STRUCTURAL AND FUNCTIONAL ANALYSIS OF THE EYE OF *BIOMPHALARIA GLABRATA* (MOLLUSCA, GASTROPODA, BASOMMATOPHORA)

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1. The eye of the snail *Biomphalaria glabrata* was studied at the light microscope level. The eye is a spherical lens bathed in humor (vitreous body) and surrounded by the corneal and retinal cell layers.

2. The retina is composed of four layers: the inner photoreceptor layer close to the ocellar cavity, a pigmented layer, a nuclear layer, and the fibrous layer. The nuclear layer contains the nuclei of the supporting cells and of two types of sensory cells that are similar to those described for other gastropod molluscs.

3. Calculations of optical properties showed that the eye of *B. glabrata* is slightly hypermetropic and has limited resolving power.

4. The results are discussed in terms of the importance of visual information for the behavior of this animal.

Key words: eye, retina, *Biomphalaria glabrata*, photoreceptor cells, physiological optics, behavior.

Introduction

The structurally simple eyes of gastropod molluscs can provide information on differences in light intensity, although their ability to form images is debated. Although the eye structure of several mollusc species of this class has been known for a long time (Willem, 1892), few recent studies have been published on their physiological properties or on the role of the eyes in the behavior of these snails (Stoll and Bijlsma, 1973).

In some species, electrophysiological studies have demonstrated responses traditionally associated with ocular detection of patterns such as lateral inhibition in *Hermissenda* (Dennis, 1967; Stensaas et al., 1969) and in *Otala* (Goldman and Hermann, 1967). Also, Suzuki et al. (1979) reported that light- and dark-adapted retinas have different spectral sensitivity curves.

Optical measurements in *Littorina littorea* suggest that the eye may be able to form images on the retina in an aerial medium (Newell, 1965). Similar measurements of the eyes of *Agriolimax reticulatus* have suggested the ability to detect only changes in light intensity. These eyes are adapted to night function and are adequate for the simple orientation behavior associated with this species (Newell and Newell, 1968). The same measurements made on the eyes of *Strophocheilus* (Oswaldo Cruz and Bernardes, 1982) have suggested a higher

resolving power than those of *Helix* (Schwalbach et al., 1963) and of *Agriolimax* (Newell and Newell, 1968), although they have limited capacity for shape discrimination. In contrast Hamilton and Winter (1982) reported that *Littorina irrorata* is able to distinguish pattern orientation with untrained animals showing a statistically significant preference for vertical rather than horizontal bars.

In addition to neurophysiological and optical studies, behavioral observations have suggested that gastropods are able to perceive biologically relevant stimuli. Light-related behavioral studies on molluscs have been reviewed by Warden et al. (1940), Milne and Milne (1956) and Fraenkel and Gunn (1961).

Several studies have been published concerning the activity of *Biomphalaria glabrata* in relation to light in attempts to correlate this form of information with various aspects of the snail's behavior. These include distribution in the environment (Pimentel and White, 1959), circadian rhythm of activity (Pimentel-Souza et al., 1976, 1984; Schall, 1980; Rotenberg et al., 1988), spawning rhythm (Joy, 1971; Barbosa, 1984) and orientation reaction (Sodeman Jr., 1973; Schall et al., 1984), among others.

There is only one description of the general structure of the eye of *Biomphalaria glabrata* (Pan, 1958) but no histological or electrophysiological studies related to vision are available for this species. The objective of the present investigation is to describe the structure of the eye of *Biomphalaria glabrata* in more detail, as well as to present some of its optical properties, thus providing data that may be used to correlate the animal's behavior and its physiology.

