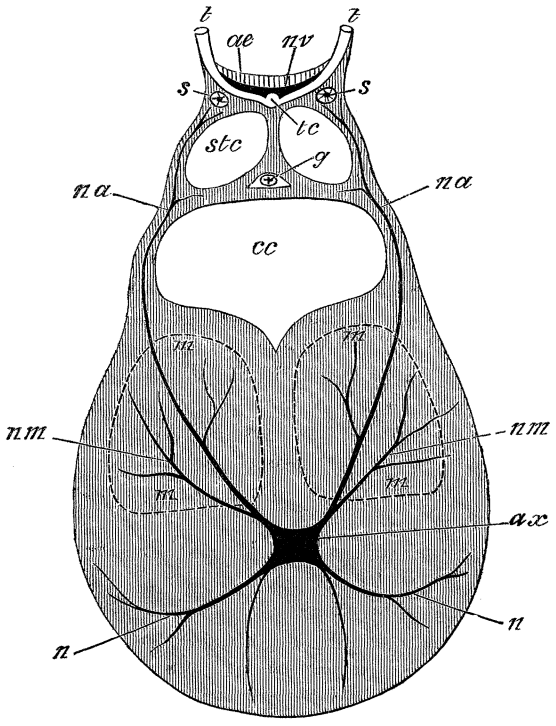
IV. On the Nervous System of the Crinoidea." By WILLIAM B. CARPENTER, C.B., M.D., LL.D., F.R.S. Received May 20, 1884.

In a Memoir "On the Structure, Physiology, and Development of *Antedon* (*Comatula*, Lamk.) *rosacea*," presented to the Royal Society in 1865, I stated* that I had ascertained that the cord (fig. 1, *g*) lying

FIG. 1.



Diagrammatic transverse section of an arm of *Antedon rosacea*. (The ventral or ascending branches of the axial cord cannot be followed continuously in any single section.) *ax*, axial cord, giving off pairs of branches, *n*, *n*, which proceed towards the dorsal aspect of the arm; *nm*, branches distributed on the ends of the muscular bundles, whose position is marked out by the dotted lines *m*, *m*; *na*, ventral branches; *cc*, cœliac canal; *stc*, subtentacular canal; *g*, genital rachis; *tc*, tentacular canal or water-vessel, giving off branches to the tentacula, *t*, *t*, between which lies the ambulacral groove, whose floor is covered by a thick ciliated epithelial layer, *ae*, immediately beneath which is the riband-like band, *nv*, supposed to be the ventral nerve; *s*, *s*, sacculi.

* "Philosophical Transactions," 1865, p. 705.

between the two principal canals (*stc* and *cc*) in the arms of Crinoidea, which had been regarded by Professor J. Müller as a nerve, really belongs to the reproductive apparatus; and further, that I had been led to regard as a nerve-trunk the solid cord (*ax*) which traverses the axial canal of each calcareous segment of the rays and arms, through finding that this cord gives off a regular system of branching fibres (*nm*, *nm*) to the muscular bundles (*m*, *m*) which intervene between the calcareous segments, and which flex the arms by their contraction.

In a further communication on this subject made to the Royal Society at the beginning of 1876, I supported this view by experimental evidence;* showing that in an eviscerated specimen of Antedon, irritation of the quinquelocular organ (contained in the centro-dorsal basin) from the walls of which the radial cords proceed, produces a sudden and simultaneous contraction of the flexor muscles of the arms, similar to that which I had mentioned in my Memoir (§ 13) as resulting in the natural condition of the animal from irritation of its oral pinnules.

That the supposed nerve of Müller is really what I stated it to be—a genital rachis—had been independently ascertained by Professor Semper, and is now universally acknowledged. But my other conclusion has not gained the same acceptance. Coincidently with the communication to which I have last referred, it was affirmed by Professor Greef of Marburg and by Dr. Ludwig, that the real nerve in the arms of Crinoidea is (as in other Stellerida), a fibrillar band (fig. 1, *nv*) that lies beneath the epithelial floor (*ae*) of the ambulacral (ventral) furrow of the arms; a conclusion at which Professor Huxley had independently arrived. And this view is now very generally received and taught in Germany.

