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Internal morphology of the camera-like eye of the gastropod *Helix pomatia* Linnaeus, 1758 (Stylommatophora: Helicidae): Retina

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Abstract. For the first time, the internal morphology of the camera-like eye of the terrestrial pulmonate gastropod *Helix pomatia*, namely the general morphology of the retina, was studied in detail using light and transmission electron microscopy. In total, 13 general morphological properties of the *H. pomatia* retina were studied, of which 11 properties were examined for the first time. It was shown that the general morphological properties of the retina of *H. pomatia*, which are available for comparison with the corresponding properties of the retina of other species of terrestrial pulmonate gastropods, are completely typical for them. The remaining properties were studied for the first time in terrestrial pulmonate gastropods. Based on the studied general morphological properties of the retina of *H. pomatia*, including for the first time for terrestrial pulmonate gastropods, its possible functions were identified. This is the first article on the general morphology of the retina of the camera-like eye of a gastropod.

Keywords: *Helix pomatia*, molluscs, morphology, non-optic part of the retina, optic part of the retina, epithelial tissue

Внутренняя морфология камерного глаза брюхоногого моллюска *Helix pomatia* Linnaeus, 1758 (Stylommatophora: Helicidae): Сетчатка

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Аннотация. Впервые при помощи световой и трансмиссионной электронной микроскопии подробно изучена внутренняя морфология камерного глаза наземного легочного брюхоногого моллюска *Helix pomatia*, а именно общая морфология сетчатки. Всего изучено 13 общих морфологических свойств сетчатки *H. pomatia*, из них 11 свойств — впервые. Показано, что общие морфологические свойства сетчатки *H. pomatia*, которые доступны для сравнения с соответствующими свойствами сетчатки других видов наземных легочных брюхоногих моллюсков, являются полностью типичными для них. Остальные свойства изучены впервые у наземных легочных брюхоногих моллюсков. На основе изученных общих морфологических свойств сетчатки *H. pomatia*, в том числе впервые для наземных легочных брюхоногих моллюсков, определены ее возможные функции. Это первая статья об общей морфологии сетчатки камерного глаза брюхоногого моллюска.

Ключевые слова: *Helix pomatia*, моллюски, морфология, незрительная часть сетчатки, зрительная часть сетчатки, эпителиальная ткань

Introduction

In terrestrial pulmonate gastropods, the camera-like eyes are located inside the tips of the upper pair of head tentacles, where they are surrounded by tentacle tissues (Lawson 1863; Meisenheimer 1912; Likharev, Rammelmeyer 1952; Runham, Hunter 1970; Oswaldo-Cruz, Bernardes 1982). These tissues are completely transparent in front of the anterior section of the eyes, through which light penetrates into the eyes. Light passes through the outer shell of the eyes — the cornea and the eye capsule, the vitreous body, the crystalline lens, the vitreous body again, and hits the inner shell of the eyes — the retina (Lawson 1863; Meisenheimer 1912; Land 1981; Messenger 1981; Oswaldo-Cruz, Bernardes 1982; Shepeleva 2011; 2013; 2019; 2021a). The retina combines the light-sensitive and light-insulating apparatus of the eyes (Lawson 1863; Eakin et al. 1980; Land 1981; Messenger 1981; Shepeleva 2011; 2019; 2020; 2021b; 2021c). An analysis of the literature on the structure of the camera-like eyes of terrestrial pulmonate gastropods shows that out of 25,000 known species (Schileyko 2016), the morphology of the retina has been studied to some extent in only 28 species (Henchman 1897; Meisenheimer 1912; Röhlich, Török 1963; Schwalbach et al. 1963; Eakin, Brandenburger 1967; 1975a; 1975b; Newell, Newell 1968; Brandenburger 1975; Kataoka 1975; Zunke 1979; Eakin et al. 1980; Oswaldo-Cruz, Bernardes 1982; Tamamaki, Kawai 1983; Zaitseva 1992; 2000; 2016; Jeong, Lee 1994; Chang et al. 1998; Koralewska-Batura 1999; Bobkova et al. 2004a; 2004b; Zieger et al. 2008; Shepeleva 2005; 2006a; 2006b; 2006c; 2007; 2008; 2010; 2012; 2014; 2015; 2017; 2020; 2021b; 2021c; 2026; Matsuo et al. 2017). Of these 28 species of mollusks, the morphology of the retina has not been fully studied in any species.

