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

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Abstract. Gastropods are considered model animals for studying the functioning of the visual system. However, gaps remain in our knowledge of the gastropod visual system itself, including the external and internal morphology of the camera-like eyes. This study presents the first detailed examination of the external morphology of the camera-like eye of the terrestrial pulmonate gastropod *Helix pomatia*, using observations of intact animals, dissected eye tentacles and isolated eyes, histological sections of eye tentacles, light and scanning electron microscopy, traditional morphometrics, and statistical analyses. The morphological characteristics of the eye of *H. pomatia* are shown to be largely, but not completely, typical of terrestrial pulmonate gastropods. Based on these characteristics, potential functions of the *H. pomatia* eye were identified. This article is the first dedicated to the external morphology of the camera-like eye of a gastropod.

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Keywords: *Helix pomatia*, external morphology, molluscs, eye tentacle, tentacular integument, eyeball

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

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Аннотация. Брюхоногие моллюски рассматриваются как модельные животные для изучения функционирования зрительной системы. Однако в наших знаниях о зрительной системе самих брюхоногих моллюсков, в том числе о наружной и внутренней морфологии камерных глаз, существуют пробелы. Впервые при помощи наблюдения за интактными животными, приготовления препаратов изолированных глазных щупалец и глаз и гистологических препаратов изолированных глазных щупалец, световой и сканирующей электронной микроскопии, традиционной морфометрии и расчета статистических показателей подробно изучена наружная морфология камерного глаза наземного легочного брюхоногого моллюска *Helix pomatia*. Показано, что морфологические свойства глаза *H. pomatia* являются в большей степени, но не полностью, типичными для наземных легочных брюхоногих моллюсков. На основе изученных морфологических свойств глаза *H. pomatia* определены его возможные функции. Настоящая статья — первая работа о наружной морфологии камерного глаза брюхоногого моллюска.

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Ключевые слова: *Helix pomatia*, наружная морфология, моллюски, глазное щупальце, щупальцевый интегумент, глазное яблоко

Introduction

All vertebrates and some invertebrates have camera-like eyes. Across different levels of evolutionary development, camera-like eyes consist of five identical main components: the cornea and sclera (or eye capsule); the retina; the pupil; the crystalline lens; and the vitreous body (Walls 1942; Land 1981; Land, Nilsson 2006; 2012; Shepeleva 2011a; 2011b; 2013; 2019; 2023; Nilsson 2021). Consequently, a comparative analysis of camera-like eyes can be undertaken for vertebrates and invertebrates to identify similarities and differences between them. Such analysis is particularly necessary to establish invertebrates as model organisms for studying the visual system. This type of analysis has been carried out for humans and terrestrial pulmonate gastropods (Shepeleva 2013; 2018a; 2018b; 2018c; 2019; 2021a; 2021b; 2025), as well as for humans and jumping spiders (Shepeleva 2022). However, a complete comparative analysis of camera-like eyes between humans and terrestrial pulmonate gastropods has not been possible due to the lack of data on the eyes of this molluscan group, including information on eye morphology.

The group of terrestrial pulmonate gastropods comprises at least 25,000 species (Schileyko 2016). Based on available publications, the study of camera-like eye morphology in these invertebrates began in earnest approximately 160 years ago (Lawson 1863). To date, the number of terrestrial pulmonate gastropod species in which eye morphology has been studied to any extent is only 28 — a negligible figure given the group's diversity. Among these species of molluscs, there is not a single one for which eye morphology has been fully documented, meaning that both external and internal morphology have been completely described. In all 28 species, eye morphology has been studied incompletely; that is, external and internal morphology are either both incomplete, or only internal morphology is incomplete.

Specifically, incomplete data exist on both external and internal eye morphology for five species. For two of these, all five eye

components have been studied (Oswaldo-Cruz, Bernardes 1982; Shepeleva 2012), and for three species, four components have been studied (Lawson 1863; Henchman 1897; Meisenheimer 1912; Röhlich, Török 1963; Schwalbach et al. 1963; Eakin et al. 1980; Zaitseva 1992; 2000; 2016). For 23 species, incomplete data exist only on internal eye morphology: for 12 species, all five components have been studied (Zunke 1979; Tamamaki, Kawai 1983; Tamamaki 1989a; Zaitseva 2000; 2016; Bobkova et al. 2004a; 2004b; Shepeleva 2005a; 2005b; 2006a; 2006b; 2006c; 2007; 2008; 2010; 2014; 2015; 2017; 2018d; 2018e; 2018f; 2020; 2021a; 2021c; 2021d; 2023; Zieger et al. 2008), for three species, four components (Eakin, Westfall 1964; Eakin, Brandenburger 1967; 1975; Newell, Newell 1968; Mortensen, Eakin 1974; Brandenburger 1975; Chang et al. 1998; Zaitseva 2000; 2016), for two species, three components (Jeong, Lee 1994; Koralewska-Batura 1999), for one species, two components (Kataoka 1975; 1977; Tamamaki 1989b) and for five species, one component (Eakin, Brandenburger 1975; Zaitseva 1992; 2000; 2016; Matsuo et al. 2017).

The external and internal morphology of camera-like eyes in terrestrial pulmonate gastropods has been investigated using several methodological approaches. To study external morphology across five species, one species was examined using observation of intact individuals, preparation of isolated eye tentacles and isolated eyes, and light microscopy (Lawson 1863); one species using observation of intact individuals, preparation of isolated eyes, light microscopy, and traditional morphometrics (Shepeleva 2012); and three species using only observation of intact individuals (Meisenheimer 1912; Eakin et al. 1980; Oswaldo-Cruz, Bernardes 1982).