Material and Methods

The data were obtained from the eyes of 10 adult animals (shell diameter = 15 to 20 mm) reared and maintained in the laboratory on a 12-h light/12-h dark schedule similar to natural conditions. Eyes were enucleated between 10:00 a.m. and 16:00 p.m. To obtain complete data for 10 eyes, the eyes of more than 40 animals were processed since data from a sequence of sections covering the entire eye are required. The specimens were anesthetized by "immersion" in a 0.1% nembutal solution. After 4 to 6 h they were removed from their shells, and the cephalopodal mass was placed in Helly fixative solution for Mallory (Heidenhein), Nissl and Masson staining of the eye. The material was dehydrated and embedded in a mixture of carnauba wax, beeswax and paraffin. Tangential sections (7.00 μm thick) were analyzed and photomicrographed with a light microscope (Ergaval, Zeiss, Jena) equipped with an ocular micrometer, a camera lucida and accessories for photomicrography. The morphological measurements were carried out in the eyes of 8 animals, taking the median portion of the eye as a reference plane for the measurement of total length and width, lens diameter, corneal aperture, and distance between the refractor and receptor layers.

Direct measurements of the optical properties of the eye are difficult because of its small size and intense pigmentation. Therefore these properties were investigated using a procedure developed by Oswaldo-Cruz and Bernardes (1982) for a closely related species. The calculations were based on the measurement of curvature radius and of the distance separating the refractive surfaces of a medium-sized eye (290 μm in diameter) among those included in the sample. The values of the refractive indices used were similar to those

reported by these investigators, which in turn were within the range of those reported in the literature for invertebrate eyes. We used an intermediate value (1.55) between that adopted for *Strophocheilus* (1.65) by Oswaldo-Cruz and Bernardes (1982) and that reported by Newell (1965) for *Littorina litorea* (1.45) for the refractive index of the lens.

The optical properties and resolving power of the eye were calculated using a computer program based on the procedures described by Oswaldo-Cruz et al. (1979). The data were processed with a Sector-IBM (PC-XI) computer.

Photoreceptor cells were counted using a slide projector coupled with an NU2 universal investigation microscope (Zeiss-Jena). Counting was performed on serial sections of two complete eyes using a mapping system for eye reconstruction. Each section was projected onto a microscope accessory screen, its outline was drawn on plastic transparent tracing foil and the nuclei of each receptor cell were marked. The subsequent section was projected onto another sheet superimposed on the previous drawing, and only the cells which did not overlap with those of the previous drawing were included.

Results

General eye structure

As described by Pan (1958), the eyes of *B. glabrata* are located on the dorsal surface of the body on the lateral surface of each cephalic tentacle and are surrounded by a perioptic cavity limited by a transparent cell layer. The eye is pear shaped (Figure 1), with an axial diameter of 265.00 to 308.00 μm ($\bar{x}$ = 290.00; SD = 15.22), by 206.00 to 250.00 μm ($\bar{x}$ = 210.00; SD = 25.40) and consists of cornea, lens, vitreous body, retina and optic nerve.

For the morphometric calculations the cornea was defined as the non-pigmented part of the eye wall, as proposed by Kataoka (1977) as well as by other investigators cited in his paper. The cornea (Figure 1) is about 5 μm thick in its central portion and consists of a single layer of transparent cuboidal cells. The refractive index of the cornea reported for related species varies from 1.36 to 1.38. Therefore the cornea may act as an important refractive layer when the animal is exposed to the air but not when it is in water, which has a refractive index of 1.33.

The transition between the retina and the cornea is marked by a gradual reduction in thickness of the former and by a forward inclination of the retinal components. The lens is 123.00 to 200.00 μm in diameter ($\bar{x}$ = 160.00; SD = 28.28) and is bathed by vitreous fluid, which may hold it in place, since no supporting structure was observed connecting it to the inner surface of the eye. The pupil (Figure 1) is approximately spherical and varies in diameter from 109.00 to 180.00 μm ($\bar{x}$ = 135.00, SD = 25.44).

