v. 2, n. 1, 2022

International Journal of Biological and Natural Sciences

OCULAR STRUCTURE OF THE GHOST CRAB *Ocypode quadrata* (Fabricius, 1787)

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Abstract: Arthropods have composed eyes that differ in their cellular structure due to their diurnal or nocturnal habits, naming the eyes of diurnal habits organisms as apposition type and those of organisms of nocturnal habits as superposition type. However, there are species with twilight habits, such as the ghost crab *Ocypode quadrata*, which suggests that the cellular structure of the eye of this species could be different. In order to determine the type of eye, ocular tissue samples were analyzed of *O. quadrata* using histological techniques and electronic microscopy. It was structurally appreciated that each ommatidium consists of four layers of tissues: the cornea, the lens, the rhabdom and the basement membrane. In the cornea three sections are appreciated: the cuticle, the corneogenous cuticle, and the distal pigment cells. The crystalline contains the interomatidial pigment, the retina cellular pigment and the retina cells. The rhabdom is made up of the rhabdomeric cells and proximal pigment cells, and finally the basement membrane that supports the ommatidium. When analyzing and comparing the structural characteristics of the ghost crab eye with those of diurnal and nocturnal organisms, both, structural similarities and differences were found, resulting in an intermediate ocular structure, which is why it was called the Interposition type. This structure allows *O. quadrata* to respond to intermittent changes in its environment like: aquatic-terrestrial and light-darkness.

Keywords: Pigment Cells, Cornea, Cone, Ommatidium and Rhabdoma

INTRODUCTION

According to their habits, the compound eyes of the arthropods, have been classified in two types: apposition, present in diurnal organisms whose eyes are exposed to the light, and of superposition, of nocturnal organisms better for darkness (Ruppert and Barnes, 1996).

The compound eyes of apposition are constituted by a set of ommatidiun, that anatomically have hexagonal facets, omatrichias in the surface, and the crystalline formed by four cells. The Rhabdoma is composed by seven rabdomeros and one retinular cell occupying the central part (Hariyama *et al*., 1986; Hariyama *et al*., 2001). The superposition eyes act as light collectors integrating an image on all the working area of the photoreceptors (Wald, 1968; Cronin, 1986; Cronin and Marshall, 2001). The advantage of a superposition eye is its greater sensitivity to light at low intensities (Warrant *et al*., 1996; Warrant, 1999; Warrant and Nilsson, 2006). The studies on the compound eyes types have been carried out especially in insects and some crustaceans (Ruppert and Barnes, 1996), the latter being of nocturnal, aquatic and terrestrial habits such as prawns and shrimp, and a semi-terrestrial - coastal crustacean (*Ligia exotica*) (Aréchiga and Huberman, 1980; Aréchiga *et al*., 1989; Mishra, 2013; Chen and Hua, 2016). On the other hand, there are few studies on the type of eyes that crepuscular crustaceans present.

The ghost crab, *Ocypode quadrata* is a species able to tolerate extreme climatic differences in the coastal zones of the American continent between the latitudes 30° and 45° North or South, during very cold winters it tends to winter, considering it as a nocturnal organism (Wolcott, 1978; Alberto & Fontoura, 1999). In the temperate zone (between the latitudes 30° North and the Equator) the organisms are always active (Wolcott, 1978; Alberto & Fontoura, 1999) and, based on their behavior, they have been considered as twilight active (Valero-Pacheco *et al*., 2007). During this period, it supports different luminance intensities during a 24 hours cycle, being active during 19 hours, of which nine hours are diurnal and ten nocturnal, this behavior shows the degree of plasticity as a response to environmental changes like temperature and light (Valero-Pacheco *et al.*, 2007).

Another characteristic of this species is their requirement to enter to the water in order to obtain the dissolved oxygen, which is why it is considered semi-aquatic and semi-terrestrial, since it can carry out its physiological functions in both environments (Wolcott, 1978; Barros, 2001; Valero-Pacheco *et al.*, 2007). The present study describes the eye's cellular structure of the ghost crab *Ocypode quadrata* by means of histological techniques and electronic microscopy. The results showed a type of eye different to the apposition or superposition types, showing how this structure is an adaptation to the behavior of this crab.

