ON THE MORPHOLOGY OF THE ARTHROPODA.

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Read before the British Association, September 5th, 1867.

THESE investigations on the Morphology of the Arthropoda were made some weeks ago at Millport, on the Firth of Clyde.

It is well known to zoologists, that the first who worked out the development of the crustacea was the late celebrated Rathke, who gave an account of the embryology of Astacus fluviatilis. At that time also Von Baer propounded the history of development of the vertebrate animals: and as it was the endeavour of that period to find out the connexion and the relations between the vertebrate and the invertebrate kingdoms, both were working out the analogies and homologies of the arthropodous and the vertebrate embryology.

These principles were objected to by Professor Weismann at Freiburg. He stated, in his excellent work on the "Development of the Diptera," that the types of development in the insects—and therefore probably in the whole arthropodous class—and in the vertebrata were as different as possible, that there were no homologies at all to be found, and that the endeavours of Zaddach in his "Development of the Phryganidæ" to work out the theories of Von Baer and Rathke were fruitless and wrong. It was he who stated at first the presence of, what he called a *faltenblatt*, a membrane of the embryo, which appears before any other process after the formation of the primitive streak (*keimstreif*). It is necessary for my purpose, that I should give an account of the manner in which this membrane, called faltenblatt, is formed. The keimstreif surrounds the vitellus. At both ends of it a thin layer of cells begins to grow out, which finally encloses the whole embryo, or rather the keimstreif, by a membrane, in which structure is hardly to be seen, because it is so close to the primitive streak that only the outlines of the margins can be distinguished. The beginning of the formation of this membrane is at the back of the embryo; on the opposite side the membrane soon splits, and the extremities grow out.

In the most remarkable book, "Für Darwin," the well-known zoologist in South Brazil, Fritz Müller, made a brilliant application of Darwinian principles to the embryology of the crustacea; and stated that the *Nauplius*, the so-called larva of copepoda and cirripedia, was also the first larval state of a decapodous crustacean, of a *Peneus*; that this *Peneus-Nauplius* then changed into a *Zoëa*, the *Zoëa* into something like a *Mysis*, and that after these stages it becomes a *Peneus*. He was of the opinion that all crustacea were the offspring of nauplius, and I think he proved it or at least made it very probable.

For the embryology of the edriophthalmous crustacea he stated, that there was a third membrane, besides the chorion and the inner egg-skin, surrounding the body and being fastened on the back to the vitellus. He called this membrane "larval-membrane," and expressed the opinion, that it was wrong to call the heap of cells, which connect, in all amphipoda and in some isopoda, the larval-membrane with the back of the embryo, micropyle-apparatus, as it was called by Professor Meissner and La Valette de St George. This larval-membrane he identified with the nauplius, and considered it to be the last remains of the earliest state of the edriophthalma.

Last year I published a paper on the embryology of *Asellus aquaticus*[1], in which I described the larval-membrane and, like Müller, declared it to be the *nauplius-membrane*. I did not find, perhaps I overlooked, the so-called micropyle-apparatus, but I found two organs or appendages developed before all other organs on the sides of the embryo, the so-called trefoil-like processes (*blattförmigen anhaenge*) of Rathke. I don't consider those appendages to have any function, but, like the larval-membrane and the micropyle-apparatus, to be the remains of the lost earlier stages of their genealogical development.

The structure of both the micropyle-apparatus and the trefoil-like processes was uniform—long outgrowing cells surrounding cavities, and giving origin to cuticular membranes.

In the same year I examined the embryology of the Phryganidæ, and discovered at the same time with Professor Weis-

[1] *Zeitschrift f. wissenschaft. Zoologie*, Bd. XVII. Heft. 2.

mann and the Russian zoologist Elias Mecznikow, a third membrane round the embryo, consisting of large distinct cells. The membrane was connected with the back of the embryo and, splitting as soon as the embryo, grew and became too large for the space within the membrane. I published a little paper on the subject in the *Medizinisches Centralblatt* of Berlin, and indicated that this membrane in the Phryganidæ and the larval-membrane in Asellus might be true homologous formations. I had the pleasure of finding that Professor Weismann in a letter to me expressed the same opinion.

