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Original Article

Extravisual opsins in the blind shrimp *Creaseria morleyi*: presence and expression

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ABSTRACT

The presence of a long-wavelength sensitive (LWS) opsin gene was demonstrated in the stygobitic crustacean *Creaseria morleyi* (Creaser, 1936) by PCR readings from genomic DNA. In order to find the expression of this gene in extraocular tissue, shrimps were collected and placed in a tank to expose them to light/dark conditions for a period of 72 hours, and immediately after, sacrificed and sampled for RNA in the eyes, cephalothorax, abdomen, and sixth abdominal segment plus uropods. The transcripts of the LWS opsin gene were found in the eyes and abdomen of individuals exposed to light. The expression of these opsins could be involved in extravisual functions such as synchronization of their biological processes with environmental cycles related to diurnal vertical migration.

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Photopigment, phototransduction, stygofauna.

INTRODUCTION

The opsins are a group of G protein-coupled receptors (GPCR), which are characterized by their capacity for photon absorption (Terakita et al., 2012). They are found on the membrane of photoreceptor cells of animals, where they capture light energy and translate it into different physiological responses; among them, an electrochemical signal which is the first step in the visual transduction cascade (Shichida and Matsuyama, 2009).

The opsins contain a protein, of a variable amino acid residue number with molecular masses of 30-50 kDa (Terakita, 2005). These form seven transmembrane α-helix regions connected by cytoplasmic and extracellular loops (Peirson et al., 2009; Lledó-Riquelme et al., 2010); that are distinguished from other GPCRs by the binding of a retinal-type chromophore (Terakita, 2005; Peirson et al., 2009).

The degree of specialization of the structures that detect light enable organisms to perform different photoreception types. Extravisual photoreception (EP) refers to the detection of the quantity of light from the environment allowing them to perform processes like phototaxis or physiological functions and behaviors related to the day phase (Alexandra and Cronin, 2016). EP can be present even though the organism lacks true eyes, such as in the case of photoreceptor cells of the pineal gland in birds or the ocelli in arthropods (Fu et al., 2005; Santillo, 2006).

Photoreceptors in crustaceans have been described in the eyes, caudal photoreceptors, and intracerebral ocelli (Meyer, 2001). Likewise, opsins with extravisual functions have been identified such as the short-wavelength sensitive opsin (SWS) and the LWS in the abdominal ganglion of the crayfish *Procambarus clarkii* (Girard, 1852); and the peropsin in the abdomen and cerebral ganglion of the Antarctic krill *Euphausia superba* Dana, 1850 (Kingston and Cronin, 2015; Biscontin et al., 2016).

Creaseria morleyi (Creaser, 1936) is a stygobitic crustacean that could possess opsins with extravisual functions. It is endemic to the Yucatán Peninsula and inhabits submerged cave systems accessed through sinkholes, locally known as cenotes (Hobbs et al., 1977). In this subterranean environment, individuals have developed multiple adaptations to the lack of light, and oligotrophic conditions. Their bodies are translucent through loss of pigments and with greatly reduced eyes (Alvarez and Illife, 2008; Botello and Alvarez, 2010; Benítez et al., 2020). Nevertheless, in cenotes that receive light at the entrance area, individuals have vestigial eyes and perform a vertical migration that seems to be synchronized with the environmental light. During daylight hours, the shrimps are more abundant in the depths, while during the night they move closer to the cenote entrances (Chávez-Solís, 2015; Chávez-Solís et al., 2018). This kind of behavior, typically synchronized with environmental light, is shown by other species, including some planktonic crustaceans (Forward, 1976; Wallace et al., 2010). Thus, the question arises whether *C. morleyi* has opsins that perform extravisual functions and enable it to synchronize with the environment. Therefore, the aim of this project is to demonstrate the presence of opsin genes and show their expression in various body regions of *C. morleyi*.

MATERIALS AND METHODS

Collection and preservation of specimens

Four specimens of *Creaseria morleyi* were collected alive from the Noh-Mozon, Tecoh, Yucatán State, México, during October 2017. They were transported to the Unidad Multidisciplinaria de Docencia e Investigación de la Facultad de Ciencias, UNAM, located in Sisal, near Mérida, Yucatán.

To demonstrate the expression of opsins, two test individuals were exposed directly to light, while two control specimens were kept in the dark. For

this purpose, four 14 L tanks were constructed with constantly circulating water taken from the Noh Mozón cenote. A RADION XR15W G4 PRO lamp was placed above two tanks to emit white light 24 hours a day. The other two tanks were completely covered so that these individuals remained in total darkness.

