On the Eyes of Some Invertebrata.

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With Plate XLV.

It is known that in the Vertebrata the percipient elements of the retina turn away from the light, while they are turned to it in the Invertebrata—an arrangement which is conditioned by the development of the organ in both the groups.

In order to attain the greatest effect and to embrace a very extended horizon the percipient elements can be arranged in two ways.

Either they form the wall of a hollow ball, into which the light falls through a very small opening, so that there is sketched a real image on the background of the eye. This kind of organ of sight is found in the vertebrates and the cephalophorous molluscs and lies below the surface of the body.

Or the parts of the eye perceiving the light are radially disposed on a more or less complete ball, which projects beyond the surface of the body. These eyes, forming a fan in vertical section, are met with among the Arthropoda and certain Lamellibranchiata.

A third form of eyes which belongs to the Arthropoda, the cup-shaped eyes with one lens, will not be considered in the present communication; nor will the organs of sight constructed upon the principle of the camera obscura be dealt with, since my purpose is merely to offer a few remarks in regard to fan-shaped (coniform) eyes.

Through Grenacher we know the construction of the eyes

(ommatidium) of Musca, while Berger first described the related layers of the optic ganglion. Already, some years ago, I myself examined both parts by means of thin vertical sections, and I can in the first place confirm Grenacher's accounts concerning the construction of the pseudoconus and of the retinula.

The whole set of eye-units (ommatidia[1]) of Musca vomitoria are enclosed in a chitinous capsule, the exterior face of which is formed of the cornea-lenses, while a thin chitinous membrane limits the eye towards the brain, being full of holes to let pass the nerve-fibres. It is only a little smaller than the cornea and nearly concentric to it. The eyes being placed on both sides of the head have their largest extension in the direction from above to below; the foremost retinulæ stand almost perpendicular on the basal membrane; in the midst of the eye they take a position more inclined backwards, and the last ones are not only set quite slantwise, but even curved in order to catch still a glimpse backwards, while all the other retinulæ are quite straight. With this setting of the eye-units the animal sees to the side, and obliquely to the front and behind, but not directly to the front. Experiments show also that a fly rests often quietly sitting if one approaches it with a fine-pointed object directly from the front; but upon approaching it from the side mostly makes off.

The eye is limited anteriorly by a fold in the membrane (Chitinpanzer) *x*, which is narrow and directed towards the inside, being specific to many insects.

Also on the dorsal margin such a fold, but less deep, is met with; whereas the posterior margin of the eye is supported by a round ledge (*y*), the transverse section of which is shown by the drawing.

[1] The term "ommateum" was introduced by Lankester in his memoir on the eyes of Scorpions to signify the entire soft parts of the non-segregate (unicorneal) eye of Arachnida and Hexapoda, consisting of a layer of nerve-end cells, and usually a layer of vitreous cells. The similar term "ommatidium" is introduced in this paper to signify the units consisting each of a retinula and a vitrella, together with their sheath of pigment cells, into which the ommateum of the multicorneal (polymeniscous) eye of Arthropods, is segregated.

The side-wall (cornea) does not project very much over the surface of the head, and is divided into a great number of plano-convex lenses (facets) which are separated from one another by narrow shallow furrows.

I will here recall to mind quite shortly what Grenacher says about the construction of the eye-units:

Below each cornea-lens is found a coniform space (Pl. XLV, fig. 1, A) filled with a liquid or jelly; its shape is apparently fixed by the enveloping pigment-cells. This is the pseudoconus. Its truncated point ends at the four crystal cells (4), which are also set together, so as to form a cone with its broad base outwards, the point inwards. They are the matrix-cells of the pseudoconus, and surrounded like it by the two principal pigment-cells (2).

The crystal cells are touched by the retinula (6), which diminishes in breadth as it passes inwards, and so represents a very much elongated cone, which surpasses the pseudoconus in length more than sixfold. The retinula consists of seven cells fused together longwise, and forming the wall of a tube, at the inside of which the staves (rhabdomeres) (5) project as circular ledges; they touch each other only at the foremost somewhat thickened end. One of the rhabdomeres always lies in the midst of the six other ones carried by a narrow ledge of the cell-body.

Between the exterior ends of the ommatidia lie clear-coloured and spindle-shaped pigment-cells (3).

Of the seven nuclei of the retinula-cells five lie in the uppermost end of the retinula, while the sixth one lies somewhat more distant from them, and the seventh one quite isolated in the lower third of the retinula, so that one can distinguish clearly in a stained vertical section of the eye, three nucleus layers, the second and third of which, formed each by one row of nuclei, are placed concentrically to one another.

At the end of the retinula, immediately above the basal membrane, lie pigment-cells with very small nuclei (7), the numerous processes of which wrap round in a subtle pigment-knot the undermost part of the retinula.

Among the matrix-cells of the cribriform basal membrane, being there proportionately thick, numerous tracheæ ramify. The thicker trunks of these are placed between the matrix-cells and the ganglion layer lying below it.

