IV. Supplemental Note to a Paper* "On the Structure, Physiology, and Development of *Antedon* (*Comatula*, Lamk.) *rosaceus*."

By William B. Carpenter, M.D., F.R.S. Received April 6, 1876.

Since my communication of the above-cited Paper to the Royal Society on the 16th December, 1875, two important contributions to the Anatomy of *Antedon* have appeared—one by Dr. Ludwig, chiefly based on his study of *Antedon Eschrichtii* ("Zur Anatomie der Crinoiden," Zeitschrift für Wissenschaftliche Zoologie, Bd. xxvi. 1876, p. 361, continued in Nachrichten von der Königl. Gesellschaft der Wissenschaften und der G. A. Universität zu Göttingen, No. 5, Feb. 23, 1876), and the other by Prof. Greef, of Marburg (Sitzungsberichte der Gesellschaft zur Beförderung der gesammten Naturwissenschaften zu Marburg, January 1876), both of which seem to have been prompted by the appearance of Professor Semper's short paper on the subject. These able observers fully concur with me, as to all essential particulars, in the account I have given of the triple canal-system of the arms, which M. Edmund Perrier not only could not himself find, but ventured to predict that no one else would find; in fact, Professor Greef's figure of a transverse section of an arm might have been copied from one of the drawings I have had by me for more than ten years, save for one slight additional feature. The German investigators also accept the correctness of the statements made by me in my First Memoir, that the "nerve" of Müller is really the genital rachis, and that Müller's "vessel" in the arms is solid, not tubular, though neither is disposed to believe with me that this "axial cord" is a nerve. The character of a nerve, on the other hand, is assigned by Ludwig to a fibrillar band lying beneath the epithelial floor of the ventral furrow of the arms; which band had been independently noticed by my son, Mr. P. H. Carpenter † (who is at present working in the laboratory of Professor Semper at Würzburg), in two of Professor Semper's Philippine species, *Actinometra armata* and *A. nigra*, as also in *Antedon Eschrichtii*, in which it had been previously discovered by Ludwig. It is not nearly so distinct, however, in *A. rosaceus*; but its existence in that species was also independently recognized by Professor Huxley, who, like Ludwig, was led by his general view of the homologies of the Crinoids to regard it as a nerve. My son regards both the ventral band of Ludwig and my "axial cord" as belonging to the nervous system, being led to that conclusion, as regards the former, by its homology with the radial nerves of other Echinoderms, and, as regards the latter, by the very definite branching he has discovered in the axial cord of the

* See *antè*, p. 211.

† "Remarks on the Anatomy of the Arms of the Crinoids," in the Journal of Anatomy and Physiology for April, 1876, p. 571.

arms of *Actinometra armata* and *A. nigra*—two pairs of branches running on each side towards the dorsal surface, and two towards the ventral, where he has distinctly traced their ramifications as far as the leaflets bounding the ventral furrow. Prof. Greef, on the other hand, describes the whole epithelial floor of the ventral furrow as a nerve, on the ground that its histological character resembles that of the nerves of other Echinoderms.

Having recently had an opportunity of examining at Würzburg the very thin sections prepared by my son, I can say with certainty that the fibrillar band is quite distinct from the layer of columnar epithelium which it underlies; but it appeared to me to send off very minute fibrils that pass up between the cells of which that layer is composed.

To myself it appears by no means improbable, looking alike to its position and to its histological characters, that this band is a nerve; but having regard to its immediate proximity to the sensory (ventral) surface, and to its separation from the muscles by the interposition of the triple canal-system, I cannot but think it more likely that it is functionally related rather to the former than to the latter—in other words, that it is an *afferent* rather than a *motor* nerve.

As it seemed to me that important evidence might be obtained on this point from experiments made on the living animal, I took the opportunity afforded by my recent visit to the Zoological Station at Naples to institute such experiments; the results of which I am desirous of appending to my Paper, as they seem to me to place the doctrine advocated in it beyond reasonable doubt.