To study internal morphology across 28 species, a variety of methods were employed. In six species, these included preparation of isolated eyes, isolated crystalline lenses, and isolated vitreous bodies; histological sections of isolated eyes or eye tentacles; light and transmission electron microscopy; traditional morphometrics; and calculation of statistical

indicators (Shepeleva 2005a; 2006a; 2006b; 2006c; 2007; 2010; 2017; 2018d; 2018e; 2018f; 2020; 2021a; 2021c; 2021d; 2023; Zieger et al. 2008). In one species, preparation of isolated eyes and isolated crystalline lenses, histological sections of isolated eye tentacles, light and transmission electron microscopy, traditional morphometrics, and calculation of statistical indicators were used (Zunke 1979; Shepeleva 2015; 2018e; 2018f; 2023). In another species, the same techniques were employed but without calculation of statistical indicators (Lawson 1863; Henschman 1897; Eakin, Brandenburger 1975; Zaitseva 2000; 2016). In three species, preparation of isolated crystalline lenses, histological sections of isolated eyes or eye tentacles, light and transmission electron microscopy, traditional morphometrics, and calculation of statistical indicators were applied (Bobkova et al. 2004a; Shepeleva 2005b; Zieger et al. 2008). In one species, preparation of isolated eyes and isolated crystalline lenses, histological sections of isolated eye tentacles, light microscopy, traditional morphometrics, and calculation of statistical indicators were used (Shepeleva 2008; 2014; 2018d; 2018e; 2018f; 2023). In one species, histological sections of isolated eye tentacles, light and transmission electron microscopy, traditional morphometrics, and calculation of statistical indicators were employed (Tamamaki, Kawai 1983; Tamamaki 1989a; Zaitseva 2000; 2016; Bobkova et al. 2004b). In ten species, histological sections of isolated eyes or eye tentacles, light and transmission electron microscopy, and traditional morphometrics were used (Meisenheimer 1912; Röhlich, Török 1963; Schwalbach et al. 1963; Eakin, Westfall 1964; Eakin, Brandenburger 1967; Newell, Newell 1968; Mortensen, Eakin 1974; Brandenburger 1975; Kataoka 1975; 1977; Eakin et al. 1980; Tamamaki 1989b; Zaitseva 1992; 2000; 2016; Chang et al. 1998). In one species, histological sections of isolated eye tentacles, light microscopy, and traditional morphometrics were used (Oswaldo-Cruz, Bernardes 1982). In two species, histological sections of isolated eye tentacles, light

and transmission electron microscopy were employed (Jeong, Lee 1994; Matsuo et al. 2017). In one species, preparation of isolated eyes and isolated crystalline lenses and light microscopy were used (Shepeleva 2012) and in one species, only histological sections of isolated eye tentacles and light microscopy were employed (Koralewska-Batura 1999).

Analysis of published studies suggests that the current limited knowledge of the external and internal morphology of camera-like eyes in terrestrial pulmonate gastropods is largely attributable to the specific experimental objectives of these studies, and to a lesser extent to a lack of technical capabilities. It may also be due to the very small size of the eyes — often not exceeding 200 μm — and the even smaller size of their components in this molluscan group (Shepeleva 2009a).

The aim of this study is to investigate the external morphology of the camera-like eye of the terrestrial pulmonate gastropod *H. pomatia*. The specific objectives are: to determine whether the morphological characteristics of the camera-like eye of *H. pomatia* are typical of terrestrial pulmonate gastropods; to ascertain the degree to which the morphological characteristics of the camera-like eye of *H. pomatia* are typical of this group; and to identify the possible functions of the camera-like eye of *H. pomatia*.

Material and methods

Animals

Nineteen adult specimens of the terrestrial pulmonate gastropod *Helix pomatia* Linnaeus, 1758 (Stylommatophora: Helicidae) with a shell height of 42–45 mm were collected in the Leningrad Oblast, Russia. The snails were placed in two plastic baskets measuring 35 cm long, 25 cm wide, and 13 cm high, containing 8 and 11 specimens, respectively. The molluscs were maintained at room temperature under natural light conditions and were fed carrots and dandelion leaves.

Prior to the experiments, the snails were placed in a refrigerator at 4 °C for about 15 min for cold anesthesia.

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

Observation of intact animals

Observation of intact molluscs was carried out directly by the author under natural conditions.

Preparation of isolated eye tentacles and light microscopy

For light microscopy, preparations of isolated eye tentacles were made by separating the upper portion of the eye tentacles containing the eyes from the remainder of the eye tentacles that lacked eyes. Dissecting scissors and saline solution were used. The resulting preparations were examined 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 molluscs were prepared and examined.

Histological preparation of isolated eye tentacles and scanning electron microscopy

For scanning electron microscopy, preparations of isolated eye tentacles were made in the same manner as for light microscopy. The preparations were fixed in a 2.5 % solution of glutaraldehyde in 0.1 M cacodylate buffer (pH=8.0) for 2 h at 4 °C, washed with buffer, and dehydrated in a graded series of alcohols of increasing concentration. The preparations were then dried by critical point drying using CO₂ for 2 h in a Leica EM CPD300 (Leica Microsystems, Wetzlar, Germany), mounted on an aluminum stub, and sputter-coated with a 20 nm thick layer of gold for 30 min in a Leica EM SCD500 (Leica Microsystems, Wetzlar, Germany). The resulting preparations were examined and photographed using a JEOL JCM-5000 NeoScope scanning electron microscope (JEOL, Tokyo, Japan). Four preparations of isolated eye tentacles from two molluscs were prepared and examined. All preparations of

isolated eye tentacles were obtained from new molluscs.