MATERIAL AND METHOD

The ghost crabs, *O. quadrata*, were collected at Playa Paraiso, which is part of the Municipality of Actopan, Veracruz, Mexico, located in the coordinates Latitude: 19º 12 '30 "N and Longitude: 96º 07' 59" W (INEGI 2016). Fifty adult crabs were collected, greater to 23 mm following other works methodology (Alberto & Fontoura, 1999; Negreiros-Fransozo *et al.*, 2002; Valero-Pacheco *et al.*, 2007), during the twilight hours. After being captured, they were immediately desensitized with ice, and fixed in Bouin medium. Later they were taken to the Hydrobiology Laboratory of the Faculty of Biology of the Veracruzana University.

The eyes of all the individuals collected were removed by means of surgery with the help of a stereoscopic microscope. Sixty percent of the extracted eyes were processed by means of a routinary histological technique, dehydrating the tissue and passing it through gradual alcohols, from 70% up to the absolute alcohol. Once the tissue was dehydrated, it was included in paraffin and cuts up to 10 microns were made in crank microtome (Reichert Mark Jung) staining them with Hematoxylin and Eosin (H&E) (Luna, 1958). The tissues were observed and analyzed in a compound microscope (Leica S6D brand), and photographs were taken using a camera Leica DM500.

The other 40% of the eyes were transferred to the Microscopy Laboratory of the Institute of Biology of the National Autonomous University of Mexico (IB UNAM), where the scanning electron microscopy technique was performed. For this analysis, the tissues were dehydrated by means of alcohols at different concentrations up to absolute alcohol. Later, the tissue is brought to a critical point by means of CO_2 and finally the tissue is covered with a thin slice of gold using cathodic pulverization (EMI Tech, K550X). The resulting tissue was analyzed and photographed using the Hitachi microscope model SU1510. (Luna, 1958).

RESULTS

The eye structure of the ghost crab *O. quadrata*, is formed by a set of omatidia, and each ommatidium is integrated by four tissue layers if viewed from the outside to the interior of the eye. The first layer, in contact with the outside, is the cornea, which has a differentiated concave tissue of hexagonal, slightly flattened in the base and with small ridges that divide each ommatidium (Fig. 1).The cornea is made up of laminated tissue divided into three sections: the external section (I) is thin and translucent, hexagonal in shape allowing light flux; the intermediate section (II) is laminated in the shape of a plate, giving to it the convex shape, and the internal section (III) which is also laminated and is the connection with the crystalline (Fig. 2).

The second layer that is observed is the crystalline, which is constituted by four crystalline cells that adhere to the internal

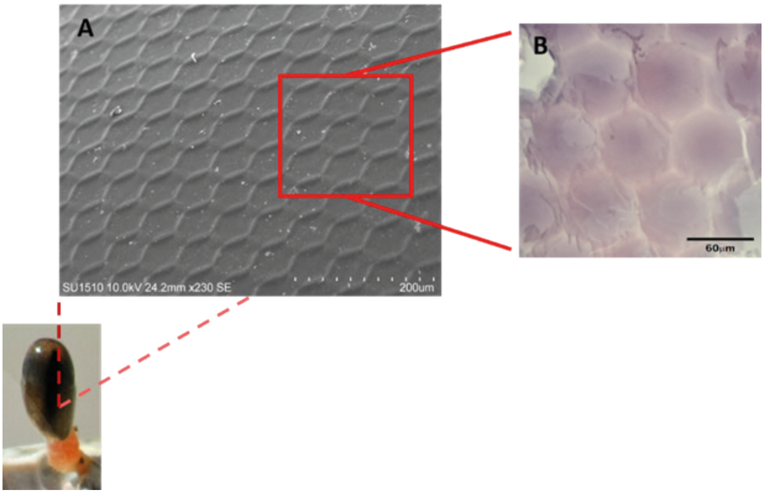

Figure 1. Compound Eye of Ocypode quadrata, **A)** Microphotography of the corneous, scanning electron microscopy **B)** Court of the cornea to 10 µm with Technical H and E Vista to 40 X.