No more about the optic and light-perceiving part of the eye. Behind it lies the ganglion apparatus which shows in Musca a typical, but, as it seems, not very frequent construction, the peripheral ganglion-opticum being spread out close to the eye as a plane.

Out of the central part of the brain passes a long and narrow string of nerve-fibres through an interposed ganglion layer into the central opticus-ganglion (13), radiating in it towards all sides.

This ganglion forms a cone turned with the point outwards, with the concave base inwards to the brain. The inside of the cone consists of several concentric layers of "Punktsubstanz" (to employ Leydig's expression), which are connected together by a great number of narrow granular strips, while the mantle of the cone is formed by the ganglion-cells or the nuclei of them.[1]

(The subtler construction of the ganglion can only be indicated in the Plate, because of the small size of the drawing, and has also been sufficiently illustrated by Berger, 'Arbeiten Zool. Anstalt. Wien.,' vol. i.)

Through the cone-point consisting of ganglion-cells the nerve-fibres come forth rectilineally, and cross each other shortly after passing out as they keep their direction (12). After crossing they extend themselves again over a larger space, and at the same time the nerve-fibres always become connected in groups so as to form bundles. Between these cord-like bundles lie numerous nuclei of the most different form and size, probably appertaining to the connective tissue.

The exterior ganglion-opticum consists of a threefold layer of small ganglion-cells (9), and a single stratum of long pali-

[1] In the embryonic state perfect cells, with much cell-body, form the bark of the ganglion in insects; the cell-substance diminishes more and more in the course of the development, the deeper layers of the ganglion increasing probably at its expense.

sade-shaped cells (10), the number of which corresponds with that of the eye-units. Every one of these palisade cells possesses an oblong nucleus at its foremost somewhat broader end, and is broken into by one of the nerve-strings mentioned above.

With a Sarcophaga carnaria which I examined shortly before the creeping out of the pupa, and the eye of which was already quite developed and brown-pigmented, while the ganglion showed still somewhat the embryonal character, I could determine by means of transverse and vertical sections that the nerve-string in each palisade cell surrounds a refracting chitinous or cuticular tube which lies in the midst of the cell.

In Musca vomitoria also, one sees that in every cell lies a cylindrical axis, but on account of the small size of the histological elements and for want of transverse sections, I could not decide here if it be the nerve-string or such a chitinous tube. Also, I did not succeed in obtaining sureness as to whether the nerve-string perforates the palisade cell unaltered, or if it only passes close to it and suffers here an interruption by the substance contained in the tube or in the axial cylinder.

Inwardly the palisade layer is limited by a membrane (11) containing nuclei; on the outside a string of several nerve-fibres passes out of every cell, penetrates the layer of the small ganglion cells (9) and reaches the central end of the retinula. In vertical sections I could not of course see more than three or four fibres in one string, but it seems certain to me, in view of what occurs in other Arthropoda, that their number answers to that of the retinula cells, and probably that already the strings or bundles, formed after the crossing, consist each of seven fibres.

Though in most cases the peripheral ganglion-opticum is not extended as a plane but more spherically, yet there is a specific character which we always find in the higher and in many lower Arthropoda with fan-eyes—namely, the existence of the two ganglionic layers, and secondly, the crossing of the nerve-fibres between them. In the Decapoda and Schizopoda there

are actually four ganglion layers successively in the ommatophor and between each a crossing of fibres takes place.

If one considers the ordering of the eye-units in Musca as the one extreme of the form of the fan-shaped eye, the other is found in the Cladocera. The eye approaches here to the spherical form and exhibits its most developed form in Leptodora hyalina, where the spherical eye is carried freely at the front end of the body like a lantern on a thin stake.

In a section which bisects the eye in the median plane (Pl. XLV, fig. 2), there lie about twenty-four eye-units set radially; the strongly pigmented retinulæ lie quite closely to one another, so that in the transverse section the thin rhabdoms appear like clear points on a black ground.

The retinulæ do not reach with their points quite to the centre of the globe, but end so as to leave empty a little central space.

The crystal cones are slender and considerably longer than the retinulæ are composed of five segments and do not lie very closely together, and at the peripheral end show distinctly their limits (*a*) whilst they fuse more and more intimately together towards the cone-point (*b*, *c*, *d*). Their transverse section is accordingly here rosette-shaped, there circular.

At about the half height the cone shows a pyriform swelling which stains intensely with colouring reagents.

The crystal cone is surrounded throughout its length by a number of cells, the "Umhüllungsschlauch" (investing tunic) of Leydig; at the outermost end they form around the base of the cone a sack-shaped envelope hanging together; in which in one plane of section are visible four nuclei (*a*), so that their number may be estimated at five, and this part of the envelope with the nuclei may be regarded as the remains of the crystal cells (Semper's nucleus).

The thinner part of the cone is surrounded by long, narrow cells, the nuclei of which are somewhat irregular. I am not able to say if the nuclei which lie close round the cones before the beginning of the pigmented retinula (*d* and *b*) belong

to these cells or perhaps to the retinulæ, or if they are homologous with the pigment-cells.

