Response to Pisani *et al*.

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Tracing the origins of dim-light vision in vertebrate evolution has important palaeobiological and molecular implications for the evolution of vision. The last common ancestor of the vertebrates is thought to have possessed a cone-based (photopic) visual system that operated in brightly-lit shallow marine water [1,2]. This assumption is mainly based on the phylogeny of the visual pigment (opsin) genes, with the cone photoreceptor opsin genes evolving first, as well as on coincident fossil evidence of photosynthetic algae found together with the earliest jawless vertebrates. The question of when dim-light (scotopic) vision evolved from the ancestral photopic state has become the subject of some controversy.

The only study to identify the complete complement of opsin genes from an extant jawless vertebrate (lamprey) found 5 visual pigment opsin genes [3]. A Neighbour Joining analysis suggested that three of the lamprey opsins are orthologous to the opsins LWS, SWS1 and SWS2, which are primarily used for photopic vision in jawed vertebrates (gnathostomes); two lamprey opsins represent paralogous genes (RhA and RhB) resulting from an independent gene duplication event within the agnathan lineage. The absence in the lamprey *Geotria australis* of an orthologue of an Rh1 opsin gene, which is used for scotopic vision in the jawed vertebrates, was consistent with early physiological and morphological studies [4,5], and collectively suggested that rod-based, dim-light vision originated after the divergence of the Agnatha and Gnathostomata.

Pisani *et al.* [6] have refuted this conclusion suggesting that the RhA and RhB opsin genes are orthologous with the Rh1 and Rh2 opsin genes of gnathostomatous vertebrates, respectively. Using a range of phylogenetic analyses (Maximum Likelihood, Bayesian, Minimum Evolution as well as equally and differentially weighted parsimony), but without providing any new sequence data, the study concludes that the last common vertebrate ancestor possessed an Rh1 opsin gene and that scotopic (rod-based) vision evolved in the stem vertebrate lineage.

These contrasting conclusions highlight the difficulty in inferring phylogenetic relationships over large evolutionary distances: Phylogenetic analysis of aligned codon-matched nucleotide sequences benefits from the inclusion of additional data from silent substitutions and less variability in evolutionary rates [1], while the analysis of amino acid sequences is less prone to multiple substitution errors [6]. Differences in sequence alignment may also contribute to the contrasting conclusions. The seemingly erroneous order of species in the LWS clade in all of the trees generated by Pisani *et al.* [6] emphasizes such problems.

Both studies [3,6] concur that duplication of the Rh opsin genes occurred early in vertebrate evolution but the function of the photoreceptors that express the lamprey Rh opsins is still unknown. Electroretinographic [4] and morphological [7] characterisation, in addition to molecular indicators of regeneration rates [8], of lamprey photoreceptors suggests they may be hybrids between both rods and cones. Whether the lampreys possess 'true' scotopic vision needs to be explored functionally (physiologically and biochemically) in combination with analyses of opsins and rod- and cone-specific phototransduction genes from other agnathans. Coupled with the highly contentious nature of the supposed monophyly of the lampreys and hagfishes, and the uncertainty of when the Agnatha split from the jawed vertebrate lineage, it may at present be premature to conclude when scotopic vision originated in vertebrates.

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