

Exploring opsin diversity and localisation in echinoderms: insights from sea cucumbers and crinoids

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Echinoderms, a group of marine invertebrates comprising sea stars and sea urchins, are intriguing because they exhibit an important light sensitivity despite lacking eyes. This makes them good models to study photoreception evolution in deuterostome metazoans. Studies in sea urchins, sea stars and brittle stars have revealed the expression of various opsins in organs like spines and tube feet or directly within the nervous system. Echinoderms possess a remarkable diversity of opsins, expressing seven out of the nine bilaterian-type opsin lineages, including uncommon lineages like Bathyopsins and Chaopsins. However, limited attention has been paid to light perception in two echinoderm classes: sea cucumbers (Holothuroidea) and feather stars (Crinoidea). Exploring crinoids is crucial for a comprehensive understanding of echinoderm photoreception evolution, as they represent the most basal lineage. Sea cucumbers, with their secondary bilateral symmetry, differ from the typical pentaradial symmetry of other echinoderms. To investigate light perception in these groups, we used a multidisciplinary approach, including behavioral experiments, transcriptome and genome mining, as well as morpho-functional and expression analyses.

Behavioural tests conducted on several shallow-water sea cucumber have shown both negative and positive phototaxis according to species, specifically for shorter wavelengths corresponding to blue and green light. On the other hand, the shallow-water European crinoid *Antedon bifida* exhibits a negative phototactic behavior for both short (blue light) and long (red light) wavelengths. The analysis of genomes and transcriptomes from various sea cucumber species unveiled a similar high diversity of ancestral bilaterian opsin lineages, as observed in other echinoderms, except for Chaopsins and Bathyopsins which appear to be absent in sea cucumbers. In contrast, the genome of a European crinoid exhibited only three rhabdomeric opsin genes. The reduction in opsin diversity suggests a pronounced specialization in the photoreception of feather stars, particularly within the antedonid family. In the European sea cucumber *Holothuria forskali*, the expression of rhabdomeric opsins was specifically detected in feeding oral tentacles, radial nerves, and locomotory tube feet. Our investigation also focused on the order of Apodida, a group of snake-shaped sea cucumbers lacking tube feet. Our study demonstrated the expression of a ciliary opsin in the photo-sensory neuroepithelial structures of large tropical species which form eyespots at the base of each oral tentacle. Additionally, we have also detected ciliary opsins in the sensory cupules located on the inner surface of tentacles in a small burrowing eye-less Apodida species. In the feather star *A. bifida*, two of the crinoid rhabdomeric opsins are expressed in various nerve plexi, as well as in the tube feet.