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Cover illustration

The eyes have it . . .

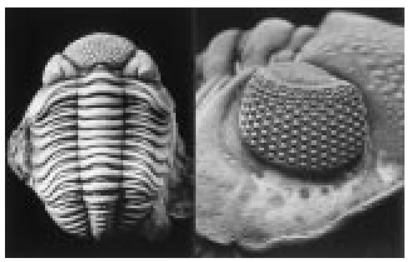
Christian Huygens (1629–95) the Dutch mathematician, and Rene Descartes, the French philosopher/mathematician who first "correctly" explained the rainbow (1596–1650), independently solved the problem of spherical aberration in a lens, with a doublet lens arrangement; a system that now bears their names. Unbeknown to them, though, evolution had already solved this problem millions of years earlier in small ancient creatures known as trilobites. This subtle, recently decoded, palaeontological tale reveals the microevolutionary principles continuously at work and capable of providing ingenious solutions to the physical problems of vision.

Trilobites arose from the evolutionary crucible of the Cambrian explosion 535 million years ago and evolved for perhaps 300 million years, only to become extinct by the mother of all dyings—the Permian extinction, 235 million years ago. Nevertheless, much is known of these animals from the fossil record because these extinct marine arthropods had hard body parts, which included calcite lenses and allowed preservation in stone. Much remains in the fossil record to assist our understanding of the visual capabilities and experiences of these oldest eyes.

From this fossil record, we know that there were at least two different morphological types of these compound eyes, including holochroal and schizochroal. A third somewhat intermediary type, known as the abathochroal eye, is somewhat less certain, but should probably be considered as a separate morphological form.

The holochroal eye is the earliest and most common model and consists of small, multiple, closely packed, round or hexagonal ommatidia. These individual visual units are covered by a single continuous blanket layer of calcite that is in essence the "cornea." This visual surface could have been shed with ecdysis (moulting), allowing for growth of the organism as well as for the eye. Identical new ommatidia were added below the existing ones in a hexagonal pattern, much like a honeycomb.

The schizochroal eye, a unique variation in compound eyes, was found only in the suborder *Phacopina*, and was seen during the Ordovician period to survive until the end of the Devonian period. These ommatidia were arranged in a hexagonal packing pattern but were found in a rectilinear pattern with vertical rows, as can be seen from the two examples of trilobites, *Phacops rana milleri* and *Phacops rana crassituberculata*, shown on this month's cover. These individual ommatidia were generally larger and had an array different from the holochroal eye. The ommatidia were of different sizes, becoming larger towards the ventral surface of the animal. The first lens in each ommatidium was spherical and was followed by an odd bow-shaped lens with a wave-shaped surface facing the first lens. These two lenses are defined in the optical world as



a "doublet." It is this second lens, or the Descartes-Huygens correction lens, that is unique, and perhaps seen in only one or two other animals, and provides for the correction of spherical aberration. This lens system would have increased the contrast sensitivity by as much as fivefold and, in effect, lowered the f-number of the eye (see the February 2001 *BJO* cover essay for a discussion of the f-number). Because of the convexity of the first lens surface, these schizochroal eyes could even have had stereopsis from adjacent ommatidia in the same eye, although it is doubtful the neurological mechanisms for this were present.

These trilobite species had unusual abathochroal lenses with the central nipple appearance creating an aspherical proximal surface that would help with spherical aberration and would create lenses with bifocal capabilities—a feat emulated by contemporary intraocular lens design. Most likely, though, this system would have created problems with internal reflection and would have limited light collecting efficiency.

Thanks to Levi-Setti *et al* (*The Eye: Palaeontology; Frontiers of Life.* London: Academic Press, 2002) the evolution of the optics of these creatures is becoming calcite clear. These investigators suggest that the first trilobite probably had holochroal eyes with only a single calcite lens in the cone of the ommatidium, although there would be optical difficulties with these eyes including diffraction limitations. With room for improvement, the evolutionary tinkering that continued would prove advantageous—especially in a mesopelagic environment—to those species which could evolve improved optics.

A second step would be the appearance of an abathochroal eye with a larger round lens as these animals extended into a dimmer environment. As the lens enlarged the optical system would be less limited by diffraction but rather would be limited by spherical aberration producing a blurred focus.

The third, and truly revolutionary, step to be taken was the formation of a lens doublet with a perfected Huygensian profile. This dramatic but logical evolutionary step would allow for dramatic increased light gathering capabilities and would eliminate spherical aberration, as Descartes and Huygens would learn in the 1600s. Chromatic aberration would probably still exist in such a doublet but in a monochromatic world of mesopelagic light or perhaps even epipelagic light—this would matter little.

Trilobites, especially because of their hard body parts, have contributed much to our understanding of the evolution of the eye and to evolution in general, even though these hardy pioneers were lost to the Permian extinction. To overcome spherical aberration, these creatures didn't need Descartes or Huygens to help them understand the principle of the doublet lens. Long before the appearance of these two scientists, the eyes had it.

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Photographs generously loaned by Riccardo Levi-Setti, PhD, from his book *Trilobites*, Chicago: The University of Chicago Press, 1993.

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