To study the morphology of the retina of the camera-like eyes of terrestrial pulmonate gastropods, different sets of methods were used. Thus, for six species, making preparations of isolated eyes and histological preparations of isolated eyes/eye tentacles, light and transmission electron microscopy, traditional morphometrics, and calculation of statistical indicators were used (Shepeleva 2005; 2006a; 2006b; 2006c; 2007; 2010; 2017; 2020; 2021b; 2021c; Zieger et al. 2008), for six species — making histological preparations of isolated eyes/eye tentacles, light and transmission electron microscopy, traditional morphometrics, and calculation of statistical indicators (Meisenheimer 1912; Röhlich, Török 1963; Schwalbach et al. 1963; Zunke 1979; Tamamaki, Kawai 1983; Zaitseva 1992; 2000; 2016; Bobkova et al. 2004a; 2004b; Zieger et al. 2008; Shepeleva 2015; 2026), for ten species — making histological preparations of isolated eyes/eye tentacles, light and transmission electron microscopy, and traditional morphometrics (Henchman 1897; Eakin, Brandenburger 1967; 1975a; 1975b; Newell, Newell 1968; Brandenburger 1975; Kataoka 1975; Eakin et al. 1980; Zaitseva 1992; 2000; 2016; Chang et al. 1998), for one species — making histological preparations of isolated eye tentacles, light microscopy, traditional morphometrics, and calculation of statistical indicators (Shepeleva 2008; 2014), for one species — making histological preparations of isolated eye tentacles, light microscopy, and traditional morphometrics (Oswaldo-Cruz, Bernardes 1982), for two species — making histological preparations of isolated eye tentacles, light and transmission electron microscopy (Jeong, Lee 1994; Matsuo et al. 2017), for one species — making preparations of isolated eyes and light microscopy (Shepeleva 2012), and for one species — making histological preparations of isolated eye tentacles and light microscopy (Koralewska-Batura 1999). An analysis of the cited works suggests that the lack of data on the morphology of the retina of the camera-like eyes of terrestrial pulmonate gastropods is due not so much to the lack of technical capabilities for conducting the relevant studies, as to the experimental objectives of these studies. In addition, this may be due to the very small size of the retina in terrestrial pulmonate gastropods. Of the species studied, retinal thickness was measured in only one species — *Strophoheilus* sp. In the thickest

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central part, it is 60 μm (Oswaldo-Cruz, Bernardes 1982).

The purpose of the work is to study the internal morphology of the camera-like eye of the terrestrial pulmonate gastropod *Helix pomatia*, namely the general morphology of the retina. Objectives of the work: to identify whether the general morphological properties of the retina of the camera-like eye of *H. pomatia* are typical of terrestrial pulmonate gastropods; to identify to what extent the general morphological properties of the retina of the camera-like eye of *H. pomatia* are typical of terrestrial pulmonate gastropods; to identify the possible functions of the retina of the camera-like eye of *H. pomatia*.

Material and methods

Animals

Seventeen adult specimens of the terrestrial pulmonate gastropod *Helix pomatia* Linnaeus, 1758 (Heterobranchia: Stylommatophora) were collected in the Leningrad Region of Russia. They had a shell height of 42 to 45 mm. All snails were placed in two plastic baskets 35 cm long, 25 cm wide, and 13 cm high for six and 11 specimens, respectively. The mollusks were kept at room temperature and natural light conditions. They were fed carrots and dandelion leaves.

Before the experiments, the snails were kept in a refrigerator at 4 °C for about 15 min for cold anesthesia.

The studies were carried out in accordance with the International Guiding Principles for Biomedical Research Involving Animals, developed by the Council for International Organizations of Medical Sciences in 1985.

Making preparations of isolated eye tentacles and light microscopy

For light microscopy, preparations of isolated eye tentacles were made by cutting of the upper part of the eye tentacles with the eyes. The obtained preparations were studied under a Leica M205 FA fluorescent stereomicroscope (Leica Microsystems, Wetzlar, Germany) and photographed with a Leica DFC365 FX digital camera (Leica Microsystems, Wetzlar, Germany). Twelve preparations of isolated eye tentacles from six mollusks were made and studied.

Making preparations of isolated eyes and light microscopy

For light microscopy, preparations of isolated eyes were made from preparations of isolated eye tentacles by separating the eyes from the tissues of the eye tentacles. The preparations were made and studied under a Leica M205 FA fluorescent stereomicroscope (Leica Microsystems, Wetzlar, Germany) and photographed with a Leica DFC365 FX digital camera (Leica Microsystems, Wetzlar, Germany). Twelve preparations of isolated eyes from 12 preparations of isolated eye tentacles from six mollusks were made and studied. All preparations of isolated eyes were made from the same preparations of isolated eye tentacles from the same mollusks described above.

