New light on photoreceptors in two echinoderm groups: Crinoids and sea cucumbers

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Echinoderms are marine invertebrates (comprising starfishes and sea urchins) which exhibit an important light sensitivity despite lacking complex photosensory organ. This extraocular photoreception is allowed by opsins (typical photoreceptor proteins) present in different part of their bodies like spines and tube feet as several studies have revealed in sea urchins, sea stars and in brittle stars. Moreover, Echinoderms possess a remarkable wide diversity of these photoreceptors with a preservation of seven out of the nine ancestral bilaterian-type opsin lineages. This makes them good models to study the evolution of light perception and opsin diversity in deuterostomes. However, the photoreception has been remained largely understudied in two major echinoderm classes: sea cucumbers (Holothuroidea) and feather stars (Crinoidea). Nevertheless, the investigation of these two groups remains of great interest, on the one hand because of the unusual bilateral derived morphology in the case of holothurians, and on the other because of the privileged basal position in the echinoderm phylogeny for crinoids. To investigate the photoreception in these groups, we used a multidisciplinary approach, including behavioral experiments, in silico gene searching, as well as morphofunctional analyses. The ethological tests conducted on several sea cucumbers have shown both negative and positive phototaxis according to species, specifically for shorter wavelengths corresponding to blue and green lights. 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 in silico analysis of genomes and transcriptomes from various sea cucumber species have shown a similar high diversity of ancestral bilaterian opsin lineages, as observed in other echinoderms. In contrast, the genome of our model European crinoid Antedon bifida exhibited only three rhabdomeric opsin genes. This reduction in opsin diversity suggests maybe a pronounced specialization in the photoreception of feather stars or at least for the Antedonid family. Finaly, the opsin localisations have been highlighted by immunodetection in different tissues of holothurian and crinoid species. 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. We have also focused on the Apodida order (a group of snake-shaped sea cucumbers). Our study demonstrated the expression of a ciliary opsin in the photo-sensory neuroepithelial structures which form eyespots at the base of each oral tentacle of the large tropical species Euapta godeffroyi. 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 Oestergrenia digitata. In the feather star A. bifida, two rhabdomeric opsins are expressed in various nerve plexus, as well as in the tube feet of ambulacral grooves.