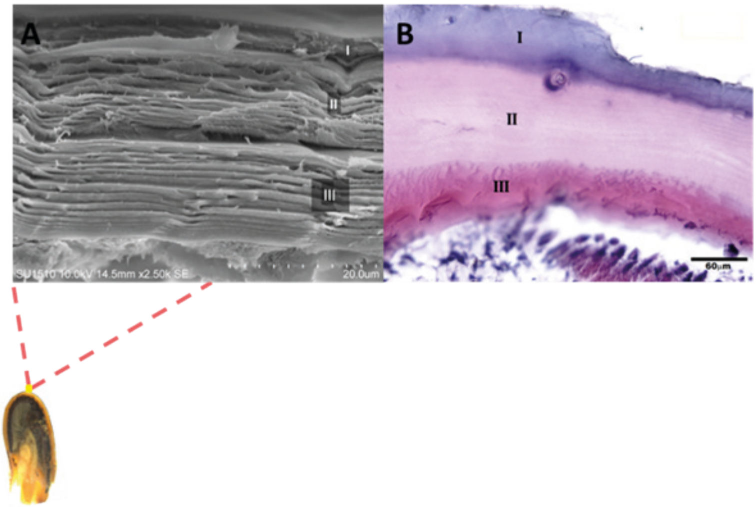

Figure 2. Sagittal section of 10 µm of the cornea of the eye compound of Ocypode quadrata, **A)** Corneous conformed of three layers: External (I) Intermediate (II) and Internal (III), by electronic microscopy of sweeping and **B)** Corneous conformed of three layers by Technique H & E seen at 40 X.

layer of the cornea and elongate decreasing its thickness or diameter, this gives the lens a cone-like appearance, which in the present work will be called cone-shaped crystalline (Fig. 3). Between each cone-shaped crystalline there is an empty space, which appears as a clear area that will be denominated naked. In a cross section at the cone-shape crystalline, it is observed the presence of grains in the exterior and interior, which could correspond to pigment grains and oil drops, respectively (Fig. 3D).

In the third layer, from the exterior to the interior of the eye, the cells of the retinular cells that form rhabdom can be observed (fig. 4). The rhabdom is constituted by four, six and seven retinular cells, which in their union form an intermediate tube-like space where small, relatively long "bars" of microvilli exist, composed by the central face of the rhabdomeric bristles that form the body of the rhabdom. The retinular cells are elongate and grouped in form of bouquet in a parallel way and ending in the fenestrated membrane.

Adhered in the external wall of the rhabdom, pigment grains are observed. These pigment grains, based on the images and observation of the cuts we can say that they migrate in an ascending and descendant way through the tissue in the superior of it since it is noticeable pigmentary cells that divide to the cone-shape crystallin cells and rhabdom (fig. 4).

Finally, the fourth layer and innermost one, corresponds to the fenestrated membrane (Fig. 5), which forms a base with holes that serve as an assemble for each of the omatidia. Within these orifices, granules can be seen these are called screening pigment, which connect the rhabdom with the dendrites, that is why these granules are considered dendritic buttons. In the posterior part of the fenestrated membrane (Fig. 5), dendritic assemblages arise, which travel to the central part of the eye and reach the region of the tapetum, which is constituted by muscle tissue and is surrounded by pigment granules. To the interior of the tapetum some somas exist, all these, as an ensemble constitutes the optical nerve in charge to sending the nervous impulses to the cerebral ganglion.