Making histological preparations of isolated eye tentacles, light and transmission electron microscopy

For light and transmission electron microscopy, histological preparations of isolated eye tentacles were made from preparations of isolated eye tentacles. The preparations were fixed in a 2.5 % solution of glutaraldehyde on 0.1 M cacodylate buffer (pH = 8.0) for 2 h at 4 °C and in a 1 % solution of osmium tetraoxide on the same buffer for 1 h at 4 °C, dehydrated in a series of alcohols of increasing concentration, impregnated with absolute acetone and a mixture of acetone and epoxy resin Embed 812 (EMS, Hatfield, USA), and filled with Embed 812. Semithin (1.5 μm) and ultrathin (70 nm) sections were cut with glass knives on a Leica EM UC7 ultramicrotome (Leica Microsystems, Wetzlar, Germany). Semithin sections were stained with 0.5 % toluidine blue solution and enclosed under a cover glass using Bio Mount HM (Bio Optica, Milano, Italy). The obtained preparations were studied under a Leica DMI 6000 inverter fluorescence microscope (Leica Microsystems, Wetzlar, Germany) and photographed with a Leica DFC360 FX digital camera (Leica Micro-

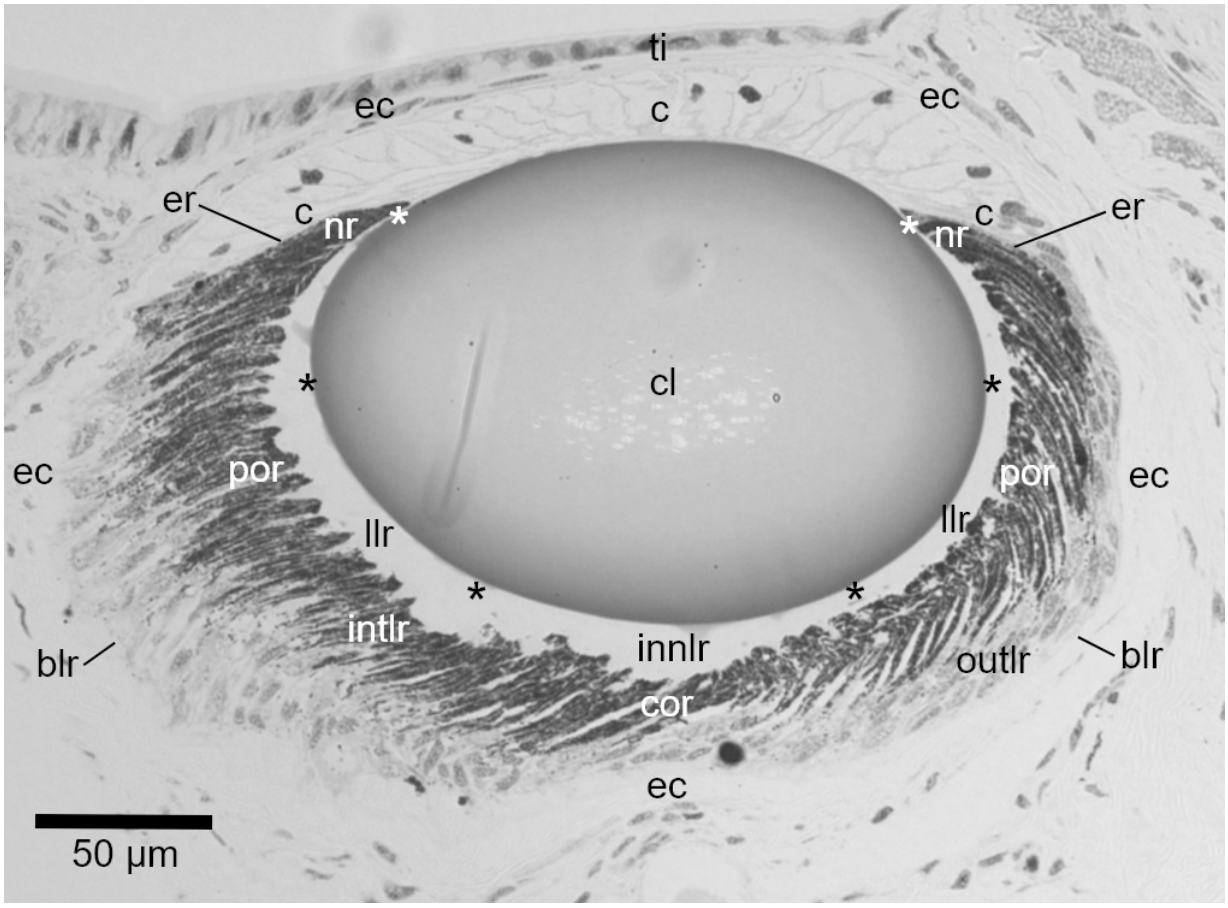

Fig. 1. Photograph of a longitudinal semithin section of the camera-like eye of *Helix pomatia*, obtained using a light microscope: *blr* — area of the basal lamina of the retina; *c* — cornea; *cl* — crystalline lens; *cor* — central region of the optic part of the retina; *ec* — eye capsule; *er* — edge of the retina; *innlr* — the inner layer of the retina; *intlr* — the intermediate layer of the retina; *llr* — light-sensitive layer of the retina; *nr* — non-optic part of the retina; *outlr* — the outer layer of the retina; *por* — peripheral region of the optic part of the retina; *ti* — tentacular integument. Asterisks indicate the apical surface of the supporting cells in the non-optic part and the vertices of the photoreceptor cells in the optic part of the retina

