Extraocellar and ocellar opsin based photoreception in sea cucumbers (Holothuroidea, Echinodermata)

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Echinoderms are an intriguing group of deuterostome invertebrates which have been known to be sensitive to light despite lacking complex eye structures. They are therefore an interesting group to study the evolution of light perception in metazoans. Previous studies on sea urchins, sea stars and brittle stars have identified photoreceptors in various body parts, such as tube feet, spines, and the nervous system (Ullrich-Lüter et al. 2011; 2013; Delroisse et al. 2014). Some studies also led to the discovery of low-resolution spatial (but eye-less) vision in some species (Blevins et Johnsen 2004; Sumner-Rooney et al. 2020). The light perception abilities of holothuroids (sea cucumbers), however, have been largely understudied, with some punctual results from ethological studies (e.g., some species flee away from a light source while other species retract their oral tentacles under strong light exposure) (Pople. 1958; Bonham & Held 1963 ; Dong et al. 2010, 2011). To investigate photoreception in sea cucumbers, we used a multidisciplinary approach focusing on opsins, which are prototypical photoreceptor proteins in bilaterians. Our analysis of genomes and transcriptomes from multiple holothuroid species revealed six ancestral opsin types. The expression of rhabdomeric opsins was specifically detected in photoreceptors located in the oral tentacles, radial nerves, and tube feet in *Holothuria forskali*, a European species of the order Holothuriida, suggesting well-developed extraocular photoreception in these animals. Our investigation also focused on the order of Apodida, a group of sea cucumbers with elongated bodies and lacking tube feet, in which some researchers have reported the presence of visual structures at the root of their tentacles (Berrill 1965 ; Yamamoto et Yoshida 1978). Our study demonstrated the expression of a ciliary opsin in the photo-sensory neuroepithelial structures of the tropical species *Euapta godeffroyi*, which form eyespots at the base of each tentacle (figure 1A, B). A similar expression of opsins in the baso-tentacular nerves was observed in the small European burrowing species *Oestergrenia digitata*. Additionally, we detected opsins in the sensory cupules, which are structures located on the inner surface of tentacles and having unknown sensory functions (figure 1C, D, E). Finally, our ethological tests on three holothuroid species showed that they moved away from (*Holothuria forskali* and *Euapta godeffroyi*) or toward (*Synapta maculata*) a light source, specifically for shorter wavelengths corresponding to blue and green light. Turning the spotlights on these amazing sea cucumbers and more broadly on all echinoderms is important to better understand the mechanisms and evolution of extraocular photoreception in the deuterostome lineage.

Figure 1: Photosensitive structures of two Apodida holothurian species

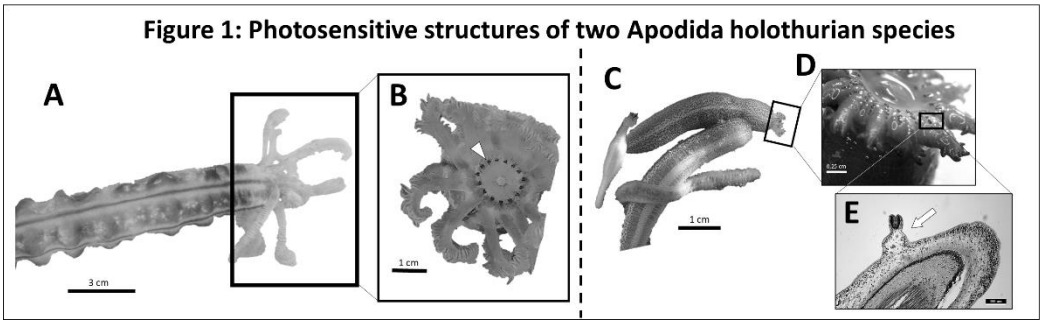

Fig1 : two types of photosensitive structures (eyespot and cupules) in two Apodida species (*Euapta godeffroyii* (A; B) and *Oestergrenia digitata* (C; D; E). A: The anterior body-part of *E. godeffroyii*; B: the peri-oral part with eyespots (one shown by arrowhead); C: Four *O. digitata*; D: Focus on the inner face of oral tentacles; E : histological cross-section of a tentacle with one sensitive cupule shown by the white arrow