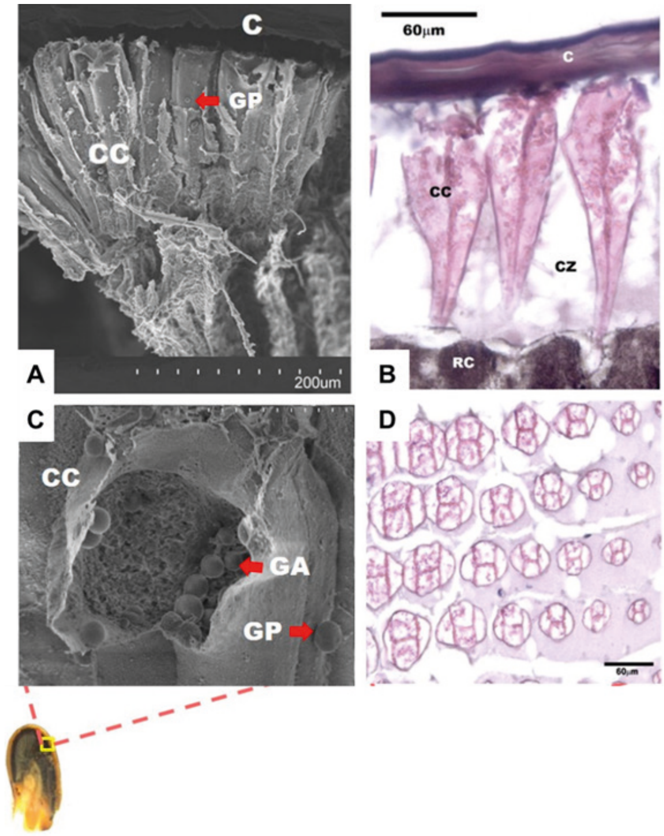

Figure 3. Cross-sectional and longitudinal section 10 mm of the crystalline in form of cone (CC) of the eye of Ocypode quadrata, **A)** Cross section, cone-shape crystalline, scanning electron microscopy, **B)** Cross section, cone-shape crystalline, H & E technique at 40 X. **C)** Longitudinal section, cone-shape crystalline scanning electron microscopy: pigment granules (GP) and oil droplets (GA) inside the cone-shape crystalline, and **D)** Longitudinal section, of the cone-shape crystalline: the cornea (C), the cone-shape crystalline (CC), the clear zone (CZ) and the cellular retinal (CR) H & E technique seen at 40x.

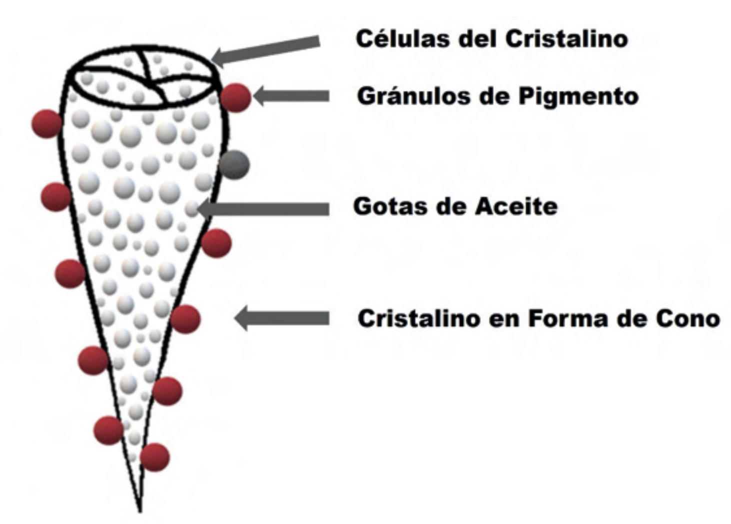

Figure 3a. Scheme representing the cone-shape crystalline, which is constituted by four cells of the crystalline. From the observations made in the histological cuts.

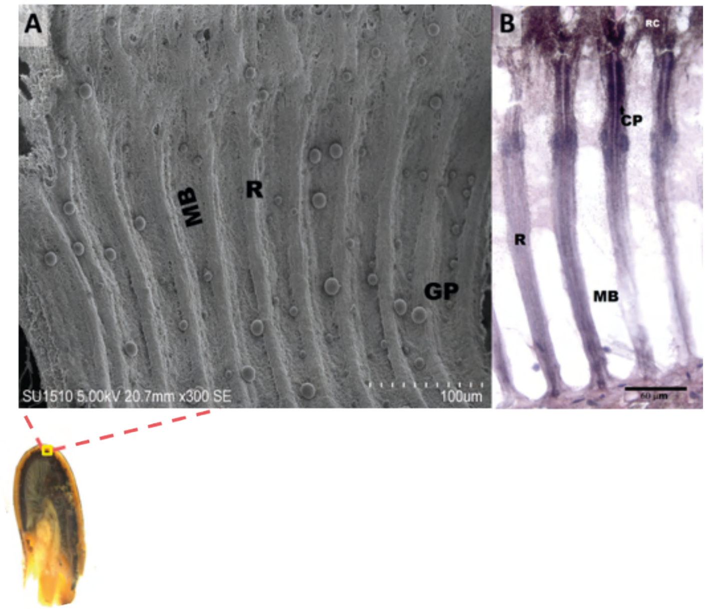

Figure 4. Cross section of 10 mm of the Rhabdom of the eye composed of Ocypode quadrata. **A)** is observed the rhabdoma (R), the basement membrane (MB), the pigment granules (GP) by Scanning Electron Microscopy and **B)** the Rhabdoma is observed together with the cellular retinae (CR) and pigment cells (CP), by Technique H & E View at 40 X.

