Note on the Eyes of Cardium Muticum *Reeve.*

by

K. Kishinouye, *Rigakushi.*

Zoologist to the Department of Agriculture and Commerce.

With Plate IX.

The eyes of the genus *Cardium* have been studied by many authors; but, so far as I know, no one has yet found such conspicuous eyes as I describe below in the molluscs of this genus. The following note may therefore prove interesting to investigators of the molluscan eye.

The mantle-edges, both right and left, of *Cardium muticum* are beset with dark brown, almost black pigment. They unite at the posterior end of the shell and form a triangular pigmented area, surrounding the siphonal openings. Over this area the right and left valves of the shell do not meet closely but leave a rather wide slit. In this triangular, pigmented area we find a great many tentacles, arranged in many irregular rows round the siphonal openings.

The tentacles are of various sizes : those on the periphery of the pigmented area are larger and longer; those towards the siphonal openings, shorter and more slender till at the margin of these they are reduced to mere fringes (fig. 1). Generally speaking the larger and longer tentacles about 100 in number bear the eyes. They are bent away from the siphonal openings, and each of them has a longitudinal band of black pigment on the siphonal side, *i. e.* on the

side exposed to the light.

The eye can easily be found without a microscope as a black spot on the siphonal side of the tip of a tentacle, opposite to the position of the eye of *Cardium edule*, which is "on the shell side of the mantle." * Along the upper, posterior † side of the eye, the epithelium is raised into a triangular screen (figs. 2, 6, 7, 9, *s.*). At one time I thought that this screen is the tip of the tentacle, but a closer examination showed that it is raised secondarily, probably to protect the eye, and that the true tip is occupied by the eye.

In the eye of *Cardium muticum* we find all the essential parts of an eye. Its structure resembles on the whole that of the eyes of *Pecten*, *Spondylus*, and *Cardium edule*; but differs in some essential points, since it is difficult to find the homology of some constituent parts.

The *cornea* (fig. 2, *c.*) consists of thin pavement cells, while that of other molluscs consists generally of columnar cells. The general epithelium becomes gradually thin as it approaches the lens and forms the thin cornea over it. The corneal cells are colourless, transparent, and polygonal in outline. The convexity of the cornea is great, its external surface being almost hemispherical.

The *lens* (fig. 2, *l.*) is large and consists of a great number of cells. Instead of the usual biconvex, flat form the lens of *Cardium muticum* is ovoid. Its longer axis is parallel to the optic axis and its broader end is directed below. It is more or less constricted at the middle part. The cells composing the lens are large, colourless and compressed in the direction of the optic axis, the degree of compression being greater nearer the cornea. In the median lon-

* Patten—Eyes of Molluscs and Arthropods. Mittheil. aus der Zool. Station zu Neapel. 1886.

† For the sake of convenience, the word *upper* is used to designate the distal end of the tentacle, and the word *anterior* that side of the tentacle turned towards the siphonal openings. The words *lower* and *posterior* naturally indicate the opposites of the above words.

gitudinal section, we find that the cells of the lens are arranged for the most part in two longitudinal columns. The cells are nucleated, having nuclei near the external surface of the lens.

The *retina* (fig. 2, *ret.*) is in contact with, and directly below, the lens. It is very simple in structure, consisting of colourless, columnar cells arranged in one layer. These cells have rods (fig. 2, *ro.*) which are not clearly found in the eye of *Cardium edule* (Patten,* Bütschli **). The rods are directed away from the retinophorae and are separated from them by a pseudomembrane. They seem to be hollow, as they appear as rings in cross section of some well preserved specimens. They are longest at the optic axis and gradually diminish in length as the distance from the optic axis increases. They are stained homogeneously and rather deeply. As regards the retinophoræ, the nuclei are deeply stained, while the protoplasm is very faintly stained. I could not find the ganglionic-cell layer, although it is stated to be present in the eyes of *Pecten* and *Cardium edule* (Patten, Bütschli).

Below the retina and continuous with it at the circumference, there is a layer of flat cells (fig. 2, *ch.*). These cells, are small and thin at the juncture with the retina, so that it is difficult to find out this connection in well developed eyes. I shall name this layer as the *choroid*, as it seems to be homologous in position to the pigment epithelium of the choroid of the vertebrates. If the tapetum (argentea of Patten) of *Pecten* and *Cardium edule* is cellular in orign, as it is stated to be, the choroid of *Cardium muticum* is probably homologous with it.