Every one who has had the opportunity of observing the habits of the living *Antedon* well knows the peculiarly rhythmical and symmetrical swimming action which it executes when it spontaneously leaves or is detached from the anchorage afforded by the grasp of its dorsal cirrhi. Each of its five rays divaricates into two arms, which may be characterized (like the two legs proceeding from the human trunk) as the *right* and the *left* respectively; and the act of swimming consists in the alternate consentaneous advancement of the *five right* and then of the *five left* arms, each of which is bent forwards in a curve which resembles that of the swan's neck in its graceful arch, and is then straightened backwards. The perfect similarity of the movements of all the five arms that work together, involving the conjoint contraction of several hundred pairs of muscles, seems to me to point almost certainly to coordination through a nervous centre; and it will be seen that experiment has fully confirmed that conclusion.

It will be recollected that the centre of what I regard as the motor nervous system is the quinquelocular organ contained in the centro-dorsal basin, which Müller (who did not recognize its cavitary subdivision) characterized as a heart. Müller's view of its nature is still

upheld by Greef (*loc. cit.*), who says that it gives off vessels to the cirrhi, and regards what I have described as a circular commissure (analogous to the "circle of Willis") as a closed blood-vascular system in connexion with this, although he admits that the axial cords of the arms, which are derived from this ring, are solid. The careful and repeated investigations I have made on this point, however, have fully satisfied me that my previous statement was correct. There is no passage whatever out of the chambers into the axial cords either of the cirrhi or the rays; and in the pedunculate Crinoids, as in the early Pentacrinoid stage of *Antedon*, there is no ventricular dilatation, the solid radial cords directly arising from the axis.

Experiment 1.—Taking up a large and vigorous specimen of *Antedon*, I turned the entire visceral mass out of the calyx, leaving behind it, therefore, as the *centrum* of the animal, only the calcareous segments of the calyx with their muscles and ligaments, the centro-dorsal basin with its cirrhi, and the five-chambered organ contained in the cavity of that basin. On replacing the animal in the water, *it executed the usual swimming movement as perfectly as the entire animal had previously done.*

Experiment 2.—I removed from a second specimen, which I took out of the water in the act of swimming, the entire centro-dorsal basin, with its contents and appendages, leaving every other part as it was. On replacing the animal in the water, *all the arms were rigidly straightened out*, apparently by the action of the elastic ligaments, which the muscles were powerless to antagonize.

This second experiment, then, not only confirmed my previous belief that the source of the perfect coordination of the swimming movements lies in a Nervous centre, but seemed to establish beyond doubt that the quinquelocular organ is the instrument of that coordination—the centre of a Nervous system, whose peripheral portion consists of the axial cords of the rays, arms, and pinnules. On the other hand, the first experiment, taken in connexion with the second, clearly shows that nothing contained in the Visceral mass is essential to the perfect coordination of the swimming movements. And since it is clearly in the oral ring that we should expect to find the centre of any nervous system lying immediately beneath the tentacular furrow, it seems to me fair to conclude that the supposed "nerve" of Ludwig, if a nerve at all, has no immediate relation to those movements.

Experiment 3.—I divided, in another lively specimen of *Antedon*, the soft parts of one of the arms down to the calcareous segment, thereby cutting through the "nerve" of Ludwig. This ought, on his supposition, to paralyze the arm so treated, or at any rate to destroy the consentaneousness between its movements and those of the other arms. But on replacing the specimen in water, *all the arms worked as usual*, without the slightest disturbance of regularity.