Preparation of isolated eyes and light microscopy

For light microscopy, preparations of isolated eyes were made from preparations of isolated eye tentacles by dissecting the eyes together with the optic nerves from the surrounding tissues of the eye tentacles using dissecting needles and saline solution. The preparations were examined 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 were made and studied from 12 preparations of isolated eye tentacles obtained from six molluscs. All preparations of isolated eyes were made from the same preparations of isolated eye tentacles and the same molluscs described in the section 'Preparation of isolated eye tentacles and light microscopy'.

Histological preparation of isolated eye tentacles and light microscopy

For light microscopy, histological sections of isolated eye tentacles were prepared from preparations of isolated eye tentacles using the following technique. The preparations were fixed in a 2.5 % solution of glutaraldehyde in 0.1 M cacodylate buffer (pH = 8.0) for 2 h at 4 °C and washed with buffer, then fixed in a 1 % solution of osmium tetroxide in the same buffer for 1 h at 4 °C and washed with distilled water. The preparations were subsequently dehydrated in a graded series of alcohols of increasing concentration, infiltrated with absolute acetone and a mixture of acetone and Embed 812 epoxy resin (EMS, Hatfield, USA), and embedded in Embed 812. Semithin sections (1.5 µm) were cut using glass knives on a Leica EM UC7 ultramicrotome (Leica Microsystems, Wetzlar, Germany), stained with a 0.5 % solution of toluidine blue with the addition of 1 % sodium carbonate, and mounted under a coverslip using Bio Mount HM (Bio Optica, Milano, Italy). The resulting

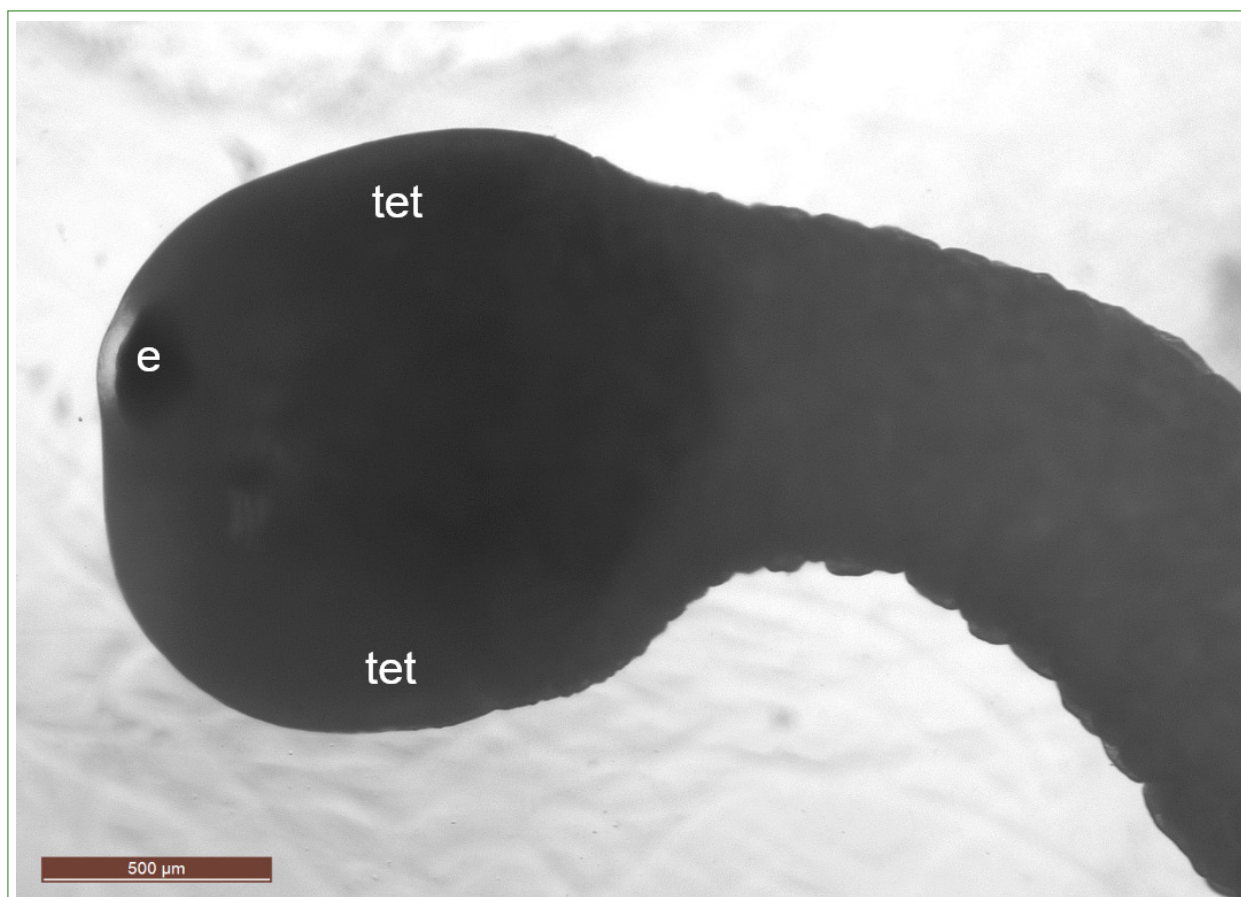


Fig. 1. Photograph of an extended isolated eye tentacle of *Helix pomatia* obtained using light microscopy. Abbreviations: *e* — eye, *tet* — tip of the eye tentacle

Рис. 1. Фотография препарата вытянутого изолированного глазного щупальца *Helix pomatia*, полученная при помощи светового микроскопа: *e* — глаз; *tet* — кончик глазного щупальца

preparations were examined under a Leica DMI 6000 inverted fluorescence microscope (Leica Microsystems, Wetzlar, Germany) and photographed with a Leica DFC360 FX digital camera (Leica Microsystems, Wetzlar, Germany). Approximately 2,340 semithin sections of eye tentacles from 22 eye tentacles obtained from 11 molluscs were prepared and examined. All semithin sections of eye tentacles were made from new preparations of isolated eye tentacles from new molluscs.