In a third communication which I shortly afterwards† made to the Royal Society, I referred to this doctrine; and, whilst admitting the probability that this sub-ambulacral band is really a nerve, I adduced what seemed to me conclusive proof that it cannot be the nerve through which the motor apparatus of the arms is called into action. For, in the first place, it is far removed from this apparatus in position; being separated from the muscles by the triple canal-system, and not being connected with them (so far as can be discerned) by any branching fibres. And, further, the loss of the visceral mass (which contains the central ring of this ambulacral nerve-system) was not found in the least degree to interfere with the rhythmical swimming actions of the animal; whilst a division of the ambulacral nerve in any individual arm produced no paralysis of that arm.

On the other hand, I stated that my son (who was then working in the laboratory of Professor Semper at Würzburg) had fully confirmed

* "Proceedings," Jan. 20, 1876, p. 226.

† *Ibid.*, April 6, 1876.

—by means of thin sections—the statement I had made ten years previously, as to the regular transmission of pairs of branches (fig. 1, *nm*, *nm*) from the axial cord of the arms to their successive pairs of flexor muscles; and I adduced what seemed to me conclusive experimental proof that these cords, which radiate from the wall of the central quinquelocular organ, and are further connected with each other by a commissural ring, have a motor function.

In the first place, I argued that the extraordinary co-ordination which is manifested in the active swimming action of Antedon, when it spontaneously leaves, or is detached from, the anchorage afforded by the grasp of its dorsal cirri, cannot be accounted for without a definite direction from a nervous centre. That this centre is not in a circum-oral ring, is clear from the continuance of the regular movements after the complete evisceration of the animal. On the other hand, that it is contained within the centro-dorsal basin, was indicated alike by the coiling-up of the arms when the quinquelocular organ was irritated, and by the complete paralysis of the flexor muscles which followed the removal of the centro-dorsal basin with its contents. And, further, the destruction of a portion of the axial cord of an arm, the ventral nerve being left uninjured, was shown to be followed by complete paralysis of the muscles of that arm beyond the injured part.

The anatomical and the experimental evidence that the quinquelocular organ, with its radiating and branching cords, constitute the motor nervous system of the arms, being thus in complete harmony, I ventured (p. 454) to profess myself "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 and spinal cord, and the white solid cords proceeding from these centres, in a Vertebrate animal."

That the sub-ambulacral band of Ludwig is also a nerve (as homology would indicate), I thought not improbable; but looking to its immediate proximity to the sensory (ventral) surface, and to the absence of any connexion with the muscular apparatus, I thought that it might probably be an afferent nerve, "the functions of the single trunk of the Asterida 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 fifth and seventh pairs."

During the eight years which have elapsed since these statements were made public, it might have been expected that my conclusions would have been either accepted or controverted. But the question has been considered by many eminent Zoologists, especially in Germany, as one which is so conclusively settled by Homology, as not

to be a matter for discussion; it being impossible (in their judgment) that the axial cords of the arms should be nerves, whatever may be the anatomical and experimental evidence that they are. I would submit, however, that the possibilities of Nature are not limited by the dicta of her interpreters;* that anatomical and experimental facts are not to be set aside by preconceived theoretical opinions; and that the morphology of the Crinoidea has to be settled upon the basis of their own organisation, before it is brought into comparison with that of other Echinodermata. Now the question whether the axial cords of Crinoidea do, or do not, form part of their nervous system, has to be decided: *first*, by their Histological character; *secondly*, by their Anatomical distribution; and, *thirdly*, by Physiological evidence; and on each of these points I have now a large body of new evidence to adduce, derived from the careful and minute investigations on which my son, Dr. P. Herbert Carpenter, has been continuously engaged during the last eight years. Of the results of these investigations, which are scattered through the various papers he has published on "Crinoid Morphology," I shall now present a summary, arranged under the above heads; referring to those papers† for a more detailed statement of them.

Histological Character.—Although the axial cords do not consist of tubular nerve-fibres—their substance being essentially protoplasmic, and showing but an indistinct fibrillation when hardened in spirit—yet, scattered through these cords and their branches, Dr. P. H. Carpenter has found distinct bi-polar and multi-polar cells; and he has further ascertained that the sub-ambulacral band presents a histological character so precisely identical, notwithstanding the difference of its origin, as to afford a strong presumption that if the latter is a nerve, the former likewise is so. On the other hand, the axial cords, which are regarded by Ludwig as merely unconsolidated portions of the basis-substance of the calcareous segments, differ essentially from that substance histologically.