The experiment was maintained for three days with amphipods and anostracans (*Artemia salina* (Linnaeus, 1758)) provided for nourishment.

Extraction, amplification and sequencing of DNA

Degenerate primers were designed to detect the long-wavelength opsins (LWS) by PCR; OpnL WCrustF: 5'-CTGGTACCARTWYCCYCCCATG-3', and OpnLWCrustR: 5'-GAACACCGTACCCCAGATGG-3'. The Forward primer binds to the initial amino region and the Reverse to the seventh transmembrane segment. The oligonucleotides were designed based on conserved regions between amino acid sequences and nucleotides of LWS opsins from decapods *Litopenaeus vannamei* (Boone, 1931), *Cambarellus schufeldtii* (Faxon, 1884), *Cambarus ludovicianus* Faxon, 1884, *Orconectes australis* (Rhoades, 1941), *Cambarus maculatus* Hobbs and Pflieger, 1988, *Orconectes virilis* (Hagen, 1870), *Procambarus clarkii*, *Procambarus seminolae* Hobbs, 1942, and *Procambarus orcinus* Hobbs and Means, 1972. The sequences were visualized using BioEdit software (Hall, 1999) and aligned with Clustal W (Thompson et al., 1994) and MAFFT (Katoh et al., 2002). The DNA was extracted from shrimp abdominal muscular tissue with a commercial kit DNeasy ® Blood and Tissue by QIAGEN ®. Amplification reactions consisted of 32 cycles of denaturation at 94 °C for 60 s, annealing at 53 °C for 45 s and elongation of DNA at 72 °C (GoTaq Green Master Mix, Promega). The PCR products were purified with the Wizard ® SV Gel kit and PCR Clean-Up System (Promega). They were inserted in the pGEM ®-T Easy vector (Promega) and the resultant plasmid constructions were propagated in *Escherichia coli* using One Shot TOP Electrocomp by Thermo Fisher Scientific. Finally, they were sequenced in both directions through automatic sequencing by Molecular Cloning Laboratories (MacLab) and the obtained sequences were edited with the BioEdit software. Homologies were analyzed with BLAST (Camacho et al., 2009), to determine whether the obtained nucleotide sequences corresponded to opsin genes. Additionally, cluster analysis of genetic distance was performed with the Unweighted Pair Group Method with Arithmetic Mean UPGMA in MEGA X software (Kumar et al., 2018), with branch support of the resampling data method of Bootstrap with 1000 replicates.

RNA extraction and expression of the opsin genes

The expression of opsin genes by *C. morleyi* in response to different light conditions was investigated by RT-PCR analysis. Given the low accessibility of the species and the difficulty to keep animals in captivity we used the tissue from two specimens pooled for each experimental condition. First, messenger RNA isolation was performed by the Trizol® method (Chomczynski and Sacchi, 1986) from four regions of the body: eyes, cephalothorax, abdomen and sixth abdominal segment/uropods (6A+U). Then, the DNA present in the sample was digested employing the Thermo Scientific DNase I, RNase-free kit by Thermo Fisher Scientific and the synthesis of complementary DNA carried out using the High-Capacity cDNA Reverse Transcription Kit by Applied Biosystems. Thereafter, cDNA was employed as a template for PCR with primers OpnWCrustF and OpnWCrustR as indicated above.

RESULTS AND DISCUSSION

Opsin detection and identification

The *Creaseria morleyi* 848 pb opsin fragment was cloned, sequenced (GenBank accession number MT265680) and homology analysis was performed with BLAST. The sequence shows homology with LWL of crustaceans with an identity greater than 90% with the opsins of the crayfish *Cambarellus shufeldtii* (Faxon, 1884) (Accession number AF003544), *Orconectes virilis* (Accession number AF003545), and *Procambarus clarkii* (Accession number S5384), among others.

The UPGMA cluster analysis located the *C. morleyi* opsin in the long wavelength sensitive opsin of crustaceans (Fig. 1). The amino acid sequence

showed some of the important elements for the GPCRs structure and the phototransduction process (Gartner and Twoner, 1995; Townson et al., 1998): two cysteine residues in the first and second extracellular domains, which are responsible for the disulfide bond stabilization, a glutamic acid residue serving as a counterion of a Schiff base in the second transmembrane domain (Terakita et al., 2004), and the motifs QAKKM and DRY which are potential sites of G protein binding in the third and second intracellular domain respectively (König et al., 1989) (Fig. 2). Also, the *C. morleyi* opsin has two residues (tyrosine and serine in the third domain) that are functionally related to the LWS/MWS spectral sensitivity (Fig. 3), that allow this protein to bond to a chromophore in cephalopods and arthropods, according to protein modeling (Chang et al., 1995).