Traditional morphometrics

Measurements were performed on photographs of semithin sections of eye tentacles passing through the center of the eyes. Twenty measurements of eye size (10 measurements along the anteroposterior axis and 10 along the horizontal axis) were carried out on 10 semithin sections of eye

tentacles from 10 eye tentacles obtained from at least five molluscs. The exact number of molluscs cannot be given, as 10 eye tentacles were selected from a total of 22 eye tentacles obtained from 11 molluscs.

Calculation of statistical indicators

Mean values of the obtained morphometric data and their standard deviations were calculated using standard formulas (Lakin 1990).

Results

Morphological characteristics of the camera-like eye of *Helix pomatia*

Observation of intact specimens, together with the study of preparations of isolated eye tentacles and histological preparations of isolated eye tentacles of *H. pomatia*, reveals the following. A pair of camera-like eyes is

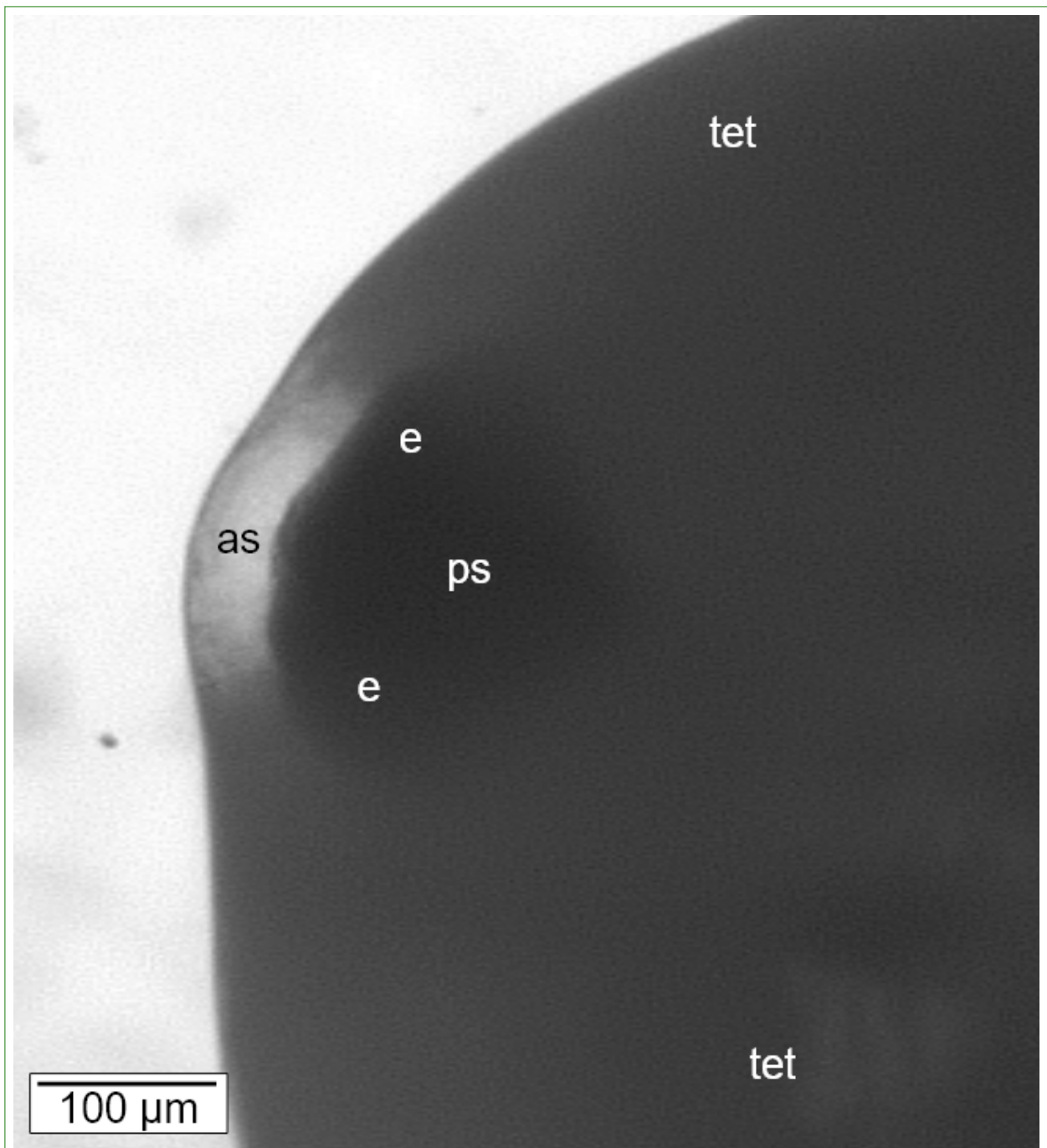


Fig. 2. Photograph of the tip of an extended isolated eye tentacle of *Helix pomatia* obtained using light microscopy. Abbreviations: *as* — anterior portion of the eye, *e* — eye, *ps* — posterior portion of the eye, *tet* — tip of the eye tentacle

Рис. 2. Фотография кончика препарата вытянутого изолированного глазного щупальца *Helix pomatia*, полученная при помощи светового микроскопа: *as* — передний отдел глаза; *e* — глаз; *ps* — задний отдел глаза; *tet* — кончик глазного щупальца

located at the tips of one of the two pairs of cephalic tentacles — the upper pair (Fig. 1). The eyes are situated inside the upper part of the tentacles and are completely isolated from the environment (Figs. 1, 2). The anterior, smaller portion of the eyes, which is adapted for light penetration, is covered

by a transparent, colorless integument of the tentacles (Fig. 2). The posterior, larger portion of the eyes, which is not adapted for light penetration, is surrounded by the internal structures of the tentacles and covered by a translucent, gray-brown integument of the tentacles (Fig. 2).