Anatomical Distribution.—Nothing can be more marked or more constant than the distribution of the branches (fig. 1, *nm*, *nm*) of the axial cords to the very definite inter-segmental muscular bundles of the arms and pinnules, alike in the free and in the pedunculate

* Every one familiar with the History of Science knows how often such *à priori* assumptions have been made and disproved.

† "Remarks on the Anatomy of the Arms of the Crinoids," in "Journal of Anatomy and Physiology" (1876), vol. x, p. 584, and vol. xi, pp. 87–93; "On the Genus *Actinometra*," in "Transactions of Linnæan Society," Second Series, Zool., vol. ii, pp. 32–37; "On the *Comatulæ* of the 'Challenger' Expedition," "Proc. Roy. Soc.," March 6, 1879, pp. 394–395; "The Minute Anatomy of the Brachiate Echinoderms," in "Quarterly Journal of Microscopical Science," vol. xxi, pp. 188–193, and vol. xxiii, pp. 614–616.

Crinoids. Moreover, in the dorsal cirri of Comatulidæ, which have a markedly prehensile power, but have no definite muscular bundles, the axial cords send branches into the contractile substance that serves the purpose of muscles. Branches of the axial cords (*na*, *na*) also proceed to the lateral surfaces of the soft parts that lie on the ventral side of the arms and pinnules, and are traceable to the very lips of their ambulacral grooves, forming also an extensive plexus along the sides of the ambulacral grooves of the disk. On the other hand, the sub-ambulacral nerves, which in Ophiurida send very distinct branches to the muscles of the arms, send no such branches to the arm-muscles of Crinoidea. And thus the evidence furnished by anatomical distribution as to the source of the nerve-power which calls those muscles into contraction, is alike positive in regard to the axial cords, and negative in regard to the sub-ambulacral nerves. At the same time, the distribution of the branches of the axial cords to the perisome of the soft parts of the arms and pinnules, would indicate that these have an afferent or sensory function.*

Physiological Evidence.—The inquiries of Dr. P. H. Carpenter, having been entirely limited to the anatomical examination of spirit specimens of Crinoidea, do not afford any direct confirmation of the statements I formerly made as to the actions of living Antedons; but they furnish most remarkable confirmatory evidence of an indirect kind—that, namely, which may be deduced from what Cuvier termed "Experiments prepared for us by Nature." For having met with numerous cases in which the ambulacral groove and the tentacular apparatus are wanting, whilst the arms and pinnules showing this deficiency are normally constructed in other respects, he has invariably found that the ventral or sub-ambulacral nerve is alike deficient, while the axial cord and its branches have their usual distribution. Among these cases, the following may be specified:—

a. The long pinnules which come off from the second brachial segments of *Antedon rosacea*, and which (from the manner in which they arch over the mouth during life) have been distinguished as oral pinnules, are destitute of the tentacular apparatus—as I pointed out in my original Memoir (§ 16). This peculiarity has been found by my son to be a general character of the genus Antedon; and he has further shown that, with the deficiency of tentacles, there is also an absence of the ordinary ciliated epithelium of the ambulacral groove, and of the subjacent nerve and nerve-vessel.†

* The observations of Dr. P. H. Carpenter upon the distribution of the branches of the axial cords, have been fully confirmed by those of M. Edmond Perrier; who has been led by his own independent investigations on *Antedon rosacea* to the full acceptance of the nervous character of these cords, notwithstanding his opposite prepossession. (See "Comptes Rendus," July, 1883, tome xcvii, p. 187.)