Рис. 1. Фотография продольного полутонкого среза камерного глаза *Helix pomatia*, полученная при помощи светового микроскопа: *blr* — область базальной пластинки сетчатки; *c* — роговица; *cl* — хрусталик; *cor* — центральная область зрительной части сетчатки; *ec* — глазная капсула; *er* — край сетчатки; *innlr* — внутренний слой сетчатки; *intlr* — промежуточный слой сетчатки; *llr* — светочувствительный слой сетчатки; *nr* — незрительная часть сетчатки; *outlr* — наружный слой сетчатки; *por* — периферическая область зрительной части сетчатки; *ti* — щупальцевый интегумент. Звездочками обозначены апикальная поверхность опорных клеток в незрительной части и вершины фоторецепторных клеток в зрительной части сетчатки

systems, Wetzlar, Germany). Ultrathin sections were contrasted with a 2 % solution of uranium acetate and a 0.1 % solution of lead citrate. The obtained preparations were studied under a JEOL JEM-1400 transmission electron microscope (JEOL, Tokyo, Japan) and photographed with an Olympus Veleta digital camera (Olympus, Tokyo, Japan). About 2,340 semithin sections of eye tentacles from 22 eye tentacles from 11 mollusks and 212 ultrathin sections of eye tentacles from six eye tentacles from at least three mollusks were made and studied. All semithin and ultrathin sections of the eye tentacles were made from new preparations of isolated eye tentacles from new mollusks.

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Traditional morphometrics

Measurements of the parameters were performed on photographs of semithin sections of the eye tentacles passing through the center of the eyes. The following number of measurements were performed: eight measurements of the thickness of the non-optic part of the retina on eight semithin sections of eye tentacles from eight eye tentacles from at least four mollusks; five measurements of the thickness of the central and peripheral region of the optic part of the retina, respectively, on five semithin sections of eye tentacles from five eye tentacles from at least three mollusks. To measure the thickness of the retina on semithin sections of the eye tentacles, both different and identical eye tentacles were taken, therefore, in total, eight semithin sections of eye tentacles were taken from eight eye tentacles from at least four mollusks. It is not possible to give the exact number of mollusks, since eight eye tentacles were selected from 22 eye tentacles from 11 mollusks.

Calculation of statistical indicators

Using the appropriate formulas, the mean values of morphometric data and their standard deviations were calculated (Lakin 1990).

Results

General morphological properties of the retina of the camera-like eye of Helix pomatia

The study of histological preparations of isolated eye tentacles of *H. pomatia* shows the following.

The retina is located between two components of the eye — the outer shell and the crystalline lens (Fig. 1). Depending on the location and functions in the retina, two parts can be distinguished: the non-optic part, which is located between the cornea, the eye capsule, the optic part of the retina and the crystalline lens and is not capable of photoreception, and the optic part, which is located between the non-optic part of the retina, the eye capsule and the crystalline lens and is capable of photoreception (Fig. 1). Within the optic part of the retina, two regions can be distinguished according to position: the central region, which is located between the peripheral region of the optic part of the retina, the eye capsule and the crystalline lens, and the peripheral region, which is located between the non-optic part of the retina, the eye capsule, the central region of the optic part of the retina and the crystalline lens (Fig. 1).

The retina is not inverted (Fig. 1, 2). The retina is formed by one morphological type of tissue — epithelial. The retinal epithelial tissue is represented by one morphological kind — a single-layer multi-row columnar epithelium (Fig. 1, 2). The retinal epithelial tissue consists of four types of cells — supporting, photoreceptor, ganglion and glial, and two forms of extracellular matrix — interstitial matrix and basal lamina (Fig. 1, 2).

The retinal basal lamina and the apical surface of all supporting cells of the non-optic part together with the vertices of all photoreceptor cells of the optic part of the retina form the outer and inner surface of the retina, respectively, the outer lateral surface of the extreme

Table 1

Morphological parameters of the retina of the camera-like eye of *Helix pomatia*

Таблица 1

Морфологические параметры сетчатки камерного глаза *Helix pomatia*

Parameter (μm)	*Helix pomatia*
Non-optic part	
Thickness	5.7 ± 1.8 (n=8)
Optic part	
Central region	
Thickness	50.6 ± 4.6 (n=5)
Peripheral region	
Thickness	45.7 ± 3.4 (n=5)

The parameters are given as the mean value ± standard deviation. n: the number of non-optic parts, central and peripheral regions of the optic part of the retina.

supporting cells of the non-optic part of the retina form the edge of the retina (Fig. 1).