Retina organization

The retina is formed by 30.00 to 40.00 μm thick epithelial tissue ($\bar{x}$ = 35.00; SD = 3.54) and can be more easily described when subdivided into four layers: an inner photoreceptor layer close to the ocular cavity, a pigment layer, a nuclear layer, and a fibrous
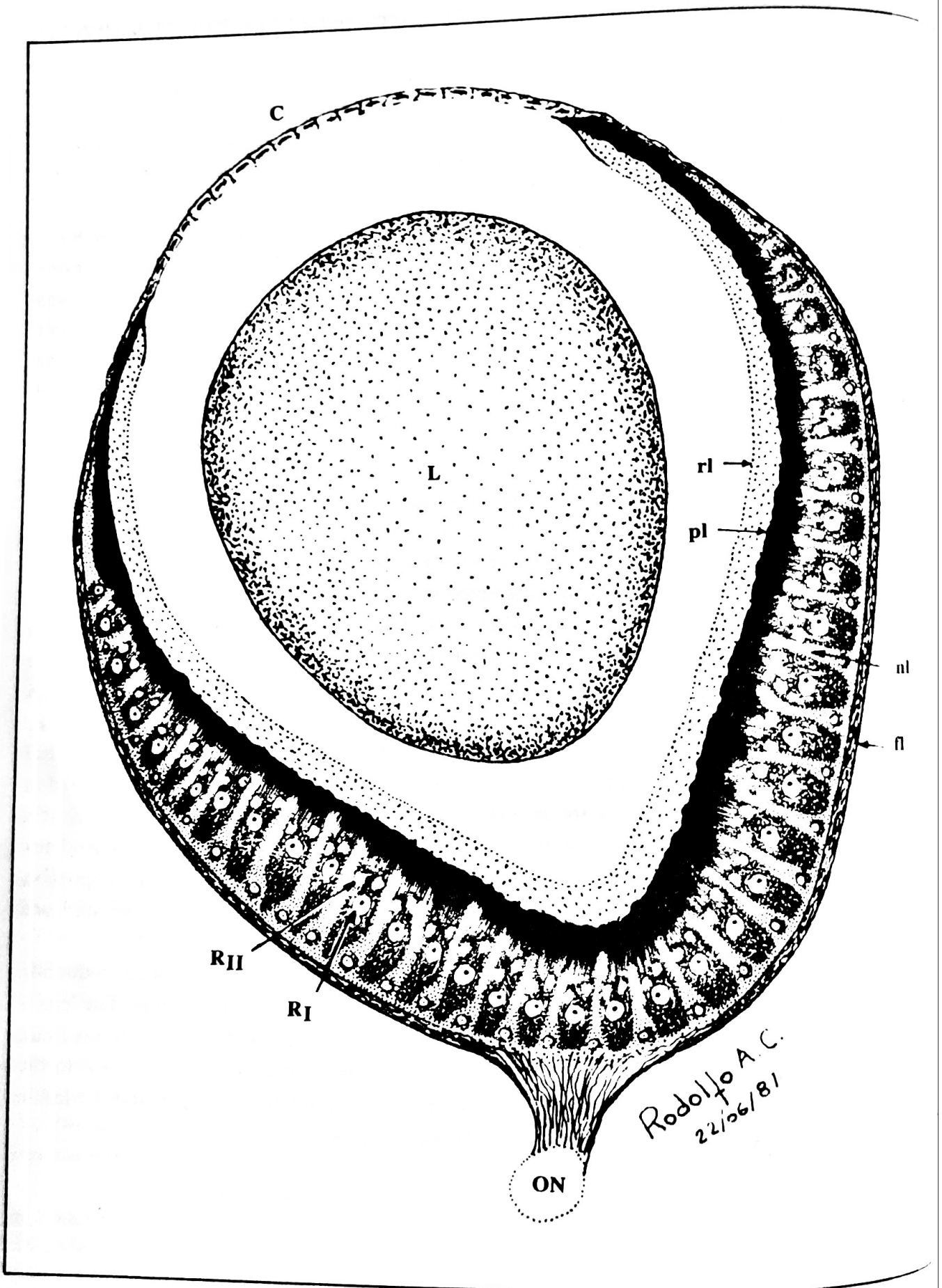
Figure 1 - Illustration of a transverse section through the center of the *B. glabrata* eye. *C*, Cornea; *fl*, fibrous layer; *L*, lens; *ON*, optic nerve; *rl*, photoreceptor layer; *R_I*, Type I receptor; *R_II*, type II receptor; *pl*, pigment layer; *nl*, nuclear layer.

layer (Figure 1). The photoreceptor layer is formed by the apical projections and microvilli of the visual cells.