† "Journal of Anatomy and Physiology," vol. xi, October, 1876, p. 89.

b. It has been noticed, as well by Ludwig as by Dr. P. H. Carpenter, that in the terminal segments alike of the arms and of the pinnules of *Antedon Eschrictii*, there is a similar want of the tentacular apparatus, with an obliteration of the ambulacral grooves by the approximation and fusion of the elevated folds of perisome at their sides; and that here also the sub-ambulacral nerve is absent.

c. The most remarkable case of this kind, however, is presented by that aberrant type of Comatulidæ which is distinguished generically as *Actinometra*. This genus differs from Antedon in the excentricity of its mouth: the anal orifice being generally in or near the centre of its ventral disk, whilst the mouth lies near its margin. This curious disposition is not related to any departure from radial symmetry in the structure either of the calcareous skeleton, of its muscular apparatus, or of the axial cords whose branches are distributed to the muscles and perisomatic surface of the arms; but it is associated with a very marked irregularity in the disposition of the tentacular and ambulacral apparatus. For, whilst in the arms given off from the *oral* side of the disk, some pairs of pinnules are usually destitute both of tentacles and of ciliated ambulacral grooves, this deficiency is generally complete in a large proportion, not only of the pinnules, but of the arms arising from the *aboral* side of the disk, sometimes amounting to one-half of the entire circle, and occasionally also on the disk itself. And wherever the tentacles and ambulacral groove are wanting, the sub-ambulacral nerve also is absent. Yet we are assured by Professor Semper, who kept *Actinometræ* for weeks together in his aquaria, that "he never saw the least trace of any irregularity in the alternating movement of their arms while swimming;" the non-tentaculated members, notwithstanding the want of sub-ambulacral nerves, acting precisely like the tentaculated.*

Thus, then, the "Experiment prepared for us by Nature," in the subtraction of the sub-ambulacral nerve-system from certain pinnules and arms of Comatulidæ, entirely confirms the conclusions which I drew from my artificial induction of the same physiological condition. For it is, of course, impossible that their oral nerve-ring can minister to the general sensori-motor actions of arms and pinnules which receive no radial extensions of it; and yet the character of those actions (as I have already pointed out) so distinctly indicates their dependence on the originating and co-ordinating power of a nerve-centre, and on the internuncial power of nerve-cords, that we must seek elsewhere for a nervous mechanism on which they depend. Those who deny that this can be furnished by the axial cords, by the dorsal centre from which they radiate (with the remarkable annular commissure on its primary trunks), and by their minute ramifications

* See Dr. P. Herbert Carpenter's Memoir on the genus *Actinometra*, in "Linnæan Transactions," New Series, vol. ii, Zoology, p. 36.

in the muscular bundles and perisomatic surface, have to account for these two facts in the ordinary life-history of uninjured animals:—*first*, the immediate and consentaneous contraction of the hundreds (or thousands) of arm-muscles in Antedon, called forth by irritation of the oral pinnules; and, *secondly*, the performance of swimming movements as regular as those of Antedon, by the non-tentaculated arms of Actinometræ—notwithstanding the absence, in both cases, of what is affirmed to be their sole nervous supply.

Thus, while the doctrine that the remarkable sensori-motor endowments of the Crinoidea depend upon their *ventral* nervous system, consisting (as in Asterida and Ophiurida) of an oral ring with radial branches, is supported only by a theoretical homology, it is in direct contradiction to the following facts:—

1. The absence of any branches from the sub-ambulacral nerves to the muscular apparatus of Crinoidea generally.

2. The absence of sub-ambulacral nerves from those pinnules of Antedon which are most distinguished by their sensory endowments.

3. The absence of sub-ambulacral nerves from a large proportion of the arms of Actinometræ, which, nevertheless, take their full share in the co-ordinated swimming movements of those animals.

4. The continued performance of these movements by Antedons from which the whole visceral mass, including the oral ring, has been removed, and by arms whose sub-ambulacral nerves have been cut near their base.

On the other hand, the dependence of the general sensori-motor endowments of Crinoidea upon what I have described as their *dorsal* nerve-system, is a doctrine which has been found to harmonise alike with every fact that the most careful and minute study of their organisation has brought to light, with the results of the "Experiments prepared for us by Nature" in the varieties of that organisation, and with those of such experiments upon the living animals as would be deemed conclusive in other cases. It is opposed only by a theoretical homology, a preconceived notion of what Crinoids ought to be,* which was adopted (as Dr. P. H. Carpenter has perti-

* Thus Baudelot, who was searching for the nervous system of the Crinoidea, and traced out the whole system of dorsal cords with their pentagonal commissure (apparently in ignorance of what I had previously done), while remarking that "dans leur disposition aussi bien que dans leur structure ces parties offrent une analogie presque complète avec les cordons nerveux des autres Échinodermes," nevertheless affirms that "*évidemment elles n'appartiennent point au système nerveux.*" ("Archiv. de Zool. Exper. et Gén.," tome i, p. 211.)