The outer and inner surfaces of the retina have the shape of a segment of an oblate ellipsoid (Fig. 1).

The non-optic part of the retina is smaller than its optic part, and the central region of the optic part of the retina is smaller than its peripheral region. According to morphometric data obtained for *H. pomatia*, the thickness of the retina decreases significantly in the direction from the central region to the peripheral region in the optic part to the non-optic part, which is confirmed by the high value of the ratio of these parameters — 8.9 (Fig. 1; Table 1).

The analysis of preparations of isolated eyes, as well as unstained and stained semithin sections of the eye tentacles of *H. pomatia* shows the following. The retina looks like a black colored structure. The pigment within the retina is unevenly distributed. The inner layer of the retina is completely transparent and colorless. The intermediate layer of the retina is opaque and colored black. The outer layer of the retina is completely transparent and devoid of color. The available distribution of pigment within the retina is such that it combines completely transparent layers devoid of color and an opaque layer colored black as a result of which the retina looks black (Fig. 1).

Discussion

General morphological properties of the retina of the camera-like eye of Helix pomatia

The retina of *H. pomatia* is located between two components of the eye — the outer shell and the crystalline lens. The location of the retina of terrestrial pulmonate gastropods has not been determined. However, in photographs of semithin sections of the eyes, it can be seen that the retina has one variant of location: between two components of the eye — the outer shell and the crystalline lens, as in *Helix aspersa* Müller, 1774 (Eakin, Brandenburger 1975a) and *Cepaea nemoralis* Linnaeus, 1758 (Bobkova et al. 2004b). Thus, the location of the retina of the camera-like eye of *H. pomatia* is the same as the location of the retina of the camera-like eyes of other species of terrestrial pulmonate gastropods.

In *H. pomatia*, depending on the location and functions in the retina, two parts can be distinguished: the non-optic part located between the cornea, the eye capsule, the optic part of the retina and the crystalline lens and not capable of photoreception, and the optic part located between the non-optic part of the retina, the eye capsule and the crystalline lens and capable of photoreception. In terrestrial pulmonate gastropods, depending on the location and functions in the retina, two parts are distinguished: the non-optic part, which is located around the pupil and is not adapted to photoreception, and the optic part, which is located around the crystalline lens and is adapted to photoreception, as in *Arion rufus* Linnaeus, 1758 (Shepeleva 2005; 2020; 2021b). Thus, the presence of non-optic and optic part in the retina of the camera-like eye in *H. pomatia* is similar to the presence of non-optic and optic part in the retina of the camera-like eyes in other species of terrestrial pulmonate gastropods.

Within the optic part of the retina of *H. pomatia*, two regions can be distinguished according to position: the central region located between the peripheral region of the optic part of the retina, the eye capsule and the crystalline lens, and the peripheral region located between the non-optic part of the retina, the eye capsule, the central region of the optic part of the retina and the crystalline lens. Within the optic part of the retina of terrestrial pulmonate gastropods, two regions are distinguished according to position: the central region, which is adjacent to the peripheral region of the optic part of the retina, and the peripheral region, which is located between the non-optic part and the central region of the optic part of the retina, as in *A. rufus* (Shepeleva 2005; 2020; 2021b). Thus, the presence of a central and peripheral region in the optic part of the retina of the camera-like eye of *H. pomatia* coincides with the presence of a central and peripheral region in the optic part of the retina of the camera-like eyes of other species of terrestrial pulmonate gastropods.

