Cover illustration

Colour me ultraviolet

Mammals arose approximately 225 million years ago in the mid to late Triassic period, as shy, small, secretive creatures springing from a reptilian lineage. At the time mammals evolved, the reptilian order that generated them probably enjoyed tetrachromacy. Most mammalian families became nocturnal (and in many cases arboreal) because of intense dinosaur predation and/or competition. These nocturnal mammalian families lost two visual pigments to become dichromats. It is believed that the now extinct, last common ancestor to the mammalian class probably gave rise to the monotremes (*BJO* March cover, 2005), the marsupials, and the placentals, although the sequence of descent and cladistic relation remains controversial.

Approximately 65 million years ago when a comet struck the Yucatan peninsula ending the Cretaceous period and snuffing out dinosaurs forever, the evolutionary door swung open for synapsids including all mammalian clades. Mammalian families extant at that time were mostly dichromatic, and only a few of the primates would later recover trichromacy (*BJO* December cover, 2001).

Evolutionary recapitulation is rare, often impossible, since metabolic solutions once lost are not randomly repeated. So, the mammalian wave that followed the dinosaurs includes only certain primates that are trichromatic, and these primates cannot have the same visual pigments as our reptilian ancestors. But, not all mammalian families became nocturnal and lost the original visual pigments.

The marsupials (metatherians) were probably well established before the radiation of the placentals (eutherians). Since most placentals are dichromats and many Australian marsupials are at least trichromats, the metatherians are a key class in understanding the evolution of colour vision. These are pivotal species among amniotes because somewhere during the march from our reptilian ancestors to placental mammals, tetrachromacy and trichromacy were lost. Metatherians, then, will help us understand this evolutionary transition.

If tetrachromacy or trichromacy remain unaltered from ancient Jurassic mammalian ancestors, the metatherians

are likely to retain those traces. Indeed, shards of reptilian trichromacy can be found in at least two marsupials although a few are thought to be dichromats, suggesting that the loss of colour vision occurred, or at least began, within the metatherians.

The fat tailed dunnart, illustrated here, and the honey possum have been found to have trichromacy, and the dunnart is believed to be close to the ancestral stock that populated Australia when that continent broke free from Gondwanaland.

The shrew-like fat tailed dunnart is an arrhythmic insectivore, which means that the animal can be active day or night. It can store fat in its tail in times of plenty to sustain itself when resources are scarce. The dunnart's vision is surprisingly good for a creature this size. This would be expected for a predator, especially one that manipulates objects. This adaptable, fierce, and opportunistic marsupial is a versatile predator that demonstrates what was probably required to retain colour vision during the Jurassic with the behemoths that populated the planet at that time.

The fat tailed dunnart has a rather pronounced horizontal visual streak and surprisingly good acuity with 2.3 cycles per degree resolution in the area centralis (foveal equivalent). This visual streak is a concentration of photoreceptors and ganglion cells in the horizontal meridian and is often seen in predators as well as in some prey species (Arrese *et al*, *Brain Behav Evol* 1999;53:111–26).

The dunnart's retina is rod dominant although not to the same extent as a nocturnal animal. Some of the cones possess transparent oil droplets, which is a trait shared with reptiles and birds,

but not placentals. These oil droplets are believed to enhance contrast, reduce glare, lessen chromatic aberration (Arrese *et al*, *Curr Biol* 2002;12:657–60), and may enhance colour vision by shifting the spectral sensitivity of the cones that have them. The dunnart also possesses double cones, a feature retained from the ancestral reptilian design, but absent from placentals. The visual system has a large binocular overlap and the creature probably enjoys stereopsis. Trichromacy, though, in such an animal is intriguing since most other mammals have lost it. Why should this creature have it?

A visual pigment is described best by the peak wavelength of light that stimulates it but for this essay we will use colour designation instead of wavelength.

The nocturnal placentals are believed to have retained a blue and a red-green sensitive photopigment along with the primary rod photopigment thus providing dichromacy. Some primates re-evolved trichromacy by the duplication of the red-green photopigment with some modification in sensitivity. The marsupials that retained trichromacy have a similar blue, a green, and a distinct red sensitive photopigment. In some marsupials, the sensitivity of the blue photopigment range extends into ultraviolet. What advantage would all of these visual pigments confer upon the dunnart, especially sensitivity into the ultraviolet?

Although the 20 g adult dunnart has been known to take small reptiles, and even young rodents, it is primarily insectivorous. So, why should it need a photopigment capable of recognising ultraviolet wavelengths? Insects are often camouflaged by the foliage they inhabit. Most leaves reflect ultraviolet, but insects do not, so the profile of an insect will stand out to any animal capable of vision into this range.

The fat tailed dunnart, then, represents a mammalian colour vision key-stone species with vision that extends into the ultraviolet.

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