Below the choroid there is a membranous layer. It is the *tapetum* (fig. 2, *t.*). It consists of many thin, shining layers, stained deeply and homogeneously by colouring solutions. I cannot find any sign of

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* Patten—*loc. cit.*

** Bütschli—Notiz zur Morphologie des Auges der Muscheln. (Zoologisches Jahresbericht für 1886).

cellular structure, though according to Patten the like-named part of *Pecten* and *Cardium edule* is said to have been produced from cell layers. The tapetum covers entirely the lower surface of the choroid, except at the spots through which the branches of the optic nerve enter. If the tapetum of *Pecten* and *Cardium edule* is cellular in origin, there is in these *molluscs* no organ homologous with the tapetum of *Cardium muticum*. Moreover, the tapetum of *Pecten* and *Cardium edule* is said to be found below the layer of retinophoræ, while that of *Cardium muticum* is below the choroid.

Lastly there comes a *layer of pigmented cells* (fig. 2, *p.*). This invests all the external surface of the above described parts of the eye below the cornea, leaving only a small round area over the upper hemispherical portion of the lens or the pupil only. The pigmented layer as a whole is cup-shaped or rather urn-shaped. It consists of flat, polygonal cells arranged in one layer. The cells at the neck of the urn are smaller and thicker than those elsewhere. The pigment is black and serves to absorb rays of light which fall obliquely upon the retina. In *Pecten* the greater part of this function is fulfilled by the iris, and its red pigment layer, probably homologous with the pigment layer of *Cardium muticum*, absorbs rays of light from the lower side alone. As the eyes of *Cardium muticum* are destitute of the iris, the pigment layer is well developed.

The eyes are *innervated* from the viscero-parietal ganglia. A nerve (fig. 2, *n.*) runs through the central axis of each tentacle. It is divided into two branches where it touches the eye. One branch (fig. 2, n^2) passes through the pigment layer near the optic axis and spreads between the choroid and the tapetum, while the other branch (fig. 2, n^1) passes through the pigment layer at the level of the retina from the shell-side and seems to innervate the retina.

As the numerous eyes of an adult individual are sometimes found

in different stages of *development*, we can study their formation from their sections. It seems to me that the eyes of *Cardium* develop in two ways. Although we must regard both as more or less abbreviated, yet we can distinguish one as *the more abbreviated process* from the other *the less abbreviated*. If an investigation into their development could be made in immature specimens, more satisfactory results would doubtless be obtained, unless they are as in the young of *Pecten* in which Patten was disappointed to find any abbreviated development of the eye. I shall describe *the less abbreviated process* of development first.

There first forms on the tip of a tentacle (fig. 3) an invagination the mouth of which then closes (fig. 4). Thus a solid mass of cells is produced, with a slight concavity at the place where the mouth of the invagination at first opened, and this is turned towards the siphonal opening. It consists of cells in many irregular rows, while the general epithelium consists of columnar cells in one row. A nerve running along the central axis of the tentacle touches the lower surface of the cell mass and there divides anteroposteriorly into two branches.

In the upper part of the cell mass, a spherical portion becomes differentiated and separated from the rest by a basement membrane (fig. 5). This spherical portion is the rudiment of the lens, which is therefore epiblastic in origin, not mesoblastic as in the case of the eye of *Pecten*, according to Patten. The cells constituting the rudimentary lens are large and some of them have nucleoli. At this stage, although the lens is differentiated and separate from the surrounding cell mass, it is still imbedded in the epiblastic thickening.

In the next stage (fig. 6) the epiblastic thickening surrounding the lens is observed to be separated into two parts—an upper and a lower. The upper part is continuous with the general epithelium and consists of flat cells in one row. It is the cornea. The lower part is cup-shaped and is not connected with the general epithelium. It consists

of cells in about two rows. It is the retina. On the upper side of the base of the eye there is formed a large hollow. This makes the eye stand out and at the same time pushes it towards the siphonal opening. Thus the hollow divides the tip of a tentacle into two—a prominent eye and a somewhat triangular screen behind it. The hollow corresponds in position with the original mouth of the invagination for the eye. Pigment is produced in mesoblast cells surrounding the retinal portion. These pigmented cells form the pigment layer. A lumen is secondarily produced between the lens and the retina.

The lens grows by the multiplication of cells in the direction of the optic axis and assumes the shape of an ellipsoid, and consequently the lumen between the lens and the retina disappears (fig. 7). The peculiar arrangement of cells in the lens begins in this stage.

Late in development, the retinal portion is divided into two layers, the retina proper and the choroid. These two layers are continuous with each other at the circumference. Soon after the separation of the choroid from the retina, the tapetum is formed below the choroid, probably by the secretion of the cells which constitute the latter. I cannot corroborate the view that the tapetum is formed of modified cell layers, for even in these early stages I cannot find any thing of a cellular nature in it. Afterwards rods are produced from the retinal cells.