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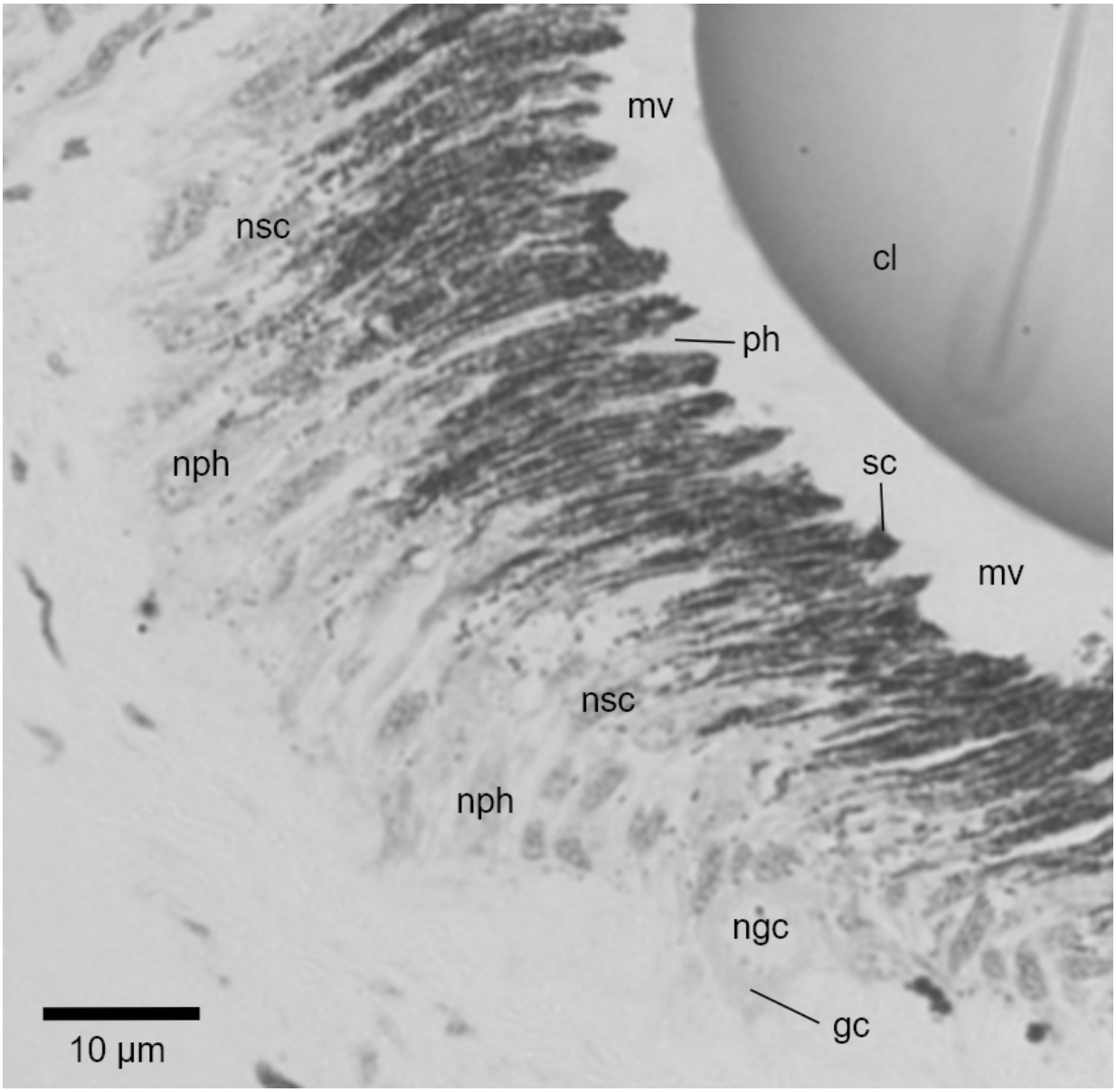

Fig. 2. An enlarged fragment of Figure 1. Photograph of a longitudinal semithin section through the central and peripheral region of the optic part of the retina of the camera-like eye of *Helix pomatia*, obtained using a light microscope. *cl* — crystalline lens; *gc* — ganglion cell; *mv* — microvilli of photoreceptor cells; *ngc* — ganglion cell nucleus; *nph* — photoreceptor cell nucleus; *nsc* — supporting cell nucleus; *ph* — photoreceptor cell; *sc* — supporting cell

Рис. 2. Фрагмент рисунка 1 в увеличенном виде. Фотография продольного полутонкого среза через центральную и периферическую область зрительной части сетчатки камерного глаза *Helix pomatia*, полученная при помощи светового микроскопа: *cl* — хрусталик; *gc* — ганглиозная клетка; *mv* — микровиллы фоторецепторных клеток; *ngc* — ядро ганглиозной клетки; *nph* — ядро фоторецепторной клетки; *nsc* — ядро опорной клетки; *ph* — фоторецепторная клетка; *sc* — опорная клетка

In *H. pomatia*, the retina is not inverted. In terrestrial pulmonate gastropods, the retina possesses a single principle of organization: it is non-inverted, as in *H. aspersa* (Eakin, Brandenburger 1975a) and *Cochlodina laminata* Montagu, 1803 (Shepeleva 2006a). Thus, the absence of the inversion of the retina of the camera-like eye in *H. pomatia* is akin to the absence of the inversion of the retina of the camera-like eyes in other species of terrestrial pulmonate gastropods.

The retina of *H. pomatia* is formed by one morphological type of tissue — epithelial. The retina of terrestrial pulmonate gastropods is formed by one morphological type of tissue: epithelial, as in *Helix albescens* Rossmässler, 1839 and *Arion silvaticus* Lohmander, 1937 (Zaitseva 2000). Thus, the morphological type of the retinal tissue of the camera-like eye of *H. pomatia* is analogous to the morphological type of the retinal tissue of the camera-like eyes of other species of terrestrial pulmonate gastropods.

In *H. pomatia*, the retinal epithelial tissue is represented by one morphological kind — a single-layer multi-row columnar epithelium. In terrestrial pulmonate gastropods, the morphological kind of the retinal epithelial tissue has not been determined. Therefore, it is not possible to compare the morphological kind of the retinal epithelial tissue of the camera-like eye of *H. pomatia* and other species of terrestrial pulmonate gastropods.