At least three types of cells in different spatial arrangements are present in the retina, their nuclei lying on the cell layer. The supporting cells have elongated nuclei which are smaller than those of the visual cells and less deeply staining (Figure 2). The nuclei of visual cells are of two types, a larger, spherical type distributed in the middle portion of the cell layer, and a smaller, more oval type closer to the pigment layer (Figure 2). On the basis of their morphological and staining characteristics, these nuclei can be considered to belong to type I and II receptor cells, respectively, as suggested by Oswaldo-Cruz and Bernardes (1982). Counting of type I cell receptor nuclei yielded mean values of 573.30 ± 23.86 cells/layer. We were unable to identify type II receptor cells with certainty in all sections. However, on the basis of counting performed on more differentiated regions in some sections, we suggest a type I/type II ratio of 1:2 (Figure 2).

The nuclei of type I cells are located in a layer approximately 16.00 μm below the inner surface of the retina and therefore are distributed over a spherical surface of 290.11 μm in diameter. The surface area of a sphere of this dimension, after subtracting the surface of the cornea where no receptors are present, is 196.92 μm^2. The retinal area for each

Figure 2 - Photomicrographs of the *B. glabrata* retina illustrating the different types of receptors and some components. *CFr*, Photoreceptors layer; *cs*, supporting cells; *cn*, nuclear layer; *CF*, fibrous layer; *(1)* type I receptor and *(2)* type II receptor. Thick arrows indicate the type I receptor with only one nucleus compared to the type II receptor with two nuclei (thin arrows).

receptor is then 343.61 μm^2, corresponding to a mean distance of 18.5 μm between type I receptor cells. The mean distance between type I receptors, determined from measurements on 76 elements taken from sections selected at random, was 14.8 ± 3.1 μm, i.e., less than the value calculated for a rectangular mosaic arrangement.

Schematic eye

The principal parameters of the schematic eye are presented in Figure 3. The data reported here indicate a focal length or posterior nodal point, N', of 120.00 μm and a posterior focal point, P', located 269.0 μm from the corneal vertex. On the basis of these dimensions for the schematic eye, a real image is formed slightly behind the receptor layer suggesting that the eye of *B. glabrata* is hyperopic (Figure 3). On this basis, the pear shape of the eye (Figure 1) indicates that the central area of receptors is the deepest one and therefore the image may be formed on the receptor layer. Consequently, the eye of *B. glabrata* may be emmetropic.

