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Cover illustration

Mirror, mirror, on the wall…

Has this happened to you? In the darkness, on a lonely country road, your headlights play across a pair of bright green, almost iridescent, spots of light; they seem to float eerily across the road without support. These furtive spots seem to move and blink, clearly alive. Eyeshine. It is all you see of the creature, as the rest of the body seems to disappear into the darkness that surrounds it. But, what exactly is eyeshine, and why did it evolve?

The *tapetum lucidum* (Latin, carpet shining) is a reflective structure found in the eyes of many diverse creatures and represents convergent ocular evolution solely for maximising photon capture. Surprisingly, the techniques for the production of these reflective mechanisms are variable, and much like the crystalline lens, seem to be drawn from whatever materials the evolutionary process found at hand.

Guanine crystals, for example, provide biological reflection and support camouflage by making a fish glisten and gleam, and hence appear invisible or at least present confusing reflections to a predator. Although we can never know for sure, this coating probably appeared very early in the development of fish as a protective mechanism, perhaps as early as the Silurian (500–450 million years ago) and certainly by the Devonian period (410–360 million years ago).

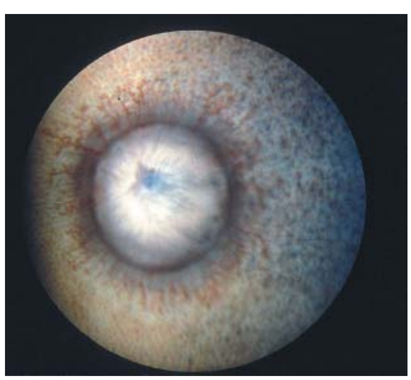
Many fish, then, must have co-opted this protein to be a biological reflective coating directly beneath the photoreceptors in the choroid, and it remains a common, and effective, mechanism among fish. Other fish such as carp, eels, lantern fish, have retinal tapeta that include reflecting materials and pigmented compounds such as pteridine. Still other fish have a tapetum cellulosum, located in the choroid, which is not seen again phylogenetically until certain mammals.

Arthropods became terrestrial during the Devonian period, and among those creatures, insects became both predators and prey and they devised ways to extend their lifestyles into the darkness. Some arthropods such as spiders use guanine for tapeta, as this protein is probably very old. Moths and butterflies found different, but no less creative, mechanisms for light reflection.

Insects deliver oxygen to ocular tissues through a series of tubes branching directly off the trachea. As this Roman aqueduct-like system of oxygen delivery grows smaller as it approaches the internal structures of the eyes, the periodicity of the chambers directly beneath the ommatidia has evolved a separation distance exactly coincident with a quarter the wavelength of light, at least in some species. As light enters the ommatidium, striking each of the 40 or so layers of these tracheal branches or tracheoles, a bit of light is reflected from each surface. With the periodicity of these surfaces at a quarter of the wavelength of light, constructive interference increases and intensifies the reflection until perhaps as much as 90–100% (at least theoretically) of the incident light is reflected back through each photoreceptive element in the ommatidium. The light, once reflected, continues back through the photoreceptive element and exits the eye on almost the identical path it entered. So, even a small torch will illuminate a moth or a spider, with two small red gleaming dots of light looking back at you.

As previously discussed (*BJO* November cover, 2004) tetrapods also ventured into a terrestrial lifestyle in the Devonian period, although curiously enough, the tapetum probably did not accompany these creatures since neither frogs nor salamanders have it. The vertebrate tapetum does not appear phylogenetically again until reptiles and mammals. As you might imagine in convergent evolution, the mechanisms were not the same (Schwab IR *et al*, *Trans Am Ophthalmol* 2002;**100**:187–200).

Crocodiles have a retinal tapetum with the reflective coating immediately beneath and within the outer retina, and specifically not within the choroid. Members of other reptilian clades such as the tuatara (*BJO* March cover, 2005) do not have a tapetum, whatsoever, illustrating that it was not a universal trait even among nocturnal animals.



Fundus photograph of elephant eye

Later, mammals, especially the hoofed mammals and their predators, the major carnivores (dogs and cats), developed tapeta. These tapeta, though, are choroidal and can be divided into pigmented and non-pigmented. The pigmented tapeta have used different light scattering pigments such as lipids, astaxanthin, and melanoid compounds to create a mosaic carpet coloured with brilliant reds and blues. The non-pigmented choroidal tapeta can be further subdivided into fibrous and cellular. The tapetum cellulosum is composed of reflecting cells stacked in depth, like tile work. The tapetum fibrosum (the Nilgiri tahr, a member of the goat family, is the cover image and has a tapetum fibrosum) is acellular and composed of stacks of densely packed collagen fibrils. Each type has evolved seemingly in tandem and whose mechanism is constructive interference as described above.

The tapetum has evolved to maximise photon capture by reflecting much of the light that traverses the photoreceptive element directly above it, but not without some sacrifice. The reflection can scatter to adjacent photoreceptive elements and, depending on shielding of adjacent photopigment may inadvertently cause that receptor to fire. This would blur an image and degrade acuity. So, most predators, since they require better acuity, have protected adjacent photoreceptors with pigment sheaths, or in the case of invertebrates, with steep walled ommatidia that never reach the angle of reflection.

These mirrors, then, are biological oddities cobbled together as necessity dictates and reflect the creativity of random evolutionary mechanisms and unfathomable lengths of time.

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Cover image of *Hemitragus hylocrius* (Nilgiri tahr) by I R Schwab; fundus photographs by Ned Buyukmihci, VMD

Cover: Nilgiri tahr on left and image of goat fundus on right.

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