The retinal epithelial tissue of *H. pomatia* consists of four types of cells — supporting, photoreceptor, ganglion and glial, and two forms of extracellular matrix — interstitial matrix and basal lamina. The structure of the retinal epithelial tissue of terrestrial pulmonate gastropods has not been studied as such. It is noted that the retinal epithelial tissue contains four types of cells: supporting, photoreceptor, ganglion and glial, as in *H. albescens* and *Achatina fulica* Bowdich, 1822 (Zaitseva 2000; 2016). Of the two forms of the extracellular matrix, only one form is mentioned: the basal lamina, as in *Strophoheilus* sp. (Oswaldo-Cruz, Bernardes 1982). Therefore, it is not possible to compare the structure of the retinal epithelial tissue of the camera-like eye of *H. pomatia* with that of other species of terrestrial pulmonate gastropods.

In *H. pomatia*, the retinal basal lamina and the apical surface of all supporting cells of thenon-optic part together with the vertices of all photoreceptor cells of the optic part of the retina form the outer and inner surface of the retina, respectively; the outer lateral surface of the extreme supporting cells of the non-optic part of the retina forms the edge of the retina. In terrestrial pulmonate gastropods, the elements that form the outer and inner surface and the edge of the retina have not been described. Therefore, it is not possible to compare the elements forming the outer and inner surface and the edge of the retina of the camera-like eye in *H. pomatia* and in other species of terrestrial pulmonate gastropods.

The outer and inner surfaces of the retina of *H. pomatia* possess the shape of a segment of an oblate ellipsoid. The shape of the outer and inner surfaces of the retina of terrestrial pulmonate gastropods has not been determined. Therefore, it is not possible to compare the shape of the outer and inner surfaces of the retina of the camera-like eye of *H. pomatia* with that of other species of terrestrial pulmonate gastropods.

In *H. pomatia*, the non-optic part of the retina is smaller than its optic part. In terrestrial pulmonate gastropods, the size of the non-optic and optic part of the retina has not been estimated. Nevertheless, the study of photographs of semithin sections of the eyes suggests the same size of the non-optic part of the retina relative to its optic part: a smaller size, as in *H. aspersa* (Eakin, Brandenburger 1975a) and *Limax valentianus* Férussac, 1822 (Matsuo et al. 2017). Thus, the size of the non-optic part of the retina relative to the optic part of the retina of the camera-like eye in *H. pomatia* is identical to the size of the non-optic part of the retina relative to the optic part of the retina of the camera-like eyes in other species of terrestrial pulmonate gastropods.

The central region of the optic part of the retina of *H. pomatia* is smaller than its peripheral region. The size of the central and peripheral region of the optic part of the retina of terrestrial pulmonate gastropods has not been estimated. At the same time, the study of photographs of semithin sections of the eyes indicates the same size of the central region of the optic part of the retina relative to its peripheral region: a smaller size, as in *H. aspersa* (Eakin, Brandenburger 1975a) and *Monachoides incarnata* Müller, 1774 (Shepeleva 2006a). Thus, the size of the central region of the optic

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part of the retina relative to the peripheral region of the optic part of the retina of the camera-like eye of *H. pomatia* is the same as the size of the central region of the optic part of the retina relative to the peripheral region of the optic part of the retina of the camera-like eyes of other species of terrestrial pulmonate gastropods.

In *H. pomatia*, the thickness of the retina decreases significantly in the direction from the central region to the peripheral region within the optic part, and further toward the non-optic part, which is confirmed by the high value of the ratio of these parameters — 8.9. In terrestrial pulmonate gastropods, nothing is known either about changes in retinal thickness, or about parameters suitable for independent calculations. Therefore, it is not possible to compare the change in the thickness of the retina of the camera-like eye in *H. pomatia* and in other species of terrestrial pulmonate gastropods.

The retina of *H. pomatia* looks like a black colored structure. The pigment in the retina is unevenly distributed. The inner layer of the retina is completely transparent and colorless. The intermediate layer of the retina is opaque and colored black. The outer layer of the retina is completely transparent and devoid of color. The available distribution of pigment in the retina is such that it combines completely transparent layers, devoid of color, with an opaque layer, colored black, as a result of which the retina looks black. The retina of terrestrial pulmonate gastropods is colored in one color: black, as in *Trochulus hispidus* Linnaeus, 1758 from Southern Sweden (Shepeleva 2008). The distribution of the pigment in the retina has not been studied. Moreover, the analysis of photographs of preparations of isolated eyes and semithin sections of the eye tentacles indicates only one way of distributing pigment in the retina: uneven, as in *Succinea putris* Linnaeus, 1758 (Shepeleva 2015). The inner layer of the retina is completely transparent and colorless. The intermediate layer of the retina is opaque and possesses a black color. The outer layer of the retina is completely transparent and possess no color. The existing distribution of pigment within the retina is such that its combines completely transparent colorless layers and an opaque layer colored black, as a result of which the retina is perceived as black. Thus, the color of the retina of the camera-like eye of *H. pomatia* is similar to the color of the retina of the camera-like eyes of other species of terrestrial pulmonate gastropods.