[Since the above was written, Dr. P. H. Carpenter has drawn my attention to a recent paper by Dr. Weinberg on the Morphology of living Crinoids ("Der Naturhistoriker," Mar.—Jun., 1883, pp. 266—307), in which Dr. P. H. Carpenter's descriptions (with illustrative figures) of the muscular branches of the radial cords are treated as "suppositions;" while his account of the absence of tentacles, of the

nently remarked) without any sufficient knowledge of the anatomy of this most interesting group. Further, that this *dorsal* nerve-system is the fundamental and essential sensori-motor apparatus of Crinoidea, and that their *ventral* nerve-system is secondary and accessory, is indicated by the universal presence of the former in every arm and pinnule, while the latter is frequently absent. And that the function of this latter is limited to the control of the tentacular apparatus, appears probable from the constancy of its association with that apparatus; being invariably present in those arms and pinnules which are provided with tentacles, and absent in those which are destitute of them.

In conclusion, I would remark that the question whether these axial cords do or do not constitute parts of the fundamental nervous system of Crinoidea, is one of far-reaching interest; since it obviously affects our whole conception of the morphology of the group. If I am right in my contention, the centre of the nervous system of the Crinoidea has its seat in that Stem which is the most distinctive feature of their structure. For the quinquelocular organ that lies in Antedon within the centro-dorsal basin, is only an expansion of the soft axis which occupies the central canal that extends through the entire length of the stem; repeating on a larger scale a similar dilatation that occurs at every node from which a circlet of cirri is given off. And the radial skeleton of the stem, of the calyx, of the arms, and of the pinnules of a Crinoid, is even more completely built up on this elongated nerve-centre and its radial extensions, than is the longitudinally segmental skeleton of a Vertebrate animal upon its cranio-spinal axis,—a consideration which must be constantly kept in view in any attempt to trace out the homologies of Crinoidea with other Echinodermata. To myself it has always appeared that

ambulacral epithelium, and of the ventral nerve, in a large proportion of the arms of *Actinometra*, is altogether ignored. As Dr. Weinberg seems to justify his disbelief of Dr. P. H. Carpenter's description, by his own failure, and that of Dr. Ludwig, to verify them on *Antedon rosacea*, it may be well for me to state that its accuracy has been verified by careful examination of Dr. P. H. Carpenter's preparations, not only by myself, but by many other experienced Microscopists in this country; whilst, as already mentioned (p. 71, *note*), Professor Perrier has been led by his own independent investigations to accept my own and my son's statements as fully borne out by microscopical evidence. As Dr. Weinberg, though he has had the opportunity of studying *Antedon rosacea* alive, and of thereby refuting my experimental results, if erroneous, refrains from discussing them, and as he also ignores the fact (though vouched for by Ludwig) that the ventral nerve is wanting in the peculiarly sensitive oral pinnules of *Antedon*, it seems as if his confidence in his theoretical Morphology blinds him to every fact which conflicts with this. The complete confirmation of my experiments by Professor A. M. Marshall and Dr. Carl F. Jickeli (see ADDENDA) may perhaps render them worthy of his more serious consideration (June 28).]

they differ much more widely both from Asterida and Ophiurida, than those Orders differ from each other; and while all recent researches tend to show that Crinoidea are closely allied to Blastoidea and probably to Cystidea, they bring into view their points of difference from all Echinoderms the aspect of whose mouths is downward,—a distinction long since put forward by Leuckart as one of fundamental value.

It was pointed out nearly twenty years ago by Sir Wyville Thomson and myself, that the canalisation or non-canalisation of the calcareous segments of the Crinoidal skeleton, for the passage of the axial cords, affords a distinctive character by which its proper *radial* portion can be differentiated from the accessory pieces by which its arrangement is often complicated and obscured. And the practical value of this character has been recognised by various students of the extinct types of the group,—with this modification, that among the Paleocrinoids the axial cords often lie in grooves which have not closed-in to form canals, just as I have shown to be the case in Antedon at a certain stage of the development of the radials. It is obvious that the morphological value of this character becomes much greater, if the axial cords are nerve-trunks which call into action the complicated muscular apparatus of the arms, than if they are to be regarded (with Ludwig) as merely unconsolidated portions of the general basis-substance of the calcareous skeleton.