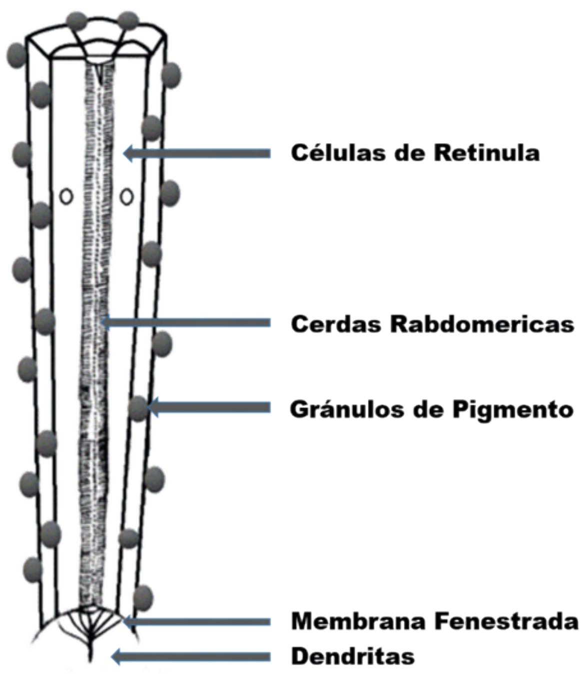

Figure 4a. Scheme or diagram of the Rhabdom of the eye of Ocypode quadrata from the observations of the histological cuts, where it is observed the Retinule Cellular (RC), the rhabdomeric bristles (CR), the fenestrada membrane (MF), the pigment granules (GP) and the dendrites (D).

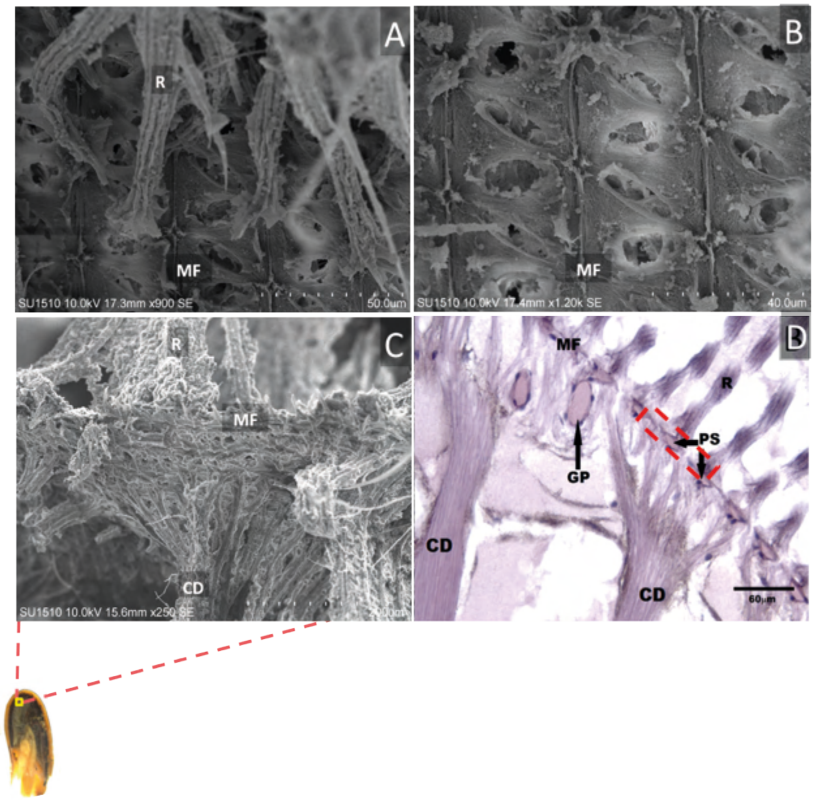

Figure 5. Sagittal cut of 10 μm of the Fenestrated Membrane of the eye composed of O. quadrata **A, B, C)** Fenestrated Membrane (MF), Rhabdom (R) and Dendritic Ensemble (CD), by Scanning Electron Microscopy and **D)** Pigment granules (GP) and proximal pigment (Screening) (PS), by Technique H & E seen at 40 X.