Possible functions of the retina of the camera-like eye of Helix pomatia

The studied general morphological properties of the retina of the camera-like eye of *H. pomatia* suggest that it can perform the following functions: shaping (for the eye and pupil), supporting, protective and delimiting (for eye components), receptor and screening (for the eye). Assumptions about some functions of the retina of the camera-like eye of *H. pomatia*, such as shaping (for the pupil) and receptor and screening (for the eye) are consistent with the literature data about the functions of the camera-like eye of this species (Meisenheimer 1912) and the camera-like eyes of other species of terrestrial pulmonate gastropods (Lawson 1863; Land 1981; Messenger 1981; Shepeleva 2011; 2013; 2019). Assumptions about the remaining functions of the retina of the camera-like eye of *H. pomatia*, such as shaping (for the eye), supporting, protective and delimiting (for eye components) were made for the first time for terrestrial pulmonate gastropods.

Conclusion

In this work, the internal morphology of the camera-like eye of the terrestrial pulmonate gastropod *H. pomatia*, namely the general morphology of the retina, was studied in detail for the first time. The following general morphological properties of the retina were studied: location in the eye; parts; regions; inversion; morphological type of tissue; morphological kind of tissue; structure of tissue; elements forming the outer and inner surface and the edge; the shape of the outer and inner surfaces; the size of the parts relative to each other; the size of the regions relative to each other; thickness change; and color (Table 2).

Table 2
General morphological properties of the retina of the camera-like eye of *Helix pomatia*
Таблица 2
Общие морфологические свойства сетчатки камерного глаза *Helix pomatia*

Properties	*Helix pomatia*
Location in the eye	Between the outer shell of the eye and the crystalline lens
Parts	Two: the non-optic part, which is located between the cornea, the eye capsule, the optic part of the retina and the crystalline lens and is not capable of photoreception; the optic part, which is located between the non-optic part of the retina, the eye capsule and the crystalline lens and is capable of photoreception
Regions	Two in the optic part: the central region, which is located between the peripheral region of the optic part of the retina, the eye capsule and the crystalline lens; the peripheral region, which is located between the non-optic part of the retina, the eye capsule, the central region of the optic part of the retina and the crystalline lens
Inversion	Absent
Morphological type of tissue	One: epithelial
Morphological kind of tissue	One: a single-layer multi-row columnar epithelium
Structure of the tissue	Consists of four types of cells and two forms of extracellular matrix: supporting cells; photoreceptor cells; ganglion cells; glial cells; interstitial matrix; basal lamina
Elements forming the outer and inner surface, respectively, and edge	The basal lamina of the retina and the apical surface of all supporting cells of the non-optic part together with the vertices of all photoreceptor cells of the optic part of the retina, respectively, and the outer lateral surface of the extreme supporting cells of the non-optic part of the retina
The shape of the outer and inner surfaces	A segment of an oblate ellipsoid
The size of the parts relative to each other	The non-optic part is smaller than the optic part
The size of the regions relative to each other	In the optic part: the central region is smaller than the peripheral region
Thickness change	Decreases significantly in the direction from the central region to the peripheral region in the optic part to the non-optic part
Color	Black: the inner layer of the retina is completely transparent and colorless; the intermediate layer of the retina is opaque and colored black; the outer layer of the retina is completely transparent and devoid of color

All the properties of the *H. pomatia* retina, except for inversion and morphological type of tissue, were studied for the first time. The studied general morphological properties of the retina of the camera-like eye of *H. pomatia* were compared, if possible, with the known/independently assessed corresponding general morphological properties of the retina of the camera-like eyes of other species of terrestrial pulmonate gastropods. Of the 13 studied properties of the retina of *H. pomatia*, eight properties could be compared — they are typical of terrestrial pulmonate gastropods, and five properties could not be com-

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pared — they were studied for the first time in terrestrial pulmonate gastropods. Thus, the general morphological properties of the retina of the camera-like eye of *H. pomatia*, which are available for comparison, are completely typical of terrestrial pulmonate gastropods. Also, based on the studied general morphological properties of the retina of the camera-like eye of *H. pomatia*, including for the first time for terrestrial pulmonate gastropods, its possible functions were identified. This article is the first article on the general morphology of the retina of the camera-like eye of a representative of the group of terrestrial pulmonate gastropods in particular and gastropods in general.

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