Another point of interest—Physiological rather than Morphological—is the existence of a definite nervous system, possessed of great functional activity, which yet shows very little histological differentiation. It can scarcely be doubted, I think, that there is here no definite distinction between ganglionic centres and nerve-trunks; almost every part of the apparatus being probably capable of originating as well as of conducting. The peripheral branches distributed to the perisome will, of course, be those by which sensory impressions will be received; while the branches distributed to the muscles will be those which call forth their motor activity. But that the axial cords of the arms are not *mere* conductors, seems proved by the performance of active spontaneous movements by arms which have been for several days detached from the body. And the connexion of these cords with each other in the annular commissure and in the quinquelocular centre, would seem to have reference rather to the co-ordination of actions which would be otherwise independent, than to a derivation of nerve-power from either of those sources.

I cannot but think that I have now given sufficient reason why the question I have raised should be no longer ignored, but should be reconsidered in the light of the new facts and arguments I have adduced in support of my views. Those who refuse to accept them, are bound, I think, either to disprove the facts, or to show that

my deductions from them are unsound. To assert that they are "evidently" erroneous, is clearly an unscientific mode of disposing of them, unworthy of any real lover of truth.

ADDENDA.

(June 11.)—I am permitted by Prof. A. M. Marshall, of Owens College, to state that having, during a recent visit to Naples, repeated for himself at Dr. Dohrn's Zoological Station the experiments which I performed there in 1876 upon the Nervous System of *Antedon rosacea*, he found their results confirmatory of my own in every particular; whilst he was further led to assign an *afferent* as well as a motor function to the *dorsal* nerve-system, as I had myself been led to do by the absence of the *ventral* nerve in the aboral arms of *Actinometræ*. Professor Marshall informs me that he hopes to publish an account of his experiments in the next number of the Quarterly Journal of Microscopical Science.

(June 28.)—I also learn from Prof. Marshall and my Son, that a further experimental confirmation of my conclusions has been recently published by Dr. Carl F. Jickeli of Jena.* Having investigated the subject four years ago at Trieste, he not only repeated and verified my experiments, but varied them by the use of electric stimulation. He found that when this was applied to the ambulacral groove of a detached arm, it produced no effect; but that if applied to the axial cord, it called the muscles of the arm and pinnules into contraction, so as to produce flexure, even though the arm had previously shown no signs of life. If applied to the axial cord of a cirrus, electrical stimulation threw the cirrus into tetanic contraction. Further, Dr. J. found that while the application of caustic to the ambulacral groove of an arm had no effect in preventing the excitation of flexure by electric stimulation of the axial cord, the application of caustic to the axial cord itself caused a straightening of the arm and a cessation of its movements, as if by the killing of its nerve.

These results, says Dr. Jickeli, can be explained in no other mode than Dr. Carpenter's; and he further states that his histological examination of the axial cord has satisfied him of its nervous character.

