# II. Wissenschaftliche Mittheilungen.

## 1. The Development of the Compound Eye of Alpheus.

By F. H. Herrick, Ph.D. Adelbert College, Cleveland, Ohio, U.S.A.

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A study of the embryology and systematic zoölogy of the crustacean genus *Alpheus* was undertaken four years ago, and abstracts of this work appeared in 1886 and 1887 [1], when the development of the compound eye received some notice. The most important details have thus for some time been worked out, and the greater part of the drawings have been ready for over a year, awaiting the publication of

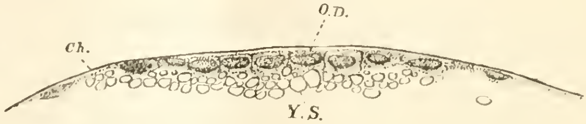


Fig. 1. Transverse section through middle of left optic disc. *Ch.* = Chorion. *O.D.* = optic disc. *Y.S.* = yolk spherule.

the final monograph. Full illustrations are almost essential for a clear presentation of the subject, but it is hoped that with the few figures at our command, together with those already published (see University Circulars, No. 54), the following account may be fairly intelligible.

The first trace of the eye in *Alpheus* is the optic disc (Kopflappen). The embryo at this time consists chiefly of 3 patches of cells, namely, the ventral plate, and anterior to this the optic discs, one on each side of the middle line. Two germinal layers can now be recog-

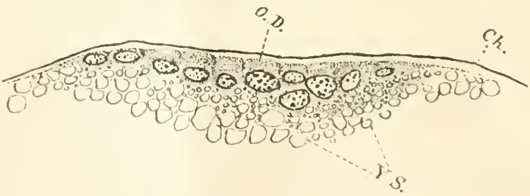


Fig. 2. Transverse section through left optic disc, to one side of middle. The thickening of the disc begun.

nized, — an outer layer which we may call the ectoderm, and secondly an inner, indifferent layer, consisting of cells scattered through the yolk. This last gives rise to all of the future endoderm, to all or greater part of the mesoderm, and to some of the ectoderm. The optic disc (*O.D.* Fig. 1) consists of a pavement or single sheet of ectoderm, resting on the food yolk. From the optic disc the whole eye, — that is the retina with its ganglia — is developed.

[1] John Hopkins University Circulars, Nos. 54, 63. Baltimore, Maryland, U.S.A.

In the next phase the embryo is triangular or V-shaped, the optic discs being united to the abdominal plate (which corresponds to the apex of the V), by a band of cells on either side. At this stage, before any of the appendages are fully budded, a thickening of the optic disc occurs (Figs. 2 and 3). It begins in the centre of the disc, and is due (1) to the emigration or crowding of cells from the surface (effected


Fig. 3. Transverse section through the optic discs and egg, from same series as Fig. 2. The left disc (*O.D.*[1]) is cut through the centre.

by cell-division in planes at right angles to a tangent at the surface); (2) to delamination or division of cells in planes parallel with a surface tangent. The initial thickening is due almost wholly to emigration, but the second method soon becomes common.

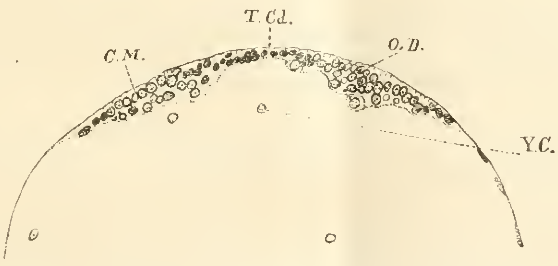


Fig. 4. Transverse section through the optic discs and egg. (A few hours younger than the egg-nauplius. Fig. 5.) Plane of section slightly oblique with respect to long axis of embryo. The posterior portion of one (*O.D.*) is divided, the anterior portion of the other.

*C.M.* = central area of optic disc, where cells are rapidly multiplying.
*T.Cd.* = transverse cord, uniting discs.
*Y.C.* = yolk cells (inner layer).

Thus two solid ectodermal plates are formed, which are soon united by a transverse bridge of cells (Fig. 4 *T.Cd.*) Elements from the yolk pass forward to the optic disc, and it is almost certain that they unite with it, so that to the processes just mentioned, by which the disc is increased, must be added a third; namely the accession of cells from the yolk (Fig. 4 *Y.C.*).