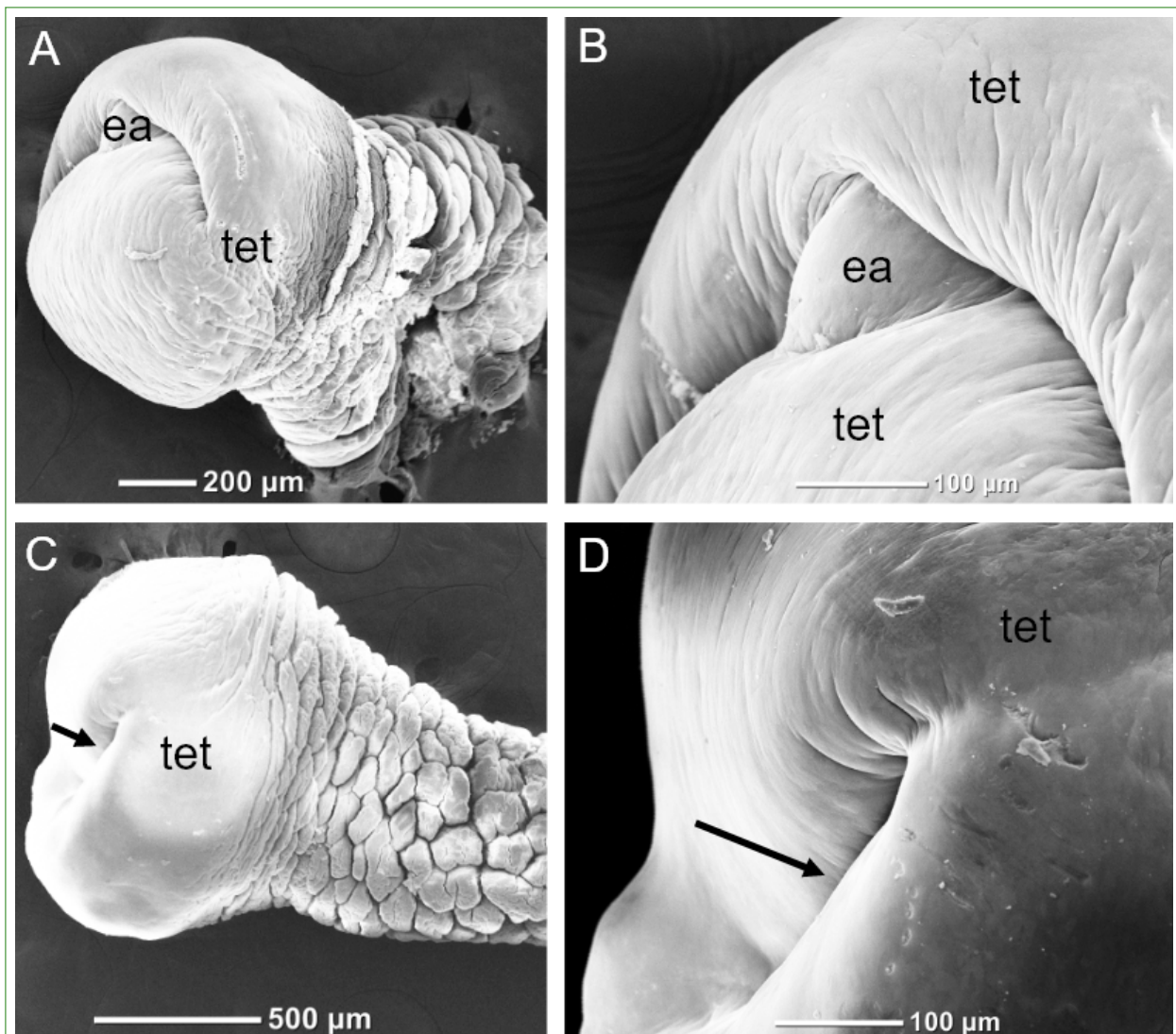


Fig. 3. Scanning electron micrographs of partially retracted isolated cephalic tentacles of *Helix pomatia*. **A** — partially retracted isolated eye tentacle with a visible eye area. **B** — tip of a partially retracted isolated eye tentacle with a visible eye area. **C** — partially retracted isolated eye tentacle with the eye area no longer visible. **D** — tip of a partially retracted isolated eye tentacle with the eye area no longer visible. Abbreviations: *ea* — eye area, *tet* — tip of the eye tentacle. The arrow indicates the region of the tentacle inside which the eye is located.

