Photoreception and Vision in Invertebrates (Nato Science Series A:)

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SYMPOSIUM

Uncovering a Gene Duplication of the Photoreceptive Protein, Opsin, in Scallops (Bivalvia: Pectinidae)

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Synopsis Evolutionary biologists have long been interested in how expansions of the photosensory system might contribute to morphological differentiation of animals. Comparative studies in vertebrate and arthropod lineages have provided considerable insight into how the duplication of opsin, the first gene of the phototransduction pathway, have led to functional differentiation and new ecological opportunities; however, this relationship cannot be examined in many invertebrate groups as we have yet to characterize their opsin content. Scallops (Pectinidae) are a promising molluscan model to study the evolution of opsin and its potential role in speciation. Recently, we discovered a second Gq-coupled, or r-, opsin gene expressed in the eyes of two scallop species. To investigate the evolutionary origin of this opsin, we screened 12 bivalve species from 4 families, representing both mobile and sessile species, with and without eyes. Although only one ortholog was recovered from the genome of the eyeless, immobile oyster, we found both genes to have been retained in 3 families comprising the order Pectinoida. Within this clade, non-mobile species of scallops appear to have lost one gene. Phylogeny-based tests of selection indicate different degrees of purifying selection following duplication. These data, in conjunction with highly divergent gene sequences and ortholog-specific retention, suggest functional differences. Our results are congruent with a Gq-opsin gene duplication in an oyster-Pectinoida ancestor, approximately 470 Mya, and suggest the likelihood of retaining both genes is associated with either the presence of eyes and/or degree of mobility. The identification of two highly divergent Gq-opsin genes in scallops is valuable for future functional investigations and provides a foundation for further study of a morphologically and ecologically diverse clade of bivalves that has been understudied with respect to visual ecology and diversification of opsin.

Introduction

Duplication of genes has played an important role in the evolution of animals' photosensory systems. Retention of diverging gene copies can result in an expansion of an organism's sensory repertoire, thus allowing a finer sampling of its environment. Most metazoans sense light using one or more opsins, seven-transmembrane G-protein-coupled receptors, that fold through the photoreceptor cell membrane and around a light-sensitive retinaldehyde-based chromophore. These two molecules are covalently bound by a Schiff base linkage via a lysine residue (Wald 1968) to form a visual pigment. The amino acids surrounding the chromophore play an important role in light sensitivity as their interaction with the chromophore influences the portion of the light spectrum that will elicit a response from the visual pigment. Thus, changes in specific amino-acid sequences can alter (or tune) the spectral sensitivity of the visual pigment (Yokoyama 2000, 2002; Hunt et al. 2004). In this way, divergence of sequences after duplication of an opsin gene is an important mechanism that increases the coverage of the light spectrum perceived by the animal. The opsin family has gone through multiple rounds of duplication early in metazoans and has generated three to five different opsin lineages that are defined, in part, by interaction with a specific trimeric G-protein (Terakita 2005; Plachetzki et al. 2007; Feuda et al. 2012; Porter et al. 2012). Subsequently, these opsin subfamilies have expanded and diversified in a lineage-specific manner both in vertebrates (e.g., fishes

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