Resolving power of the eye

Using the criterion of Rayleigh for the resolution of the diffraction pattern of *B. glabrata*, with a mean pupil diameter of 135.0 μm and a wavelength of 480 mm (peak of the sensitivity curve for other gastropods as reported by Dennis, 1967, and Susuki et al., 1979), we calculate that the
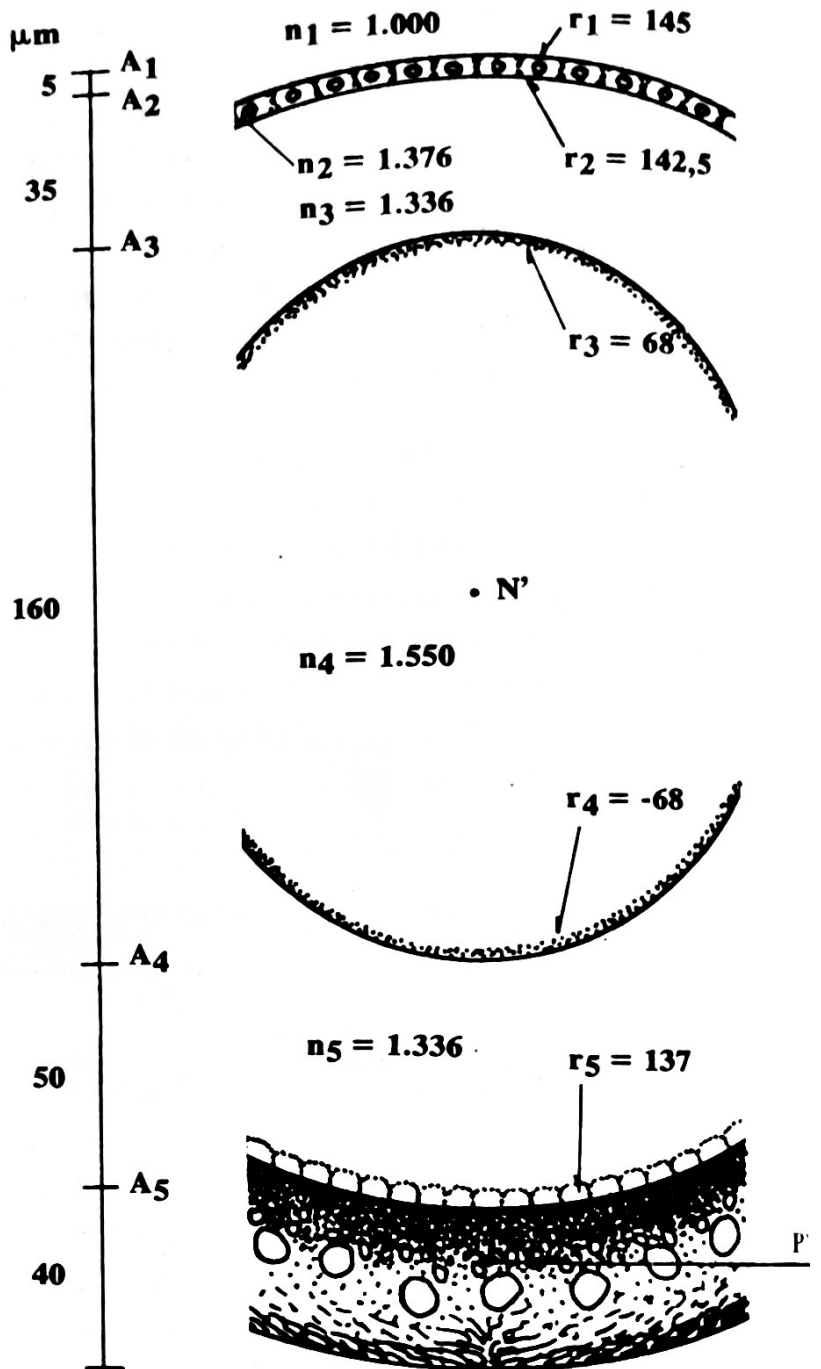

Figure 3 - Optical properties of the *B. glabrata* eye. The distance separating the refractive surfaces and the radii of curvature are given in μm. The posterior nodal point (N') and the posterior focal point (P') are located 120 μm and 26^0 μm behind the corneal vertex, respectively, indicating a hyperopic eye. A_1, Anterior corneal surface; A_2, posterior corneal surface; A_3, anterior lenticular surface; A_4, posterior lenticular surface; A_5, receptor surface; A_6, posterior scleral surface; *n*, refractive index of air (n_1), cornea (n_2), aqueous humor (n_3), total lens (n_4) and vitreous humor (n_5); *r*, radius anterior corneal (r_1), posterior corneal (r_2), anterior lenticular (r_3), posterior lenticular (r_4), receptor (r_5), and posterior scleral (r_6).

optical system of this animal can discriminate between objects separated by an angle of approximately 0.21 degrees.

The physiological resolving limit of the snail eye, estimated on the basis of the mean distance between receptors (15 μm) and of the focal length of the optical system (120 μm), indicates that *B. glabrata* is capable of discriminating only between points separated by approximately 7.00 degrees, a value similar to that calculated for the eye of *Strophocheilus* (Oswaldo-Cruz and Bernardes, 1982). Therefore, the optical performance of the dioptrical system of this animal should be higher than the sampling data provided by the receptor mosaic. This performance is much inferior to that of the vertebrate eye.