In opposition to this view Mecznikow in his elaborate work "Embryologische Studien an Insecten" contended, that there was no homology at all between the membranes in insect and in crustacean embryos. He rather preferred to advocate the old opinions of Zaddach, Rathke, and Von Baer, of the supposed homologies between arthropoda and vertebrata, and not only compared the third embryonic membrane in insects with the amnion of vertebrata, but named it Amnion Insectorum.

As a means to elucidate still further the subject, I undertook further investigations, and compared the embryology of almost all genera and species of edriophthalma I could get in the Baltic at Kiel, and in the St George's Channel at Millport I studied the development of Palæmon, Crangon, Lithodes, Portunus, and at last added most special researches on Mysis and Cuma.

I am happy to say, that Cuma has furnished me with the material, which seems to justify me in bringing out a new theory on the morphology and the homologies in the whole class of Arthropoda. Though in this brief communication I cannot enter into all the arguments which might be advanced in support of my theory, I hope shortly to publish a more extensive account of my investigations.

The most remarkable fact in the anatomy of Cuma is the manner in which the respiratory apparatus is shaped. There is in the cavity between the body and the carapace a large and complicated instrument, called by my predecessors branchia; it is described, though not quite correctly, in Henry Goodsir's paper[1] on the matter. But it is not a branchia in the true sense,

[1] *Edinb. New Phil. Journal*, January, 1843.

and is only used to excite a current of water, which enters behind and goes out near the top of the head in a most striking way. The whole apparatus is fastened to the third maxilla and moved by its movements up and down. If it is elevated, twenty laminæ on the upper side push out the water through the long channel to the top of the head; the orifice there being formed by a most remarkable little joint connected with the whole instrument. If it is depressed the laminæ give way to the water and the little joint shuts the orifice, so that no water could go out behind, or come in in the opposite direction.

The blood goes out of the heart by an aorta and by two large blood-vessels on the sides. After several bifurcations, and the giving off to the abdomen of a great vessel, these blood-vessels enter the carapace, which is constructed of two walls, connected one with the other by a great number of little links, which are the hardened processes of the cells of both walls. Round the margin there is a broad channel opening into the pericardial sinus. The blood-vessels bifurcate many times before they lose their walls and allow the blood to pass into the space between the two walls of the carapace. Here the blood-corpuscles interchange the carbonic-acid with the oxygen, enter afterwards the marginal channel, and are brought back by the pumping movement of the heart to the pericardial sinus.

The complex form of respiratory apparatus just described in Cuma is to be regarded as a high degree of elaboration of the simple and fundamental form met with in Zoëa.

But as Cuma has in all parts a great affinity with the isopoda, as is proved by the embryology, which I have made out, I now obtained an explanation both of the micropyle-apparatus and of the trefoil-like appendages in Asellus. *The micropyle-apparatus in the back of Cuma and the Edriophthalma is nothing but the remains of the dorsal spine of Zoëa, or rather, as I have reason to believe, of the larval form of the Cirripedes, which I call Archizoëa, being of the opinion that it is from this larval form Zoëa has taken its origin.*

The second conclusion is: *the larval-membrane of Edriophthalma and Cuma is nothing but the last remains of the carapace of Nauplius*, I mean the nauplius of the cirripeds, which differs

from the nauplius of copepoda by possessing already the dorsal spine on the back of the body and a fork on the underside. I further will distinctively apply to this shape of nauplius the name of *Nauplius;* and to the copepod-nauplius, as being the more simple, the name of *Archinauplius.*

The third conclusion is : *the trefoil-like appendages of Asellus are the last remains of the Zoëa state, representing the carapace, the spines on the sides of the carapace and the respiratory apparatus of the Zoëa.*

After these results I had to apply the inductive method to get further advances in regard to the other classes of the Arthropoda. It is known, that the so-called micropyle-apparatus is to be found in the embryo of Scorpio, of Ixodes, of Pentastomum, and of almost all Araneidæ. *That is one of the indubitable signs, that these animals originate from the Archizoëa.*

The excellent work of Newport on the development of Myriapods furnishes me with the material to state quite the same of this class of Arthropoda.