Рис. 3. Фотографии препаратов частично сократившихся изолированных глазных щупалец *Helix pomatia*, полученные при помощи сканирующего электронного микроскопа: **A** — частично сократившееся изолированное глазное щупальце, на котором еще видна область глаза; **B** — кончик частично сократившегося изолированного глазного щупальца, на котором еще видна область глаза; **C** — частично сократившееся изолированное глазное щупальце, на котором область глаза уже не видна; **D** — кончик частично сократившегося изолированного глазного щупальца, на котором область глаза уже не видна; *ea* — область глаза; *tet* — кончик глазного щупальца, стрелка показывает область щупальца, внутри которой находится глаз

Observation of intact specimens, combined with analysis of preparations of isolated eye tentacles and histological preparations of isolated eye tentacles of *H. pomatia*, shows that, depending on the state of the tentacles,

of which there are three, the camera-like eyes exhibit two established types of spatial orientation. In extended tentacles, the anterior portion of the eyes faces the tip of the tentacles (Figs. 1, 2). In partially retracted

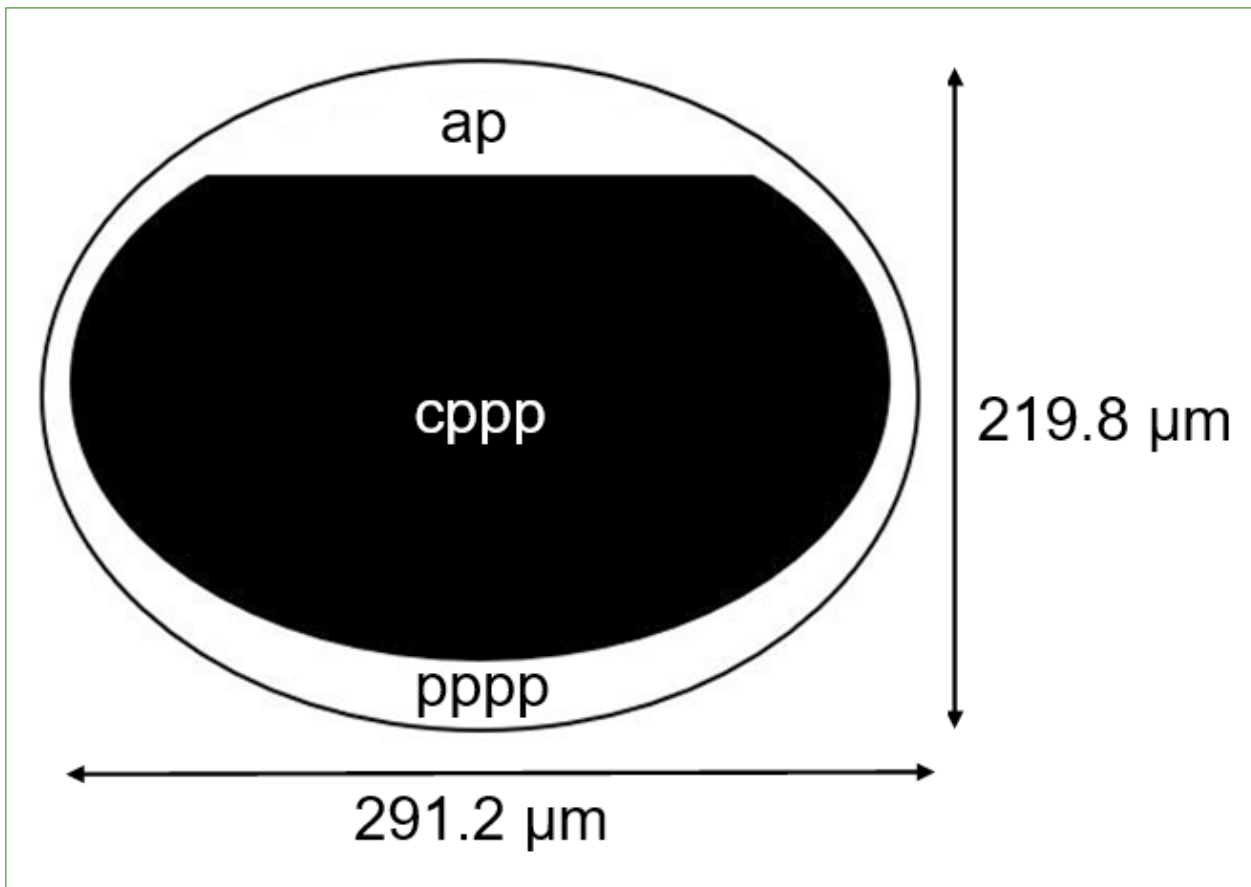


Fig. 4. Schematic diagram of the camera-like eye of *Helix pomatia*. Abbreviations: *ap* — anterior portion of the eye, *cprp* — central part of the posterior portion of the eye, *pprp* — peripheral part of the posterior portion of the eye

Рис. 4. Схематичное изображение камерного глаза *Helix pomatia*: *ap* — передний отдел глаза; *cprp* — центральная часть заднего отдела глаза; *pprp* — периферическая часть заднего отдела глаза

tentacles (Fig. 3), the eyes are deployed such that their anterior portion is directed toward the wall of the tentacles. In fully retracted tentacles, it was not possible to determine the spatial orientation of the eyes.

Examination of preparations of isolated eyes of *H. pomatia* indicates that the paired camera-like eye consists of a single eyeball as the main structure.

Viewing preparations of isolated eyes of *H. pomatia* demonstrates that the camera-like eye has the shape of an oblate ellipsoid (Fig. 4).

According to morphometric data obtained for *H. pomatia*, the size of the camera-like eye is $219.8 \pm 10.1 \mu\text{m}$ ($n=10$) along the anteroposterior axis and $291.2 \pm 25.8 \mu\text{m}$ ($n=10$) along the horizontal axis (values are presented as mean \pm standard deviation, n — number of eyes) (Fig. 4).

Observation of intact specimens of *H. pomatia* reveals that the camera-like eye appears as a black structure. The study of preparations of isolated eye tentacles and isolated eyes of *H. pomatia* suggests that the pigment within the camera-like eye is unevenly distributed. The anterior portion of the eye is completely transparent and colorless (Figs. 2, 4). The posterior portion of the eye can be divided into two parts based on location, size, transparency, and color: the central part, located inside the eye, is large, opaque and black in color; the peripheral part, located along the border of the eye, is smaller, completely transparent, and colorless (Figs. 2, 4). The observed pattern of pigment distribution combines completely transparent, colorless areas with an opaque, black area, resulting in the eye appearing black overall.