The cone penetrates with its point deeply into the retinula. The latter surrounds a thin rhabdom which is probably four-edged.

The ganglion lies in front of the brain ganglion, separated from it only slightly by a narrow furrow. Its rind consists in the front and at the sides only of a thin, at the back of a thicker, layer of nuclei through which the nerve-fibres enter from the brain-ganglion into the ganglion-opticum. The medullary substance of the latter can be separated into a front and a back segment.

The outgoing nerve-fibres pass as a spindle-shaped string into the centre of the eye, where they touch the ends of the retinulæ. The string is without pigment until it subsides between the crystal cones, and is surrounded by a pigment envelope between the retinulæ.

With the exception of the entrance of the nerves, which occupies the space of about one or two eye-units, the eye-units radiate equally towards all directions, both forwards, sidewards, and backwards, being directed to the translucent body.

Just as the camera obscura eye is common to the vertebrates and the molluscs, so there are also met with in the molluscs organs of sight of the type of the fan-eyes.

For a long time past eyes have been attributed to the Lamellibranchiata. If these animals possess such organs they can only lie on two places of the body: at the mantle border or on the siphon. At the latter place modern zoologists have not been able to find any organs of sight, whilst at the mantle border are situated, in many species, organs of different form and composition, which are considered partly wrongly (Pinna) partly rightly as eyes.

Their construction is the simplest in Arca and Pectunculus. In Pectunculus glycimeris there occur on the edge of the interior mantle fold small spherical dark-brown

pigment spots at a distance of about 0·5 mm. from one another. In Arca Noae they are black-brown, close crowded, at the back end of the mantle larger and more distant from one another, about thirteen in a length of 2 centimetres. These organs consist (Pl. XLV, figs. 3 and 4) of a small number of large cells of the form of an elongated cone, with the point directed inwards. From their lying close side by side results the outwardly convex form of the organ.

The pigment is found in the periphery of the cells, and surrounds as a sheath the cell body; the nucleus lies in the exterior half of each cell.

In Pectunculus the cuticular border is tolerably thick, and the exterior surface of every cell is convexly arched; the organ distinctly contrasts by its colour with the mantle fold, which is here without pigment.

The optic cells of Arca are larger, and the whole organ higher developed, for every cell possesses a kind of lens formed by its cuticular border, which is convexly arched, not only outwardly, but also inwardly, Since the pigment sheath reaches the exterior end of the cell this lens is only visible in cells, the pigment of which has been removed in the cutting of a section. Here the substance of this cuticular lens is distinguished plainly from the cell body by its power of refraction and its behaviour when treated with staining reagents.

The cells which form the organ of sense, the optic cells, are not limited sharply against the epithelial cells of the mantel, but pass quickly through long and narrow intermediate forms into the epithelial cells. Consequently the eyes of Arca and Pectunculus, as much as those of Patella and the Ocelli of the medusæ Oceania and Aurelia aurita, may be classed among the most beautiful examples for the study of the origin of organs of sight by the modification of epithelial cells.

Moreover, I think that these simple fan-shaped eyes of Arca and Pectunculus offer us a new proof of the truth of the view that similar organs of sight in different classes and orders of the animal kingdom may have originated independently, and in fact may still originate without in any way implying that

such eyes have been inherited from an ancestor common to these different classes and orders.

EXPLANATION OF PLATE XLV.

Illustrating Dr. Justus Carrière's Memoir "On the Eyes of Some Invertebrata."

FIG. 1.—Vertical section of the eye of Musca vomitoria. Stained with Haematoxylin. A. An ommatidium (eye-unit), more highly magnified. *c*. Cornea. *f*. Fold of the chitinous membrane. *g*. Ledge of chitin. 1. Pseudoconus. 2. Pigment-cells (i). 3. Pigment-cells (ii). 4. Crystal-cells. 5. Rhabdomere. 6. Retinula. 7. Pigment-cells on the base of the retinula. 8. Basal membrane, with its matrix-cells. 9. Layer of little cells. 10. Layer of palisade cells of the peripheral ganglion-opticum. 11. Membrane. 12. Chiasma of nerve-fibres. 13. Central ganglion-opticum. 14. Intermediate ganglion.

FIG. 2.—A vertical section through the midst of the eye of Leptodora hyalina. B. An ommatidium of it, more highly magnified. *a*—*d*. Transverse sections through the crystal cone. *a*. Near the base. *b*. In the first third. *c*. In the second third. *d*. Close before the retinula. *g*. Ganglion-opticum.

FIG. 3.—Vertical section of the eye of Pectunculus glycimeris. 1. Epithelial cells. 2. Optic cell (nerve-end cell). 3. Connective tissue and nerve-fibres. 4. Transverse section of three nerve-end cells, in two of them the nucleus.

FIG. 4.—Vertical section of the eye of Arca Noae. 1. Epithelial cells. 2. Nerve-end cell, tangential section. 3. Nerve-end cell, median section. 4. Transverse section of a nerve-end cell. 5. Connective tissue and nerve-fibres.