It is further known and especially stated by Mecznikow, that in the embryo of Scorpio we meet with the so-called "amnion," and that this amnion consists of two walls connected one to the other by small cellular processes. Mecznikow tells us, that the outer wall was an epithelium and the inner a muscular membrane, which is an error, for the whole amnion is nothing but the carapace of Zoëa, which always consists of two walls connected by small processes for the purpose of respiration.

And further, since the "amnion" of scorpio consists of the same cells as the amnion in insects, we are forced to apply the same character to that and to take it for the remains of the Zoëa-carapace. We are the more authorised to do so, because I found out after lengthened enquiry, that even the larval-membrane in Edriophthalma is not quite destitute of cells, or a mere cuticular formation, as it was considered to be, but that in the Oniscidæ and in Idothea cells are visible, which in the other species are soon lost. The "amnion" in insects and the larval-membrane in crustacea are both fastened to the back of the embryo, and if the heap of cells, now known as the remains of

the dorsal spine of Archizoëa be compared with the relics of the amnion in the back of the Phryganea-embryo and of almost all other insect-embryos, their identity will be recognised.

If this be the case, and I hope I have given some proof of it, and will give much more in my longer paper, the homologies of all parts of the insects, spiders, myriapods and crustacea, may be decided. Where then are the homologous parts of the two pairs of antennæ of the crustacea, since in insects we only meet with *one* pair of antennæ ?

In considering this question, it is well to examine along with these two pairs of extremities in the crustacean the next pair, the *mandibles*, because these three are developing at first in the crustacean embryos and in a peculiar manner quite different from the next two pairs; and these next two pairs are different in their development from the following pairs. The difference is this. The first three are growing from the back of the embryo, the next two to the ventral side; the first three diverge, the second two converge. *The first three pairs are homologous to the three pairs of the extremities of Nauplius.* In the embryo of insects the first three pairs of extremities are formed exactly in the same manner as in the crustacea; a fact, that is already stated by Professor Zaddach in the Phryganidæ. But into which parts in the full-grown larva of Phryganea do these three pairs develope? It is usually thought into the antennæ, the mandibles and the maxillæ. But this is not the case, for the first pair become the mandibles, the second pair the maxillæ, the third pair, in connexion with another formation, which corresponds to a similar formation in the crustacea, the under-lip.

But where are the antennæ? In a very early stage of the Cuma-embryo a small and almost imperceptible line above the insertion of the second and third pair of maxillæ may be found. This line bends upward at both corners and forms a little plate, which after some time grows on towards the head, so that its under-corner on the side of the antennæ is prolonged, and a small appendage comes out of its under-side and grows on to the ventral side. The plate grows further and further, turns round till it reaches the top of the head and the appendage follows this direction. *The plate developes into the carapace,*

and its appendage into the already described branchial-apparatus.

The way in which the antennæ of insects develope is the following. On the sides of the head a part of the so-called faltenblatt, already mentioned as a first formation in the embryo of insects, remains. On the under-corner of this part, which forms a plate, a little appendage is to be seen, which grows in the direction towards the ventral side. During the further development of the embryo this plate changes its position, and in the same period, when the forehead with the upper-lip—a mere prominence in all Arthropoda—is bent backwards, the plates are growing on forwards and ultimately the outgrowing appendages are situated beyond the mandibles. If we now remember that the faltenblatt is homologous to the inner wall of the Zoëa-carapace, and therefore to the inner wall of the Cuma-carapace, *the plate in Cuma and Phryganea are identical; in the first it becomes the carapace, in the second the head-plate* (*Scheitel, or Kopf-platte of the German embryologists*). *The appendage in Cuma becomes the top of the branchial apparatus, in Phryganea the antennæ.*

These observations will I think cause the study of the Morphology of the Arthropoda to enter on a new direction. It is by the application of those principles which science owes to Darwin, that difficulties may be overcome which have been in in our way for more than half a century, since Savigny at first undertook in vain to point out the homologies of the segments and extremities of insects, spiders, myriapods, and crustacea, in which fruitless though very arduous exertions he was followed by almost all the leading zoologists down to this day.