Discussion

Morphological characteristics of the camera-like eye of Helix pomatia

A pair of camera-like eyes of *H. pomatia* is located at the tips of the upper pair of cephalic tentacles. The eyes are situated inside the upper part of the tentacles, completely isolated from the environment. The anterior, smaller portion of the eyes, adapted for light penetration, is covered by a transparent, colorless integument of the tentacles. The posterior, larger portion of the eyes, which is not adapted for light penetration, is surrounded by internal structures of the tentacles and covered by a translucent, gray-brown integument of the tentacles. This location of the camera-like eye in *H. pomatia* is consistent with that observed in other terrestrial pulmonate gastropods. A pair of camera-like eyes in this group is invariably located at the tips of the upper pair of cephalic tentacles, as documented in *Helix aspersa* Müller, 1774 (Eakin, Brandenburger 1975) and *Limax maximus* Linnaeus, 1758 (Lawson 1863). Although the precise position of the eyes within the upper tentacles has not been determined for all species, unpublished data from the author, obtained during the preparation and examination of isolated eye tentacles of molluscs, indicate that the eyes occupy a consistent position: inside the upper part of the tentacles, completely isolated from the environment, as observed in *Helix lucorum* Linnaeus, 1758 (Shepeleva 2012) and *Succinea putris* Linnaeus, 1758 (Shepeleva 2015). In these species, the anterior, smaller portion of the eyes, adapted for receiving light, is covered by a transparent, colorless integument of the tentacles, while the posterior, larger portion of the eyes, not adapted for light reception, is enveloped by the internal structures of the tentacles and covered by a translucent, gray-brown integument of the tentacles. Thus, the location of the camera-like eye of *H. pomatia* is identical to that found in other terrestrial pulmonate gastropods.

In *H. pomatia*, depending on the state of the tentacles, of which there are three, the

camera-like eyes exhibit two established types of spatial orientation. In extended tentacles, the anterior portion of the eyes faces the tip of the tentacles. In partially retracted tentacles, it is directed toward the wall of the tentacles. In fully retracted tentacles, the spatial orientation of the eyes has not been established. Among terrestrial pulmonate gastropods, depending on tentacle state, two groups of spatial orientation types have been identified: those with two orientation types (toward the tip of the tentacles and toward the wall of the tentacles) and those with one orientation type (toward the tip of the tentacles only) (Burch 1968; Eakin et al. 1980; Zaitseva 2004). Most mollusc species exhibit two types of spatial orientation. Although the spatial orientation in extended tentacles has not always been explicitly considered, examination of drawings from semithin sections of eye tentacles suggests that in extended tentacles, the anterior portion of the eyes is directed toward the tentacle tip, as shown in *Agriolimax reticulatus* Müller, 1774 (Newell, Newell 1968) and *Achatina fulica* Bowdich, 1822 (Tamamaki 1989a). In partially retracted tentacles, invagination and inversion of the tentacle tip occur, causing the eyes to change their spatial orientation (Burch 1968; Eakin et al. 1980; Zaitseva 2004). This phenomenon has been described and illustrated for two species — *A. reticulatus* (Newell, Newell 1968) and *A. fulica* (Tamamaki 1989a). In both these species, the anterior portion of the eyes turns toward the tentacle wall at nearly a right angle (Newell, Newell 1968; Tamamaki 1989a). In fully retracted tentacles, the spatial orientation of the eyes has not been described. In some mollusc species, only one type of spatial orientation has been identified. In extended tentacles, the anterior portion of the eyes is directed toward the tentacle tip, as in *Athoracophorus bitentaculatus* Quoy et Gaimard, 1832 (Eakin et al. 1980). In partially retracted tentacles, invagination and inversion do not occur, so the eyes retain their spatial orientation. In fully retracted tentacles, the spatial orientation repeats that of extended and partially retracted tentacles (Eakin

et al. 1980). Thus, the spatial orientation of the camera-like eye in *H. pomatia* is similar to that observed in other terrestrial pulmonate gastropods.

The paired camera-like eye of *H. pomatia* consists of a single eyeball — the main one. In terrestrial pulmonate gastropods the paired camera-like eye exhibits two structural variants: a single eyeball (the main one) or two eyeballs (main and accessory). Many mollusc species possess a pair of eyes, each formed by a single eyeball, as in *Helix albescens* Rossmäslar, 1839 (Zaitseva 1992; 2000; 2016) and *Cochlodina laminata* Montagu, 1803 (Shepeleva 2006a). Fewer species are known to possess a pair of eyes, each formed by two eyeballs. These include representatives of different life forms, both snails and slugs. Among snails, only one species is known — *A. fulica* (Tamamaki, Kawai 1983; Tamamaki 1989a). Among slugs, several species have been documented: *L. maximus* (Henchman 1987), *A. reticulatus* (Newell, Newell 1968), *Limacus flavus* Linnaeus, 1758 (Kataoka 1977; Tamamaki 1989b), and *Deroceras agreste* Linnaeus, 1758 (Zieger et al. 2008). Thus, the structure of the camera-like eye of *H. pomatia* corresponds to that found in other terrestrial pulmonate gastropods.