DISCUSSION

The results showed that the cellular structure of the ghost crab (*Ocypode quadrata*) eye presents characteristics of the two types of compound eyes described for nocturnal and diurnal arthropods, that is, overlapping and apposition, respectively. Therefore, our findings support the hypothesis that the ghost crab, due to its twilight and semi-aquatic habits, will exhibit a compound eye with cellular structural characteristics of both eyes types (apposition and overlap), considering it as an intermediate eye type and denominating it as a Interposition compound eye. This structure demonstrates that the ocular structure of this species is an adaptation to the changes between an illuminated and dark environment, as well as to alternating its activities between the aquatic and terrestrial environment.

The fact that the ghost crab has an eye that combines features of both, an apposition eye and an overlapping eye, reinforces what was proposed by Land (1981), Cronin (1986) and Torralba & Pérez (1997), who refer to the existence of species that have a third type of eye, or modifications in basic characteristics such as an adaptive response to a medium with contrasting light changes. Such is the case of the ghost crab, a species with twilight habits, which supports different luminance intensities during a 24-hour cycle, being active for 19 hours, of which nine hours are during the daytime period and ten during the nighttime period (Valero- Pacheco *et al.*, 2007). Also, its semi-aquatic and semi-terrestrial habits force thecrab to respond efficiently to wavelengths changes in a terrestrial and an aquatic environment (Wolcott, 1978; Barros, 2001; Valero-Pacheco *et al.*, 2007).

The first structure that constitutes the ommatidium of the eye of the ghost crab is the cornea. This is the window of the facet through which the light enters the ommatidium and gives protection to the internal tissues (Bernard & Miller, 1968). The cornea of the ghost crab eye, like in other arthropods, exhibits a differentiated tissue composed of chitin, the first layer being the one that allows refraction and transmission of light into the ommatidium (Bernard & Miller, 1968).

The corneal surface of the eye of the ghost crab lacks the inter-omatidial bristles described in the compound eyes of other nocturnal, twilight invertebrates or in diurnal butterflies, which present a great amount of these structures (Bernard, 1967). Instead, it has a convex cornea that exhibits ridges in the terminal part between each ommatidium. The lamination in the division of the intermediate and internal layers of the cornea, the convex shape of the ridges in the terminal portion of each ommatidium are structural features not described in compound eyes of other arthropods.

The cornea seen from outside, presents a hexagon form that constitutes an omatidial facet, also documented in Diptera according to Bernard & Miller (1968) who report that the omatidial facets can be colored individually and grouped in clusters or rays which can be red, orange, yellow, green or blue.

The cornea of the eye of *O. quadrata* does not present any microvilli in the ommatidium or in the facets, unlike what authors like Trujillo-Cenoz & Bernard (1972) and Land (1993) mention for the long-legged flies (Dolichopodidae) that, in omatidia, a vertically and horizontally oriented microvillus are present. These are the first elements of a system that improves the color where the facets with vertical microvilli would be good for the detection of prey against shining surfaces and horizontally polarized (Land, 1993). Through field observations of *O. quadrata* it is possible that other structures are performing the same functions that the microvilli in the omatidia of long-legged flies, since it efficiently detected its prey against shiny surfaces.

It is known that, in the Cornea, the alternating layers of low and high cuticle intervene in the refractive index and that in each interface a certain fraction of incident light is reflect again, tolerating a constructive or destructive interference with respect to the light of other layers. In the cornea of the eye of *O. quadrata*, three layers are differentiated, which according to Land (1972), could be generating interference during light penetration (photons). This supports what is proposed by Bernard & Miller (1968), who mentioned that the reflected light color depends on the optical thickness of the layers and the angle of view or illumination of the colored regions, those that denominate reflectors. However, in *O. quadrata* it is observed that the intermediate and internal layers are laminated as well, for that reason it is still a question on how these layers are afecting the amount and the wave length allowed to arrive at the crystalline. Due to the lack of research in this area, it should be important to study in detail the reflicting light of the *O. quadrata* eye as well as the viewing angles, to be able to determine which is the perceived light wavelength.

