedestrian, and yet these creatures may hold the secrets to the differences between the eyes of vertebrates and invertebrates. At least one rather well studied polychaete (many bristles or legs) annelid may provide the background to understanding the origins for the profound differences in ocular morphology found between chordates and non-chordates and can shed light on the question of the monophyletic versus polyphyletic appearance of eyes.

Platynereis dumerilii (closely related to our cover species—*Platynereis bicaniculata*) spends its adult life in a self spun silky tube in the sublittoral zone, between the seashore and the edge of the continental shelf, and represents a frequent tasty morsel for many of the wading birds. The immature *Platynereis*, called atokes, are free swimming and must attach to the bottom as an adult, or epitoke, to spin a tube. The animal has lifelong development of segments and may have up to 75 segments through a process known as homonymous segmentation, each segment having a pair of appendages called parapodia. The head, or prostomia, has peristomal cirri (specialised appendages seen on the cover image), two pairs of sensory appendages, and two pairs of eyes

These are old organisms—very old! These animals have probably changed little since the Cambrian explosion (*BJO*, February 2004), and may well have existed in a similar form since well before that, in the Precambrian fauna as represented in Ediacaran fossils.

Ediacaran fossils are Precambrian and are from the late Proterozoic (perhaps 600 million years ago to 543 million years ago when the Cambrian began). The animals represented by these fossils were soft bodied and little remains of them except traces or imprints. Many of the individual traces found in the Ediacaran fossils probably represent worms, which were early bilateralians. Most of the other fossils of this era represent animals based on radial symmetry, such as starfish.

Bilateral symmetry is not an evolutionary ‘‘given’’ and understanding the first bilateralian will help in understanding the development of two symmetrical eyes among other features.

Molecular clock data are controversial, but hint that the first bilateralian diverged between 1.6 billion to 650 million years ago, and that represents quite a range. But, the last common ancestor of invertebrates and vertebrates (already a bilateralian) probably lived between 600–540 million years ago in the Ediacaran Precambrian. So, *Platynereis* is probably a direct descendent of the animal that immediately predated the split into vertebrates and invertebrates, and consequently, can teach us much about visual development.

The eyes of *Platynereis* are not complicated and are best described as pigment cups, although there is a very simple lens in front of the cups. This lens is little more than a condensation of tissue. In life, these pigmented depressions are burgundy or maroon in colour, principally because of orange visual pigment overlying more proximal black pigment in the supporting cells lining the cup. Although the eyes are interesting since they represent an early evolutionary step from eyespots to eyecups and exhibit the beginnings of a lens, the rather profound secrets of these eyes are found with the visual pigments of the prostomia, or head.

Metazoans possess basically two different types of photoreceptor cells which are divided along the lines of vertebrates and invertebrates, in general. Although both groups have transmembrane opsins permitting photoreception, invertebrates have rhabdomeric photoreceptors and vertebrates have ciliary photoreceptors. The rhabdomeric cells are microvillous cells and the visual pigment lines the numerous microvilli of the cell. In the ciliary cells, the single cilium of each cell is modified with many folds creating a stacked appearance with the photoreceptive transmembrane protein lining the infoldings of the modified cilium. The difference extends beyond the cell type and distribution of visual pigment, however, since the rhabdomeric opsin is different from the ciliary opsin.

Since *Platynereis* is an annelid, it is an invertebrate, and has the traditional rhabdomeric photoreceptors in all four of its eyes. Surprisingly, however, recent work shows that the ciliary cells and ciliary opsins exist within the brain somewhat more rostral and medial from the two pair of eyes (Arendt D, *et al*, *Science* 2004;**306**:869–71) It is doubtful whether these ciliary cells and their complement of photoreceptive pigment have any true visual function, but probably relate to setting the circadian rhythm. So, this worm has both the ciliary and rhabdomeric forms of visual pigment. But, it goes beyond this.

Vertebrates may not be so far away from these annelids after all. These same investigators suggest that the invertebrate visual pigment, opsin, is present in vertebrate eyes, albeit in the ganglion cells of the retina. That is, the rhabdomeric photoreceptive cells have been retained in the vertebrate eye in the form of retinal ganglion cells! A remnant of photoreception is present in these ganglion cells in the form of melanopsin. This ganglion cell visual pigment probably does not have a visible light function that we recognise, but may contribute to circadian rhythm control. It is also found in the pineal body and pineal eye in animals that have a pineal eye (reviewed in *BJO*, March 2005).

Interestingly, the vertebrates keep both forms of visual pigments (invertebrate and vertebrate) and have evolved an eye that unites these two different opsins from two different anatomical sources.

So, to see some of the wormy secrets of our beginnings we have only to look to our inner retina.

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