In *H. pomatia*, the camera-like eye is shaped as an oblate ellipsoid. Among terrestrial pulmonate gastropods, camera-like eyes exhibit four shapes: oblate ellipsoid; prolate ellipsoid; irregular, and normal spheroid (Shepeleva 2013; 2019). The most common shape is the oblate ellipsoid, as seen in *Helicigona lapicida* Linnaeus, 1758 (Shepeleva 2006b). The prolate ellipsoid is somewhat less common, as in *Arianta arbustorum* Linnaeus, 1758 (Shepeleva 2006c). Irregular shapes are sometimes observed, typically due to the presence of an accessory eyeball, as in *L. flavus* (Tamamaki 1989b). The least common shape is the normal spheroid, as in *Strophoheilus* sp. (Oswaldo-Cruz, Bernardes 1982). Thus, the shape of the camera-like eye in *H. pomatia* is consistent with that found in many other terrestrial pulmonate gastropods.

The size of the camera-like eye of *H. pomatia* is 219.8 μm along the anteroposterior axis

and 291.2 μm along the horizontal axis. According to calculations performed in this study, the size of the camera-like eyes among terrestrial pulmonate gastropods with an oblate ellipsoid shape varies by a factor of 1.5 along the anteroposterior axis and 1.4 along the horizontal axis. The maximum eye size reaches 199 μm along the anteroposterior axis and 270 μm along the horizontal axis, as in *Monachoides incarnata* Müller, 1774 (Shepeleva 2006a). The minimum eye size is 130 μm along the anteroposterior axis and 190 μm along the horizontal axis, as in *Trochulus hispidus* Linnaeus, 1758 from southern Sweden (Shepeleva 2008). Thus, the size of the camera-like eye of *H. pomatia* with the oblate ellipsoid shape is not directly comparable in magnitude to that of other terrestrial pulmonate gastropods with the same shape.

In *H. pomatia*, the camera-like eye of intact individuals appears as a black structure. The pigment within the eye is unevenly distributed. The anterior portion of the eye is completely transparent and colorless. The posterior portion of the eye can be divided into two parts based on location, size, transparency, and color: the central part, located inside the eye, is large, opaque, and black in color; the peripheral part, located along the border of the eye, is smaller, completely transparent, and colorless. This pattern of pigment distribution — combining completely transparent, colorless areas with an opaque, black area — results in the eye appearing black overall. In terrestrial pulmonate gastropods, the camera-like eyes of intact individuals are uniformly black, as observed in *H. lucorum* (Shepeleva 2012) and *Cepaea hortensis* Müller, 1774 (Shepeleva 2017). Although pigment distribution in the eyes of terrestrial pulmonate gastropods has not been systematically studied, analysis of photographs from isolated eye preparations indicates a single pattern of uneven distribution, as seen in *H. lucorum* (Shepeleva 2012) and *T. hispidus* from southern Sweden (Shepeleva 2008). In these species, the anterior portion of the eyes is completely

Table 1
Морфологические свойства камерного глаза *Helix pomatia*

Morphological characteristics of the camera-like eye of *Helix pomatia*

Characteristic	<i>Helix pomatia</i>
Location	At the tips of the upper pair of head tentacles and inside the upper part of the tentacles in complete isolation from the environment: the anterior, smaller portion of the eye, which is adapted for light penetration, is covered by the transparent, colorless integument of the tentacles; the posterior, larger portion of the eye, which is not adapted for light penetration, is surrounded by the internal structures of the tentacles and covered by the translucent, gray-brown integument of the tentacles.
Spatial orientation	Two established types: in extended tentacles, the anterior portion of the eye faces the tip of the tentacles; in partially retracted tentacles, the anterior portion of the eye is directed toward the wall of the tentacles; in fully retracted tentacles, it was not possible to determine the spatial orientation of the eye.
Structure	Consists of a single eyeball (the main one).
Shape	Oblate ellipsoid.
Size (anteroposterior × horizontal axis)	219.8±10.1 × 291.2± 25.8 μm (<i>n</i> =10)
Color	Black: the anterior portion of the eye is completely transparent and colorless; the posterior portion of the eye can be divided into two parts based on location, size, transparency, and color: the central part, located inside the eye, is large, opaque, and black in color; the peripheral part, located along the border of the eye, is smaller, completely transparent, and colorless.

transparent and colorless, while the posterior portion can be divided into a large, opaque, black central part and a smaller, completely transparent, colorless peripheral part along the perimeter of the eyes. Thus, the color and pigment distribution of the camera-type eye in *H. pomatia* are identical to those observed in other terrestrial pulmonate gastropods.

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

The morphological characteristics of the camera-like eye of *H. pomatia* examined in this study suggest that for this mollusc, the eye may perform the following functions: determining the light intensity and determining light direction when the tentacle is extended. These proposed functions are consistent with published data on the functions of the

camera-like eye in *H. pomatia* (Willém 1892) and in other terrestrial pulmonate gastropods (Wheeler 1921; Newell, Newell 1968; Gál et al. 2004; Shepeleva 2006c; 2009b; Zieger et al. 2008).

Conclusion

In this study, the external morphology of the camera-like eye of the terrestrial pulmonate gastropod *H. pomatia* was examined in detail for the first time. The following morphological characteristics of the eye were investigated: location, spatial orientation, structure, shape, size, and color (Table 1). These properties were compared with the corresponding known or independently assessed morphological characteristics of camera-like eyes from other terrestrial pulmonate gastropod species. Of the six, all were comparable: five properties

are typical of terrestrial pulmonate gastropods, while one property is atypical. Thus, the morphological characteristics of the camera-like eye of *H. pomatia* are largely, but not entirely, typical of terrestrial pulmonate gastropods. Additionally, based on the morphological characteristics studied, potential functions of the camera-like eye of *H. pomatia* were identified. This article is the first article dedicated to the external morphology of the camera-like eye in a representative of terrestrial pulmonate gastropods specifically and of gastropods more broadly.

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