Discussion

Few studies have been performed to evaluate the optical properties of gastropod eyes. Among them are those of Newell (1965), Newell and Newell (1968), Land (1981), Oswaldo-Cruz and Bernardes (1982) and Hamilton et al. (1983). The general structure of the eye of *B. glabrata* resembles that of the other species reported in the literature. Because of the technical difficulties in obtaining direct measurements of the optical properties of *B. glabrata* eyes, which are very small, we adopted the computational procedures developed by Oswaldo-Cruz et al. (1979) for the study of vertebrate optics and adapted for the eye of *Strophocheilus* by Oswaldo-Cruz and Bernardes (1982).

For the calculations of the refractive indices of the various eye surfaces we used values reported for other gastropods, which do not show marked variations for the cornea and vitreous humor but which vary for the lens. Thus, a refractive index of intermediate value between that experimentally measured by Newell (1965) for the eye of *L. littorea* and that estimated by Oswaldo-Cruz and Bernardes (1982) for *Strophocheilus* was adopted for the present study. Furthermore, since the calculations for a schematic eye should be made from values reflecting those of an intact eye, the processing of the material (anesthesia and fixation), which may produce small alterations in dimensions in relation to the *in vivo* eye, may have been a source of error. Therefore, although different measuring methods were used, comparisons of equivalent factors may be made among *B. glabrata*, *L. littorea*, *L. irrorata* and *Strophocheilus* (Table 1). The differences among the eyes of these four related species, having specific periods of activity in different media, i.e, air and water, should be considered. Analysis of the data in Table 1 indicates that, even though the values for *B. glabrata* are intermediate between those for *L. littorea* and for *Strophocheilus*, its optical characteristics are closer to those of *L. littorea* . It should be pointed out that both *B. glabrata* and *L. littorea* are more active in water, whereas the other species move predominantly in air. Among the four species, the one with the best resolving power and smallest receptor separation is *Littorina irrorata* (Hamilton et al., 1983). Other data reported by Hamilton and Winter (1982) suggest an ability to visualize shapes for *L. irrorata* . In contrast, according to Oswaldo-Cruz and Bernardes, the eyes of *Strophocheilus*, although larger in size than those of other snails, including the three species compared here, do not appear to have good spatial resolution, being adapted to operate at low levels of light intensity in accordance with the simple orientation behavior of the species. An important result of the present study concerns

Table 1 - *Comparison of the optical characteristics of four gastropod mollusc species based on average adult measurements.*

Optical characteristics	*Biomphalaria glabrata* (present paper)	*Littorina irrorata* (Hamilton et al., 1983)	*Littorina littorea* (Newell, 1965)	*Strophocheilus* sp. (Oswaldo-Cruz and Bernardes, 1982)
Size of the eye (µm)	290-308	270-240	-	420-450
Cornea thickness (µm)	5-7	7-13	40	35-40
Aperture diameter (µm)	135	132	55-60	190-200
Lens diameter (µm)	160	170	110	-
f/r	2.2	2.71	2.82	-
Lens core refractive index (µm)	1.55	1.51	1.45	1.65
Receptor separation distance (µm)	14.0	4.37	12.0	24.0
Receptor diameter (µm)	8.0	3.44	6.0	-
Posterior nodal distance (air) (µm)	120	149	87	206
Distance from posterior nodal point to retina (air) (µm)	120	149	87	190
Angular receptor sparing (degrees)	7.2	1.7	7.9	7.0

the relationship between the larger number of type I cells and the behavior of the animal, which, according to Jaeger (1965, apud Oswaldo-Cruz and Bernardes, 1982), is more active at low levels of luminosity.