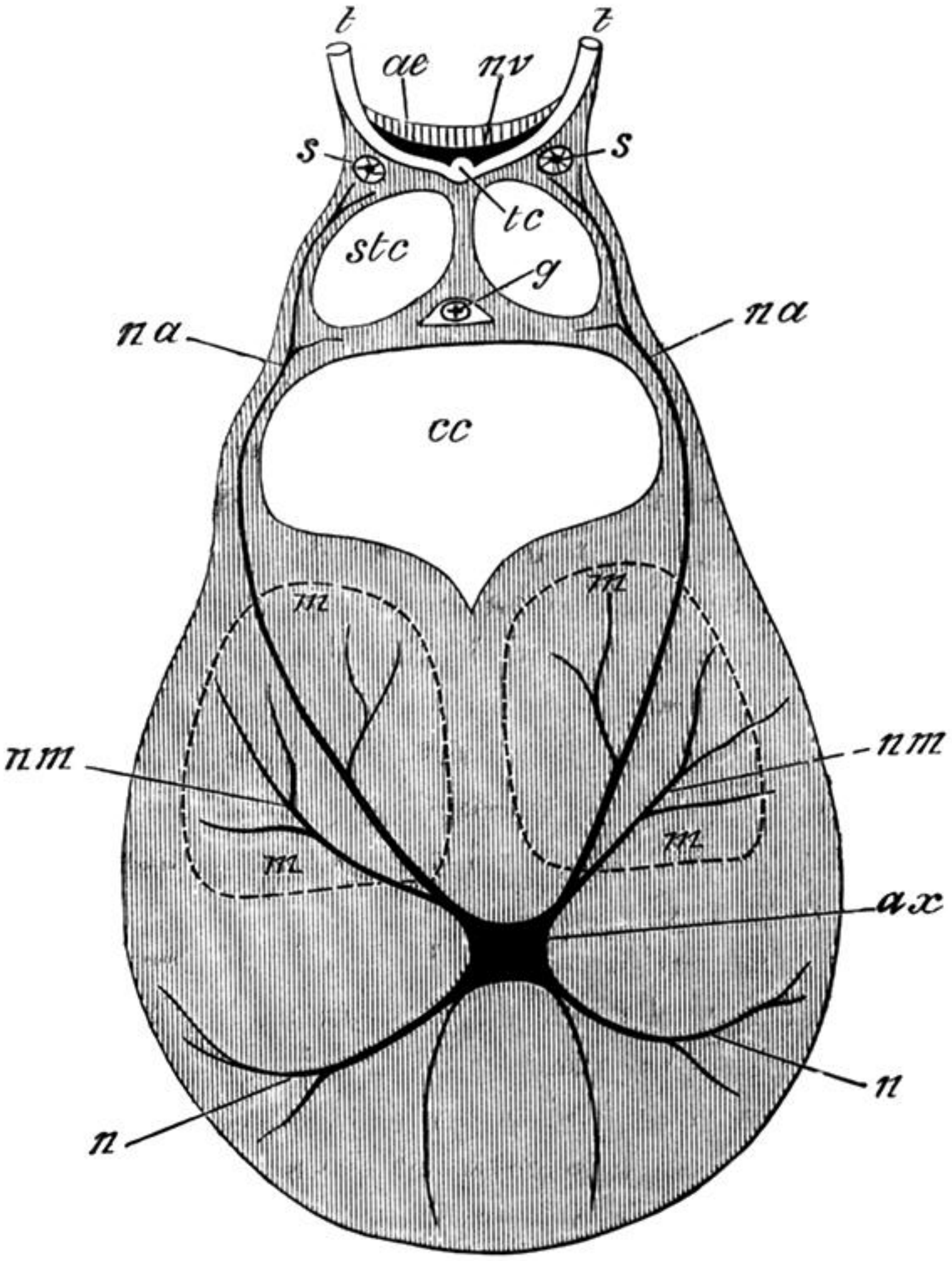
In claiming to be the first, after my Son, who has publicly adopted my view, Dr. J. seems unaware that Professor Perrier has been led to accept it, by his study of the anatomical distribution of the pairs of branches given off from the axial cord. (See note, p. 71.)

W. B. C.

The Society adjourned over the Whitsuntide Recess to Thursday, June 19.

* Über das Nervensystem und die Sinnesorgane der *Comatula Mediterranea*," in "Zool. Anzeiger," 7 Jahrgang, No. 170, p. 346.

FIG. 1.



Diagrammatic transverse section of an arm of *Antedon rosacea*. (The ventral or ascending branches of the axial cord cannot be followed continuously in any single section.) *ax*, axial cord, giving off pairs of branches, *n*, *n*, which proceed towards the dorsal aspect of the arm; *nm*, branches distributed on the ends of the muscular bundles, whose position is marked out by the dotted lines *m*, *m*; *na*, ventral branches; *cc*, cœliac canal; *stc*, subtentacular canal; *g*, genital rachis; *tc*, tentacular canal or water-vessel, giving off branches to the tentacula, *t*, *t*, between which lies the ambulacral groove, whose floor is covered by a thick ciliated epithelial layer, *ae*, immediately beneath which is the riband-like band, *nv*, supposed to be the ventral nerve; *s*, *s*, sacculi.