Evolution of extraocular photoreception in Crinoids (Crinoidea, Echinodermata)

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Light perception is a fundamental sense in most organisms living in marine ecosystems. This capacity is mainly mediated by photoreceptor proteins known as opsins. While photoreception is well understood in many animal groups with specialised visual organs, such as eyes or ocelli, it remains relatively underexplored in organisms which primarily rely on extraocular photoreception, such as echinoderms. In this marine phylum, only sea stars and a few snake-shaped holothurians have also specialised photosensory organs named respectively optic cushions (Garm and Nilsson 2014) and eyespots (Yamamoto and Yoshida 1978). Other echinoderms like sea urchins and brittle stars present only photoreceptors expressed in different anatomical structures such as spines tube feet or directly associated with the centralised nervous system (Ullrich-Lüter *et al.* 2011; Delroisse *et al.* 2014). Paradoxically, these eyeless marine animals possess one of the greatest diversities of ancestral opsin types (seven of the nine existing types) among bilaterian lineages (Ramirez *et al.* 2016). To gain a deeper understanding of opsin evolution in this deuterostome group, it is essential to study the most phylogenetically basal echinoderm class, the crinoids. These filter-feeder animals use branched arms to capture small planktonic particles in their feeding grooves, which lead to the mouth. Their photoreception remains largely understudied, although it is known that some shallow-water comatulid species are sensitive to daylight (Rutman and Fishelson 1969, Meyer 1973). We conducted a comprehensive study of the photoreception in the European species *Antedon bifida*, examining both morpho-functional and molecular aspects. An analysis of its chromosome-scale genome revealed the presence of only three opsin genes, all of which belong to the rhabdomeric type (i.e., the type containing most arthropod visual opsins). The low opsin diversity contrasts with that observed in other echinoderm classes. The three crinoid opsins were expressed in vitro, and their measured absorbance corresponded to blue and green light (respectively 464, 426 and 525nm). These results are largely consistent with behavioural tests that revealed a negative phototaxis with a large peak sensitivity to blue light (463nm) in this species. Finally, two of these opsins have been localised through immunostaining, one in the basiepithelial nervous system of the feeding grooves and the second at the tip of the tube feet. This opsin expression pattern suggests a complex extraocular photoreception system in these feather stars, like that observed in other echinoderms.

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Keywords

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