In an embryo approximately 3 days old, rudiments of three pairs of appendages are present, and the triangular area between the optic discs and abdominal plate is closed over. The disc continues to grow in the way described, but chiefly as before, by the emigration or inclusion of superficial cells. The cells in the outer central portions of the disc are large and granular, and actively multiplying. Spores at this juncture make their appearance in various parts of the embryo (see University Circular, No. 63).

We now pass to the »Egg-nauplius« stage (embryo 1 week old), as the intermediate stages are not specially important, as regards the eye. The optic disc has attained to the dignity of a lobe. It is an oval, dense mass of ectoderm, swollen or protruding slightly from the surface, and it is united closely to the »brain«, or ganglia of the antennae (Fig. 5).


Fig. 5. Transverse section of the egg-nauplius, cutting the optic lobes (*O.L.*), near their middle points, and the anterior end of the brain (*S.O.G.*).

*O.L.* = optic lobe. *S.O.G.* Supra-oesophageal ganglion. *O.G.* = gangliogen. The retinogen, the superficial layer of large cells soon becomes very distinct.

The next stage to consider is when there are 7 pairs of rudimentary appendages. The optic lobes (using this term now instead of optic discs) have grown very large and prominent, superficial layer of large granular cells is clearly defined from the mass of cells below. This differentiation has begun in Fig. 5. The outer layer is the retinogen, since all parts of the eye external to the basement membrane, are developed from it. The cell mass below, that is, the remainder of the lobe, is appropriately called the gangliogen, since it gives rise to the ganglia of the eye stalk.

When 10 pairs of appendages are present, the optic lobes are of enormous size. The retinogen is a concavo-convex cellular disc, consisting of elongated cells arranged radially with respect to a centre in the gangliogen. It is no longer one cell thick, except at its edges. A delicate, structureless membrane is now developed in the optic lobe. This is the basement membrane, a topographical boundary of great importance, separating the retinogen or eye proper, from the parts below. It is without doubt a secretion product of the ectoderm cells.

Dark brown pigment also appears in certain cells of the retinogen, in its postero-inferior part, next the basement membrane. The pigment cells develop over the entire inner convex surface of the retinogen, and lengthen rapidly, growing outward from the basement membrane. These are the retinulae, or pigment cells of the retina. Meantime the outer, elongated cells of the retinogen multiply actively and produce group or strings of cells, which are arranged radially with respect to a centre in the deeper parts of the gangliogen. The cells of the latter next the basement membrane also assume a corresponding arrangement. The cell strings mentioned above are the first step in the blocking out of the retina into its elements, the ommatidia. The following changes occur now in the retinogen. An outer layer — corneal layer -- is marked off, the function of which is to secrete the facetted cornea. Below this there is differentiated a second layer — the retinophoral layer, of which the crystalline cones are the secretion products. The cells of the corneal layer are arranged in twos, a pair to each ommatidium. The elongated retinophoral cells are grouped in fours. The retinulae grow forward, and meet the crystalline cones. They are arranged in tubular bundles, each tube or bundle consisting of 7 slender rods, coloured dark brown by pigment. The crystalline cone tapers inward into a slender stalk, which enters the lumen of the tube made by the 7 retinular. In the larval stages, but most noticeably in the adult the retinulae fuse to form a solid rod, covered with pigment, and fluted with 7 longitudinal ridges, which reveal its compound structure. A chitinous framework is developed by the time the animal is ready to hatch, in those parts of the eye most needing support, namely at the basement membrane, and at the outer part of the retinular zone where the delicate ends of the cones enter the tube formed by the retinulae. At the latter point the chitin forms a net, through the meshes of which, the bundles of retinulae regularly pass. Pigment appears in a slight quantity below the basement membrane. There are also seen certain spindle shaped cells, wedged in between the basement membrane and gangliogen. These may be either ectoderm or mesoderm, but their rare occurrence would indicate that they are not important. There are numerous undifferentiated ectodermal cells packed between the ommatidia. Each ommatidium consists of 13 cells, namely:

2 corneal cells, which secrete a single facet.
4 retinophorae, which secrete the crystalline cone.
7 retinulae.