The LWS opsin genes have been detected previously from the genomes of several Mysida including *Archaeomysis grebnitzkii* Czerniavsky, 1882, *Holmesimysis costata* (Holmes, 1900), *Mysis diluviana* Audzijonyte and Väinölä, 2005, and *Neomysis americana* (S.I. Smith, 1873), and also in the Euphausiacea *Euphausia superba* (Porter et al., 2007). Although it would not be expected for stygobitic shrimp such as *C. morleyi* to express opsins, nor to perform visual functions, the presence of an opsin gene in its genome is entirely not surprising since those genes are found and expressed in other phylogenetically related crustaceans with epigean habits such as *P. clarkii*, *Litopeneaus vannamei* and *Macrobrachium nipponense* (De Haan, 1849) (GenBank: Access number DQ825437; Kingston and Cronin, 2015; Li et al., 2018).

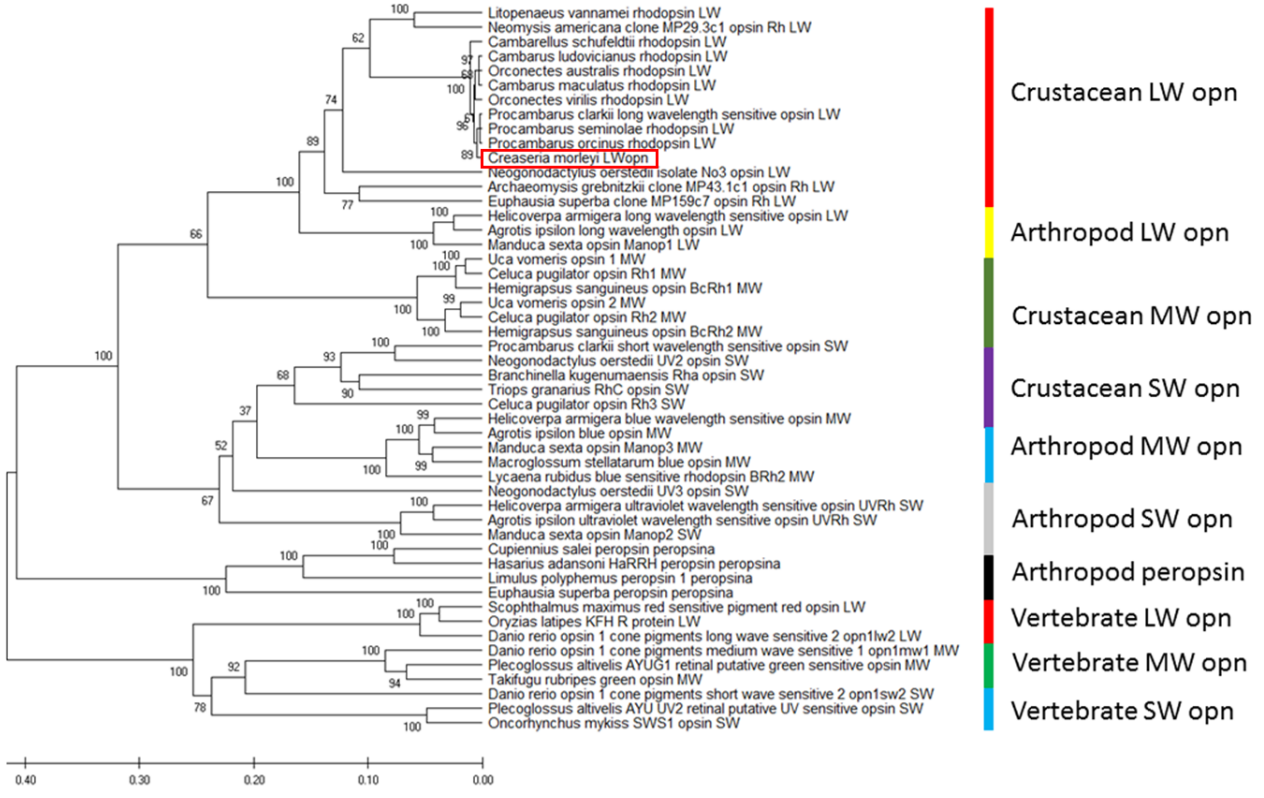

Figure 1. Opsins cluster diagram. UPGMA clustering diagram with bootstrap values of 1000 replicates for each node. The lower bar indicates the genetic distance. The *Creaseria morleyi* opsin is in the red square, in the group of the long wavelength sensitive opsins of crustaceans. LW: long-wavelength sensitive opsin; MW: medium-wavelength sensitive opsin; SW: short-wavelength sensitive opsin; opn: opsin.