Using various arguments, Newell (1965) raised the possibility that *L. littorea* can discriminate shapes, i.e.: 1) the lens may form an image without distortion, with a focal length/curvature radius ratio (f/r = 2.82) approaching that of more developed animals; 2) when the animal is exposed to air the frontal surface of the eye may cause an appreciable convergence and thus the images of distant objects could be in focus at the retinal level; 3) the 7-degree angle with the eye fundus in relation to the center of the lens may correspond to the limit of acuity imposed by the retinal mosaic, which may have a smaller value than the diopic system, producing a sharper image than the retina can detect; 4) the diffraction effects are not important, since the aperture of the pupil (55-60 μm) is 100 times the wavelength of light.

On the basis of the data in Table 1 and the general results of the present study, it is clear that there are more similarities than differences between the eyes of *L. littorea* and *B. glabrata*. Therefore, following the reasoning of Newell (1965), we may suppose that *B. glabrata* can visualize shapes, although with a performance inferior to that of *L. littorea*. However, in spite of this possibility, only behavioral tests can provide definite information since "the organ may precede the function".

On the basis of the arrangement of the nuclear layer of the retina of *B. glabrata*, two types of receptor cells, type I and type II, were observed, as described by Oswaldo-Cruz and Bernardes (1982). Type II cells, located close to the pigment layer, differ in position from those of *Strophocheilus,* which are located close to the basal lamina. Despite the different location, the general and staining characteristics of these cells, the proportion of number and spacing are similar, suggesting that they are of the same type. These two types of cells may be related to the perception of light intensity, as suggested by Suzuki et al. (1979). They demonstrated the presence of two spectral sensitivity curves in *Limax flavus,* which may be associated with the two morphologically distinct cell types (type I and type II).

Even though cell nuclei corresponding to the description of type I and II cells have been observed in *B. glabrata*, it was only possible to count type I cells, i.e., those more sensitive to light. However, in the more differentiated regions of the histological sections, a 1:2 relationship was observed between type I and type II cells. According to Suzuki et al. (1979), type II cells are active in darkness, so that a similar role may be postulated for these cells in the twilight and nocturnal activity of the animal. Studies of the biological rhythms of locomotion of the animal in relation to various lighting schedules have demonstrated that the species shows peaks of motility after dawn and dusk (Schall, 1980; Pimentel-Souza et al., 1984). Changes in the activity associated with light transition (from light to dark) and greater motion in dark bands have also been observed by Rotenberg et al. (1988) for *B. glabrata.* The greater locomotion during these periods may reflect a change in preferential region over the night-day cycle. Experiments conducted by Pimentel and White (1959) have demonstrated that the animal moves from the bottom to the surface more frequently at night, as was also observed by Pieri (1979). It is interesting to point out that the maximum absorption values of the spectral sensitivity curves recorded by Suzuki et al. (1979) for gastropods are between 460 and 480 nm, which is close to the maximum emission wavelength band

during twilight (Beck, 1980). This suggests an adaptive advantage that guarantees greater visual acuity during this period of the day.

Stoll (1973) made an attempt to answer the question of the use of light made by *L. stagnalis*. He suggested that the use of light may be related to the type of pulmonary respiration of this aquatic animal, since it occasionally needs to breathe air. Thus, the ability to locate brighter, not covered, parts of the water surface may be important. Light may also affect oviposition in this species (van der Steen, 1967) as well as the endocrine processes of molluscs which are mediated by the eye or by neural photoreception as demonstrated by Kennedy (1960) and Arvannitaki and Chalazonitis (1961). Preliminary data reported by Stoll (1973) have also suggested the participation of the eye of *L. stagnalis* in the photoneuroendocrine system. *B. glabrata* has the same type of respiration as *L. stagnalis* and therefore detection of a free water surface by identifying lighter areas may have become an adaptative factor. There are reports that *B. glabrata* migrates from the bottom to the walls and surface of the aquarium when horizontal illumination is changed to vertical illumination (Deschiens, 1957; Barbosa, 1970; Williams and Coelho, 1973; Pimentel-Souza et al., 1976, 1984; Schall et al., 1985) which implies reorientation according to light incidence. Furthermore, Joy (1971) reported the influence of light on the oviposition of *B. glabrata*, although the role of the eyes in the neural pathway of this process has not yet been established.

Acknowledgments

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