ornata, costellis in medio nullis, lineolis concentricis incrementi striolata; margine ventrali crenulato.

Hab. Mino-Sima; 63 fathoms.

A small species, very nearly similar in form to Crenella, but with the middle of the valves plain.

Nagasaki, July 10, 1861.

XXVII.—On Vision in the Arthropoda. By Dr. H. Dor*.

Compound eyes occur in nearly all Crustacea, in all winged and some aperous insects, and even in the aquatic larvae of the Neuroptera, and in the larvae of the Hemiptera. They are two in number, and form a segment of a sphere; and each is composed of an agglomeration of more simple organs, of which the number varies almost infinitely (from 50 to 25,000 in a single eye). The facets formed by the single eyes resemble the cells of a honeycomb: they are usually hexagonal, but sometimes pentagonal, rectangular, or irregular; and these various forms may be met with in the same eye.

On making an antero-posterior section of the eye, each facet is found to correspond with a more or less lenticular organ, exactly resembling in some species the crystalline lens of the Vertebrata. This has been called the cornea. Behind it is the crystalline body, a transparent and strongly refractive cone, enclosed in a cupuliform envelope, which is also transparent and is perfectly continuous with the nervous fibre. The union of all the nervous fibres, which in their course almost constantly present a dilatation and afterwards traverse several masses of ganglionic cells, forms the optic ganglion. The spaces between the different nervous fibres are filled up with a dark pigment.

The author gives a summary of the different views put forward by writers on the mechanism of vision in the Arthropoda. Cuvier supposed that the nervous filaments, although each corresponding to a facet, lost themselves in the layer of pigment; and he found it difficult to understand how impressions could be produced upon them through this opake matter. Marcel de Serres did not recognize the conical crystalline bodies, the discovery of which is due to Treviranus (Verm. Schriften, iii. p. 152), who, however, did not perceive their importance. According to him, the compound eyes act like a convex mirror, upon which objects are reproduced enlarged, the entire cornea reflecting images of distant objects, and each facet those of neighbouring objects.

J. Müller considered that each facet, with its conical body and the nervous filament attached to it, forms an apparatus which transmits to the optic ganglion only the impression of that luminous ray emanating from an external body which penetrates it in the direction of its axis, the oblique rays being absorbed by the pigment. The impressions transmitted to the optical centre by all the filaments will form a common and continuous image. The extent of the field of vision will depend on the more or less hemispherical form of the eye; and the distinctness of the image produced, upon the length of the cones, the nearness of the object, and the number of the facets. The curvature of the surface of the cornea, which enabled Leuwenhöeck to obtain reversed images with the eyes of insects, is only sufficient, according to Müller, to concentrate the rays in each cone towards the point of insertion of the nervous fibre.

As early as 1759, Porterfield had stated that the compound eyes of insects consist of as many simple eyes as they present facets; that these animals see with their innumerable eyes in the same way as Man with two and Spiders with eight, and that the number of these organs was destined to replace the movements of the eye in Vertebrata. In 1843, Brants adduced the fact, already demonstrated by Leuwenhöeck, of the presence of a reversed image corresponding to each facet, but invented a theory of interlacement of the nervous fibres in order to bring this fact into accordance with the general theory of Müller.

Of the authors who endeavoured to combat this theory, one of the first was Gottsche, who, in 1852, proved that when the crystalline body and the cornea are placed together in the microscope, an image is obtained at the conical extremity of this body. His conclusion is that the compound eyes are organs of a nature sui generis, and not to be compared with the visual organs of the members of other classes of animals.

In 1855, Leydig put forward a theory which has taken the place of that of Müller. He assumes, with Gottsche, that the crystalline body, its envelope, and the soft layer described by Will between the crystalline and the cornea, are not organs corresponding with and attached to the nervous fibres, but that they are the anterior extremities of these fibres themselves, of which the form alone is altered, there being no difference between them and other parts of the nervous system, either chemically or optically. In this view the optic ganglion becomes the analogue of the retina in the higher animals, the crystalline bodies being analogous to the bacillar coat. Leydig compares the facetted eye of an Arthropod to the eye of a vertebrate animal, as follows:—

"The cornea with its posterior convexity corresponds to the cornea and crystalline of the Vertebrata; the crystalline body (with the so-called vitreous body) and the nervous fibre which is attached
to it, to the bacillar coat; and lastly, the optic ganglion to those layers of the retina which are composed of granulations, cells, and nerve-fibres. The pigments are the analogue of the choroid and the iris; and the transversely striated muscular fibres have their equivalents in the muscular elements of the choroid and iris.”