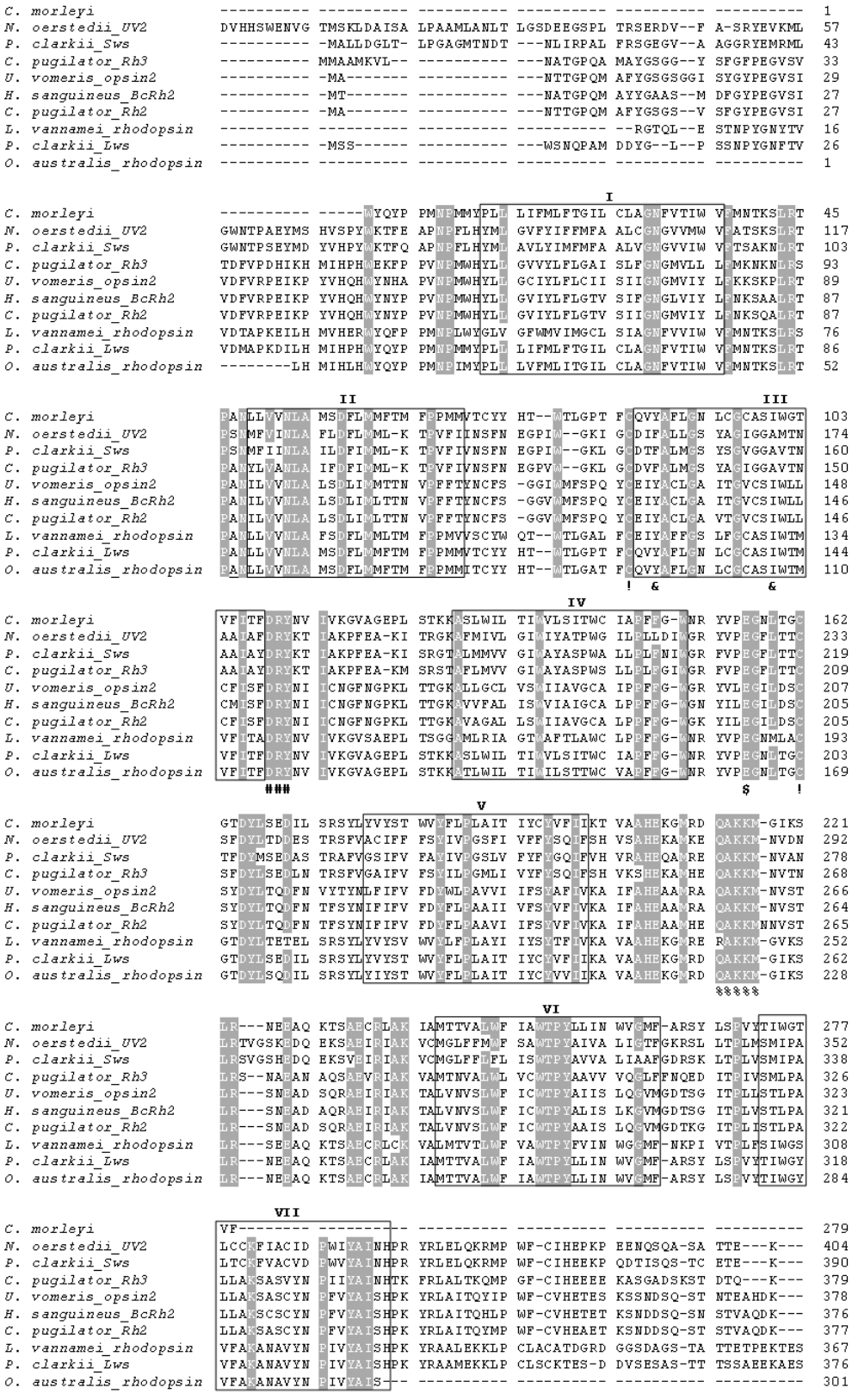

Figure 2. Amino acid sequence alignment of the *Creaseria morleyi* long wavelength opsin and other crustacean opsins. The conserved residues are shadowed, and the gaps indicated by dash (-). Amino acid numbers per individual sequence are indicated on the right. The transmembrane helix is shown as roman numeral and enclosed in squares. The "DRY" and "QAKKM" motif, which are important for the union to the G protein are shown by # and % symbols respectively. The cysteine residues responsible of the disulfide bond stabilization are indicated by ! symbol. The glutamic acid that acts as a counterion on the Schiff base is shown as $. The Y and S amino acids with the LWS/MWS spectral sensitivity are shown with the symbol &.