The more abbreviated process of development (see p. 283) is as follows :

At the top of a tentacle the epithelium becomes thickened and forms a little knob within (fig. 8). The little knob is next cut off from the epithelium (fig. 9). In this stage a hollow is produced behind the little knob and thus the triangular screen (fig. 9, *s.*) is formed. The little knob cut off is spherical in form and consists of a few, large

cells. It enlarges by the division of the cells and assumes an ellipsoidal form (fig. 10). Cells forming the lower part of the ellipsoidal mass become small by division. These smaller cells are not clearly distinguished from larger cells, as there are many cells of intermediate size. Later, however, the smaller cells are separated from the larger ones and form the retinal portion, while the larger become the lens. The later stages of development are quite like those in the first process.

In the two process of development, both the lens and the retina are produced from the epiblast. The process of their formation is probably abbreviated. Originally they were perhaps produced by two separate invaginations as in the case of the Vertebrata, one invagination for the retina and one for the lens. The invagination for the retina must have been the first to be closed and cut off from the epithelium ; it formed a hollow sphere, the upper wall of which became the retina and the lower wall the choroid. The invagination for the lens was next formed and cut off in its turn from the epithelium, and had its lumen obliterated.

The eyes of *Cardium* differ from those of *Pecten** chiefly by the presence of the choroid between the retina and the tapetum and by the mesoblastic origin of the pigment layer ; but I am inclined to think that in *Pecten* the choroid disappeared after secreting the tapetum, and that the red pigment layer is mesoblastic in origin, and not directly in connection with the retina.

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* It is hard for me to accept Patten's observation that the lens of *Pecten* is mesoblastic in origin.

PLATE IX.

Explanation of Figures.

List of Abbreviations.

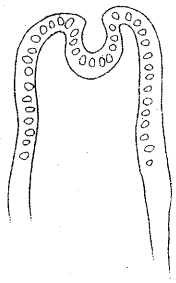
c.	Cornea.	ret.	Retina.
ch.	Choroid.	ro.	Rod.
l.	Lens.	s.	Triangular screen.
n, n^1, n^2.	Optic nerve and its branches.	t.	Tapetum
p.	Pigment layer.		

FIG. 1. Inhalent siphon of *Cardium muticum*, magnified. One longitudinal half of it is cut away.

FIG. 2. Median sagittal section of a fully developed eye (constructed from two sections).

FIGS. 3-7. Semi-diagrammatic representations to illustrate the less abbreviated process of the development of the eye (sagittal sections).

FIGS. 8-10. Semi-diagrammatic representations to illustrate the more abbreviated process of the development of the eye (longitudinal sections).



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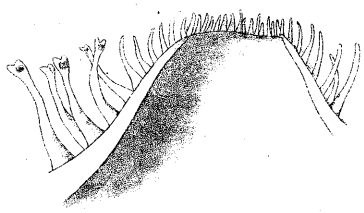

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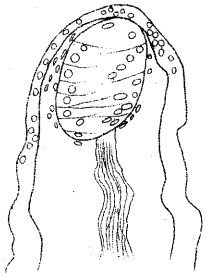

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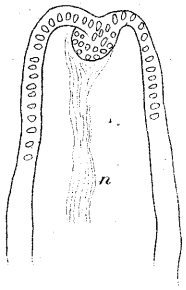

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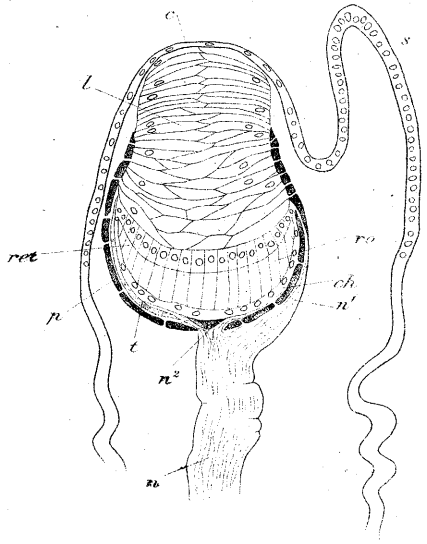

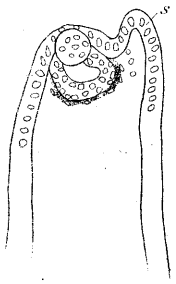

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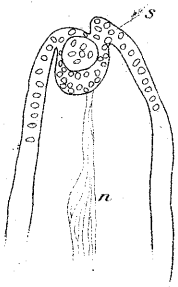

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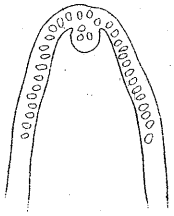

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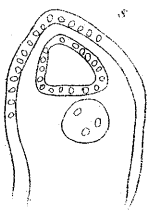

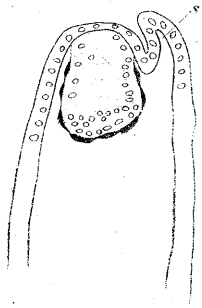

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K. Kishinouye del.