The researches of Leydig were followed by investigations of the anatomy of the compound eye by Zenker, Gegenbaur, and Leuckart, and on its embryology by Claparède. Zenker found the curvature of each facet of the eye in Dytics to equal 160°. The index of refraction of the cornea = 1·50, and that of the the crystalline body = 1·40. He concludes that the vitreous body is placed behind the cornea only to prevent the convergence of the rays behind the cornea, so as to form an image before reaching the summit of the crystalline body. In this view, opposed to Leydig, the compound eye is an aggregation of simple eyes. Gegenbaur, on the contrary, adopts Leydig’s view, and thinks he has demonstrated an uninterrupted communication of the crystalline body and nervous fibre with the optic ganglion in a Hyperid Crustacean.

Leuckart, on the other hand, not content with the various hypotheses amongst which he had to choose, adopts another, still more difficult to understand. He states that between the cornea and the crystalline body there is a space containing a vitreous gelatinous body enclosed in a proper envelope. Some muscular fibres found in this envelope may, by their contraction, approximate the crystalline body to the cornea; in other words, there exists a special organ of accommodation. Besides all this, in the genera Saphirina, Coryceus, &c., the crystalline is said to be composed of two distinct parts, exactly like the crown and flint glass in achromatic lenses. These observations the author has been unable to verify. Leuckart compares each facet of such eyes, not to a camera obscura, but to a telescope with a simple object-glass (cornea) and eye-piece (posterior lens); and he considers this view to be the more probable as movements of the posterior lens may be observed which can have no other object than to adapt the apparatus to different distances.

Claparède thinks Müller’s theory untenable, and also cites some facts which speak against Leydig’s views; but he avoids giving his own.

This being the state of the question, the author endeavoured, by fresh researches, to solve the problem, How is vision effected in the Arthropoda? For this purpose it was necessary to confirm or refute Leydig’s theory, Müller’s being already upset by the observations of Leuwenhoeck; whilst Leuckart’s seemed untenable to him, because, if insects really possess a telescope, they would require an eye behind it to enable them to see. It is by optical processes that he attempts the solution of his problem.
It is easy to calculate the focal distance, $ab$, of a lens, when we know the size of the object $cd$, its distance from the lens, $af$, and the size of the image, $gh$. We get two triangles, $cad$ and $hag$, of which the sides and perpendiculars are proportional. Thus we get $x : f a = h g : c d$. As these three quantities are known, it is perfectly easy to find the focal distance $ab$.

The author commenced by making numerous preparations, until he had the cornea of many insects in a sufficiently clean state to show the images very distinctly. He then pasted upon a window a rectangle of black paper of known dimensions, and measured accurately the distance from the stage of the microscope to the window. When the facets were in focus, they were seen very distinctly, but without images of the black paper; on their removal from the focus, their outlines became less clear; but gradually small images of the black rectangle made their appearance, and grew more and more distinct, until by one or two turns of the screw they again disappeared. It was therefore evident that each facet formed an image, and that this was at a sensible distance behind its posterior surface. It was therefore a true lens, and the image must be reversed, which proved to be the case on examining another object.

This observation proves that the image is not produced, as stated by Leydig, on the anterior surface of the crystalline body, acting as a bacillus, for the latter is often in immediate contact with the surface of the lens. Nevertheless, it might be urged that although the image is no doubt formed behind the optical centre of the lens, by the admission of even a thin layer of the so-called vitreous body the image might really be formed very close to the anterior surface of the crystalline body; or the crystalline body itself might be at once refractive and nervous, and the image might be formed at different depths in it according to the distance of the objects observed. To determine these points, the author entered upon a series of accurate measurements, of which the results are given in his paper. The following are those which bear most directly upon the subject:

**Cornea of Musca vomitoria.**

Magnifying power 560 diameters.
Size of the image seen under microscope $= 0.058$.
Real size of image $= 0.0082 = \frac{1}{122}$ mill.
Distance of object $= 68.8$ centim.
Size of the object $= 120$ mill.

Whence $x : \frac{1}{122} = 688 : 120$, from which $x = \frac{1}{21}$ mill.
This calculation leads to a very conclusive positive result. Leaving out the determination of the optical centre, the image was formed far behind the posterior face of the lens, the focal distance $\frac{1}{2^\circ}$ being exactly twice the thickness of the lens, which was $\frac{1}{1^\circ}$ mill.