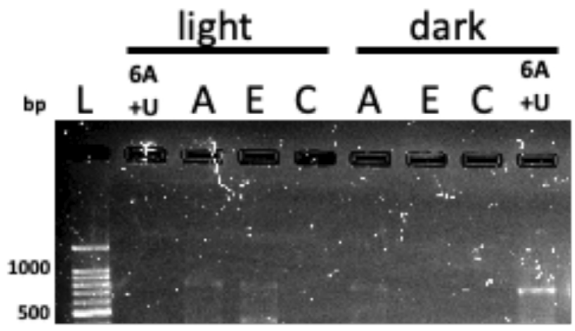

Figure 3. Electrophoresis of cDNA of amplified long wavelength opsin products by PCR from cDNA obtained by RT-PCR performed on RNA samples of *Creaseria morleyi*. cDNA from the sixth abdominal segment plus uropods (6A+U), abdomen (A), eyes (E), and cephalothorax (C), showed PCR products using specific primers for long wavelength opsin 1. The smallest band shown from the DNA ladder (L) is 500 bp, a 100 bp distance separates each band between the band corresponding to 500 bp ant and the band of 1000 bp. The expected amplicon was of 848 pb and can be observed in eyes and abdomen in continuous light condition, and in abdomen and in sixth abdominal segment plus uropods in total darkness condition.

Opsin expression localization

To determine the LW expression on different tissues and light exposure conditions from *Creaseria morleyi*, RT-PCR was performed using the eye, cephalothorax, abdomen and the sixth abdominal segment plus uropods (6A+U) RNA. The LWL detected on the genome was expressed in the vestigial eyes and abdomen of one of the individuals exposed to continuous light. Regarding *C. morleyi* specimens kept in total darkness, LWL was expressed in the abdomen and 6A+U (Fig. 3).

The existence of an extraocular photoreceptor in decapods was demonstrated for the first time by Prosser in 1934. In his study on the action potential in the astascid *Procambarus clarkii*, Prosser (1934) described the activity of a photoreceptor cell located in the sixth abdominal segment. This photoreceptor is part of the pacemaker system for circadian rhythm that includes the supraesophageal ganglion and eyes and participates in the synchronization of the circadian rhythm of locomotion in decapods with day and night cycles (Rodriguez-Sosa et al., 2012).

The opsin expression, of both LWS and SWS opsin in the retina and in abdominal photoreceptors, has been observed in *P. clarkii* using immunohistochemical techniques during the search for opsins in the sixth ventral ganglion and along the central nervous system. It was found that the LWS and SWS opsins are expressed in the nerve fibers that extend from the brain throughout the central nervous system. This leads to the conclusion that these two photopigments are involved both in retinal vision and in extravisual functions by *P. clarkii* (Kingston and Cronin, 2015) among other decapod crustaceans such as *Cherax destructor* Clark, 1936, *Orconectes virilis*, *Panulirus interruptus* (Randall, 1840), *Penaeus setiferus* (Linnaeus, 1767), *Crangon septemspinosus* Say, 1818, *Upogebia pugettensis* (Dana, 1852), and *Galathea strigosa* (Linnaeus, 1761) (Kingston and Cronin, 2016).

Our data show for the first time that *Creaseria morleyi*'s genome contains a gene sequence corresponding to at least one type of LWS opsin. This opsin is expressed in the eyes, abdomen and 6A+U of shrimp, where, in the last case, its expression is modified by light exposure. The question arises whether, like in other crustaceans, the expression of these opsins could be involved in diverse extravisual functions such as the synchronization of their biological processes with environmental cycles.

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ADDITIONAL INFORMATION AND DECLARATIONS

Author Contributions

Conceptualization and Design: AB, JAPL, MAR, NS, REMC. Performed research: JRPC, NS. Acquisition of data: JRPC, NS. Analysis and interpretation of data: AB, JAPL, JRPC, MAR, REMC. Preparation of figures: JRPC, MAR, REMC. Writing - original draft: JRPC. Writing - critical review & editing: AB, JAPL, MAR, NS, REMC.

Consent for publication

All authors declare that they have reviewed the content of the manuscript and gave their consent to submit the document.

Competing interests

All authors declare that they have no conflicts of interest.

Data availability

The LW opsin sequence of *Creaeseria morleyi* (accession number MT265680) used in the present study is available at GenBank.

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Study association

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Study permits

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