Experiment 4.—I then endeavoured to make a corresponding section of *my* nerve, the "axial cord," by cutting from the dorsal side of the arm, with the blade of a very thin knife, sufficiently deep between the segments to divide that cord without injuring the "nerve" of Ludwig. Having been repeatedly baffled in this endeavour, however, by the throwing-off of the half-divided arm, I had recourse to another method, the application of nitric acid. Carefully drying with a bit of blotting-paper the part to be thus burned away, so as to prevent the spreading of the acid, I applied it with a finely pointed camel-hair pencil, until I had reason to feel sure that it must have reached the axial canal. On replacing the animal in the water, *that arm remained rigidly stretched out, while all the other arms worked as usual.*

Now if these experiments, taken in connexion with the one described in my Paper, which I have again repeated with the same result, are not admitted as valid evidence that the quinquelocular organ with its radiating cords constitute a Nervous system, I am at a loss to understand what is the superior probative force of the evidence which is universally held to justify the assignment of such functions to the Brain, Spinal Cord, and the white solid cords proceeding from these centres in a Vertebrate animal. And I should feel it necessary to enter a strong protest against the refusal of a similar character to what I hold to be the Nervous system of the *Crinoida* (if based on no other objection than that its position does not correspond with that of the accredited Nervous system of other Echinodermata), were it not that an investigation which I commenced seven years ago into the structure of the *Ophiurida* showed that they will probably afford the means of bridging over this difficulty; for the calcareous segments of their arms, instead of being perforated by a central canal, have a deep notch on their ventral margin, which is sometimes almost completed into a canal; so that there is here an easy passage on the one hand towards the *ventral* nerve-cord of the *Asteroida*, on the other towards the *central* nerve-cord of the *Crinoida*. Further, it is to be borne in mind that in the early stage of the development of the Pentacrinoid larva of *Antedon*, as described in the First Part of my Memoir (Phil. Trans. 1855), the "axial cords" lie on the *ventral surface* of the Radials and Brachials, which are then mere flat plates; by an endogenous thickening of the calcareous network of those plates, the axial cords come to lie in *furrows* channelled out in their ventral surfaces; while by a further endogenous growth of that network these ventral furrows are completed into *canals*; and it is by a still further endogenous thickening that these canals finally come to occupy the *centre* of each Radial and Brachial calcareous segment.

At the same time I would repeat that I see no reason for refusing to believe that the subepithelial band of Ludwig is a sensory nerve, the functions of the single trunk of the *Asteroida* being here divided between

two, an afferent and a motor, just as, in Man, the double function of an ordinary spinal nerve is divided in the head between the 5th and 7th pairs. And it seems not unlikely that while the "axial cords" (motor nerves) of the arms are derived from the peripheral part of the Crinoidal axis, the "ventral bands" (sensory nerves) are derived from the central part of that axis, which has been shown to be continued, as the "axial prolongation," to the oral ring.

The Society then adjourned over the Easter Recess, to Thursday, April 27, 1876.

April 27, 1876.

Dr. J. DALTON HOOKER, C.B., President, in the Chair.

The Presents received were laid on the table, and thanks ordered for them.

THE BAKERIAN LECTURE, "On the Gaseous State of Matter," was delivered by Prof. T. ANDREWS, LL.D., F.R.S., Vice-President of Queen's College, Belfast. The following is an Abstract:—

After referring to certain modifications in his former method of working at high pressures, the author describes some preliminary experiments which were undertaken to determine the change of capacity in the capillary bore of the glass tubes under the pressures employed. From these experiments it appears that, on raising the pressure from 5 to 110 atmospheres, the capacity was increased for each atmosphere by only 0·0000036, and that this change of capacity was chiefly due to compression of the internal walls of the glass tube. Another set of experiments was made to ascertain whether air or carbonic-acid gas is absorbed at high pressures to any appreciable extent by mercury. For the method of operating and other details reference must be made to the original memoir; but the general result is that no absorption whatever takes place, even at pressures of 50 or 100 atmospheres. The pressures are given according to the indications of the air-manometer in the absence of sufficient data (which the author hopes will be soon supplied) for reducing them to true pressures. In the mean time it is probable, from the experiments of Cailletet, that the indications of the air-manometer are almost exact at 200 atmospheres, and for lower pressures do not in any case deviate more than $\frac{1}{80}$ from the true amount.

In a note which was published last year in the 'Proceedings' of the Society (No. 163), it was stated that the coefficient of expansion (α) for heat *under constant pressure* changes in value both with the pressure and