The next point was to determine the length of the crystalline body, and to calculate at what part of it the image might be formed. The most favourable species for this purpose appeared to him to be the *Macroglossus stellatarum*, as its eyes are hard and prominent. The results are given from the mean of three measurements.

*Macroglossus stellatarum.*

**First measurement.**—Magnifying power 838 diam.

Apparent size of the image 3·48, real size $0·0089 = \frac{1}{1^\circ}$ mill., from which $x$ (focal distance) $= \frac{1}{1^\circ}$ mill.

**Second measurement,** the same eye, magn. 255 diam.

Apparent size of the image 2·44, real size $0·0091 = \frac{1}{1^\circ}$ mill., from which $x = \frac{1}{3^\circ} \cdot \frac{9}{10} = \frac{1}{1^\circ}$ mill.

Thickness of lens $= \frac{1}{2^\circ}$ mill.

**Measurement of crystalline bodies** (mean of five measurements of different crystalline bodies).—Apparent size $= 15·59$, real size $0·061 = \frac{1}{1^\circ}$ mill.

The author was the more struck with this coincidence of the focal length of the lens and the length of the crystalline cone, as his only endeavour had been to prove whether the image was formed immediately behind the cornea, as was necessarily assumed in Leydig's theory. The focal distance of the cornea measured in the air being $= \frac{1}{1^\circ}$ mill., and the summit of the cone being at the same distance from the posterior surface of the lens, the difference between the refraction of the air and that of the crystalline body is sufficient to shift the position of the image for a distance equal to that between the posterior surface of the lens and its optical centre. Thus, if, as stated by Zenker, the index of refraction of the crystalline body be 1·40, we should have, in the preceding case,

$$1·00 : 0·0625 = 1·40 : x;$$

from which $x = 0·0875 = \text{circum} \frac{1}{1^\circ}$.

Hence the optical centre would be placed forward in the cornea by the whole difference between $\frac{1}{1^\circ}$ and $\frac{1}{1^\circ}$, or about $\frac{1}{1^\circ}$ mill. Now, as the antero-posterior diameter of the cornea in the *Macroglossus* is $\frac{1}{3^\circ}$, the optical centre would be about $\frac{1}{6^\circ}$ mill. behind the anterior surface of the cornea.

The author concludes his paper with the following remarks:

—"We assume without hesitation that each facet is a complete
eye, perfectly analogous to the simple eye of the Vertebrata. The lenticular cornea corresponds with the cornea and the crystalline apparatus; the cone with the vitreous body; and the cupuliform envelope—which up to the time of Leydig was considered as conjunctive tissue, as neurilemma (J. Müller), and which Leydig regards as an integral part of the bacillus—is for us a true retina, a dilatation of the optic nerve. We have not ascertained the presence of muscular fibres. The pigments replace the choroid, and the multiplicity of eyes the small muscles destined to move the eyes of the superior animals in various directions. If, as M. Claparède points out with reason, there be some species in which Leuwenhoek's images are not observed under the microscope, it must be owing to the convexity of their facets being very slight. The image is formed nevertheless, but much further backwards than it is usually looked for. We find such eyes in the Tabani; and in these the length of the crystalline bodies corresponds with the slight curvature of the cornea, for they are about seven times as long as the thickness of the cornea. The mechanism of vision is therefore the same as in Man. One fact alone is not yet clear—namely, how distinct images can be formed upon a conical retina. But is the retina of Man always perfectly spherical? In any case, we no longer admit, with J. Müller, that the only point sensible to light is the entrance of the optic nerve; for, to judge at least by analogy with the Vertebrata, this may very probably be the only blind point; and we cannot understand how this distinguished physiologist could assume that, the pigment absorbing all the luminous rays which fall upon the sides of the cones, there could be no perception of light upon these points, as if the choroid in Man prevented the functions of the retina.

"Lastly, it is not more difficult to explain simple vision with 12,000 eyes, as in the Libellula, than with the two eyes of Man. Each eye in insects gives an image slightly different from that of the eye which is immediately in contact with it. But does not Wheatstone's admirable discovery, by throwing down the old doctrine of identical points, prove that the same thing takes place in our two eyes? It is owing to the presence of two different images for the two eyes that we possess stereoscopic vision, that we appreciate distances, perspective, &c. This is the case also in insects, which will see the more exactly in proportion as they have more facets. Thus the Ant, which moves slowly, does not require so exact an appreciation of distances as Butterflies, Dragon-flies, and other winged insects. For this reason probably we only find in the former 50 facets, whilst the Dragon-fly has 12,000, and the Butterfly 17,000."