The conditions of the eye now reached belong either to the larva or to the embryo, at the point of hatching. I purposely omit here a description of the development of the gangliogen, and of the histology of the adult eye, but wish to emphasize the following points:

1) The optic disc is at first a unicellular layer of ectoderm:

2) This disc becomes thickened by emigration of cells from the surface; by delamination, and probably also by the addition of cells from the yolk (inner layer as distinguished from the outer ectoderm).

3) The lobular mass of ectoderm thus formed (optic lobe), is differentiated into two parts, separated by a structureless membrane (basement membrane). The latter is probably secreted by the ectoderm cells along the line of division.

4) From the outer portion or retinogen, which is at first a single layer, the retina is developed. The rest of the lobe (gangliogen), gives rise to the ganglia and parts of the eye below the basement membrane.

5) Retinulae, retinophorae and corneal cells are differentiated ectodermal elements belonging to the retinogen.

6) The retinophorae are prolonged inwards with the cone but a short distance, and do not enter the retinular bundle.

7) There is no swollen pedicel, and nothing answering to pedicel, »rhabdom«, or »spindle« has been detected. If anything corresponding to it exists, it must be the inner solid cone of the retinular bundle, which is a product of the retinulae themselves.

8) No invagination or cavities of any kind occur in the development of this eye.

9) The ommatidium or element of the compound eye consists of 13 cells disposed in 3 layers, as follows.

a) corneal layer — 2 cells.

b) retinophoral layer — 4 cells.

c) retinular layer — 7 cells.

10) No nerve fibres have ever been detected in the crystalline cones. — (The section method was used entirely. The eggs and larvae were preserved in picrosulphuric acid, Perenyi's fluid, and alcohol.)

It is undoubtedly true that the development of *Alpheus* has undergone secondary changes in the course of its history, but there is no reason to suppose that it has diverged in this respect more than related species of Macroura. Much less would we be led to think that it was peculiar in the development of its eye. Studies upon other Macroura (*Hippa*, *Palaemonetes*) have led me to suspect that the method here described is the common one.

There is no evident homology between this eye and the structure of the ocelli of Arachnids, where there is an invagination, and consequent inversion of the parts which form the retina. Even if it is proved that in some of the prawns, the initial step in the development of the compound eye is an invagination of ectoderm, this case of *Alpheus* shows how little importance a fact like this can have. There seems to be a tendency to exaggerate the significance of an invagination of ectoderm. In the first place it is improbable that at the time when most of these infoldings occur, that a cell has any true upside or downside, or that an included cell is differentiated from one next it, which does not participate in the invagination.

It seems to me that for the present the following may be a good working hypothesis. All invaginations of ectoderm, whereever they occur in the animal kingdom, are primarily of no morphological importance, but simply mechanical expedients for introducing rapidly a large number of ectoderm cells below the surface. Where they have any significance, this is a secondary acquirement.

January 11th, 1889.

## 2. Zur Anatomie der Blattiden.

Von Dr. Erich Haase.

eingeg. 10. Februar 1889.

Vor Kurzem beschrieb E. A. Minchin[1] an der Küchenschabe (*Periplaneta orientalis*) zwei taschenartige Einstülpungen am Anfange der sechsten Rückenplatte und wies zu diesen gehörige Epitheldrüsenzellen nach, welche sich in spitze, verästelte Haare fortsetzten. Über die Bedeutung dieser Einrichtungen sagt derselbe l. c. pag. 231: »it is probable that it is a stink-gland, though I have not been able to satisfy myself of this«.

In der That ist diese Deutung der in beiden Geschlechtern schon bei den Larven vorkommenden Einrichtung als richtig zu bestätigen. Drückt man nämlich das Abdomen einer Küchenschabe derart, daß die Leibeshöhlenflüssigkeit nach hinten gedrängt wird, so treten zwischen dem fünften und sechsten Hinterleibssegment vor den harten Rückenplatten des letzteren zwei kleine, durch das eindringende Blut gelblich durchscheinende Säckchen hervor und verbreiten sofort ganz intensiv den bekannten Schabengestank; daß dieser seine Quelle in den beiden Stinkdrüsen hat, wird durch vorsichtige Auslösung der letzteren leicht nachgewiesen. Die Haare, welche das Secret dieser

[1] Quart. Journ. Micr. Sc. No. 115. Dec. 1888. p. 229—233.