From the outside in, the second structure identified in the eye is the cone-shape crystalline, which differs from the crystalline of the apposition eye described in the *Scaphidium japonum* beetle, which lacks pigment cells around the crystalline (Mishara, 2013). Likewise, the eye of the crab *O. quadrata* lacks corneagenic cells observed in the crystalline of the superposition eye of the species of *M. heliconiaria*, (Hallberg & Elofsson, 1989; Meyer-Rochow, 2001), on the contrary, it exhibits a clear zone between each crystalline cone. This same condition has also been documented by Meyer-Rochow (1977), in the superposition eye of the *Sericesthis geminata* beetle, which is devoid of distal pigment cells.

Externally, between the cone-shape crystallines, some pigment grains are identified. Its function could be related to the absorption of photons by the visual pigment molecules (rhodopsin) contained in them (Labhart and Nilsson, 1995), as has been described in arthropods such as in the *Scaphidium japonum* beetle (Mishara, 2013). Inside the cone-shape crystallines of *Ocypode quadrata*, granules were found that can fulfill the function of oil drops, however, it is important to analyze the function of these granules.

In *O. quadrata*, the rhabdom is constituted by four, six and seven retinal cells, which in their union form an intermediate space in the shape of a tube, where small "bars" relatively long of microvilli can be found, conformed by the central face of the rhabdomeric bristles that shape the body of the rhabdom. These are visualized as elongated, aligned structures and are receptors with membrane systems that house the photosensitive layer. As in the eye of apposition in which the rhabdom is formed by five or more cells of retinule, which in their central position have specialized stripes that participate in the luminance transduction, so because of this, the rhabdom is a structure of light, generally of all the sensorial cells (Wolken &Gallik, 1965; Meyer-Rochow, 1981; Gokan, *et al*, 1998; Gokan &Meyer-Rochow, 2000; Meyer-Rochow & Lau, 2008 & Fischer *et al.,* 2014). >On the other hand, in the superposition eye it is observed the rabdoma as a group of contracted cells of retinal, with specialization of membrane, being light-sensitive elements of the ommatidium and containing photopigment (Hallberg and Elofsson, 1989; Meyer-Rochow, 2001).

In the ommatidium of the *O. quadrata* eye, it was observed the presence pigment grains which, due to the images and analysis of the cuts we can deduce that they migrate in an ascending and descending way through the tissue. It is known that the apposition eye as well as the superposition one has pigment grains. In the eye of apposition these grains migrate up and down from the rhabdom edge, adhering to the tissues upon exposure to light, while in the superposition eye the pigment granules migrate up and down from the ommatidium to exit the bright area during darkness, and the bright area under illumination focuses the image and narrowing the aperture (Meyer-Rochow, 1975; Ficham, 1984, Nilsson *et al*., 1986; Warrant & Nilsson, 1998; & Mishra *et al*., 2006). Based on the observation in *O. quadrata*, it can be supposed that they behave as has been described in the superposition eyes, nevertheless, it is necessary to make a more detailed study to analyze their behavior.

CONCLUSIONS

The ommatidium histo-architecture of the *Ocypode quadrata* eye is of intermediate type, having characteristics of the superposition and apposition eyes. The eye described here showed that the cornea is segmented in three sections, which in turn are laminated. The crystalline has cone form, characteristic of a composed eye of superposition. They present internal grains or oil drops. The rhabdoma, presents characteristics of the apposition type, however, regarding the pigment granules it can be assumed that they are like the apposition type, but further analysis is required. Due to the previous characteristics, it is considered as an intermediate eye, which is label as "interposition composed eye".

ACKNOWLEDGMENT

To CONACYT for the scholarship No.714837.

To the Institute of Neuroethology of the Veracruzana University.

To the Institute of Brain Sciences of the Veracruzana University.

To the Microscopy Laboratory, of the Institute of Biology of the National Autonomous University of Mexico.

To the anonymous reviewers.

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