

VIII. *On the Structure, Relations, and Development of the Nervous and Circulatory Systems, and on the Existence of a Complete Circulation of the Blood in Vessels, in Myriapoda and Macrourous Arachnida.—First Series.* By GEORGE NEWPORT, Esq., President of the Entomological Society of London, and Member of the Royal College of Surgeons, Corresponding Member of the Philomathic Society of Paris. Communicated by P. M. ROGET, M.D., Sec. R.S. &c.

Received April 6,—Read April 6, 1843.

THE increasing importance that is daily attached to the study of the comparative anatomy of the Invertebrata, and the interest with which every microscopic examination of structure is now regarded, as assisting to elucidate the great problems of life in the higher animals, have encouraged me through several years to prosecute a series of investigations, in the articulated classes, on two of the most important portions of the body,—the nervous and circulatory systems. These investigations have afforded me, from time to time, some interesting results, part of which, on one of these structures, I have already had the honour of communicating to the Royal Society. I now propose to communicate the results of my examinations of both these structures, and to illustrate their development, and the relations which they bear to each other, in some of the principal classes, commencing, in the present paper, with the Myriapoda and Arachnida.

The objects to which my attention has been directed in this paper are three:—*First*, the minute anatomy of the nervous system in the Myriapoda and Macrourous Arachnida, more especially with regard to the structure of the cord and its ganglia, and the means which these afford us of explaining the physiology of the nervous system, and the phenomena of the reflected movements in articulated animals. *Secondly*, to demonstrate the existence of a complete system of circulatory vessels in the Myriapoda and Arachnida. *Thirdly*, to show the identity of the laws that regulate the development of the nervous and circulatory systems in these Articulata, and their dependence on the changes which take place in the muscular and tegumentary structures of the body, as I formerly showed in regard to the changes in the nervous system of insects\*.

1. NERVOUS SYSTEM.—*Theory of Development.*

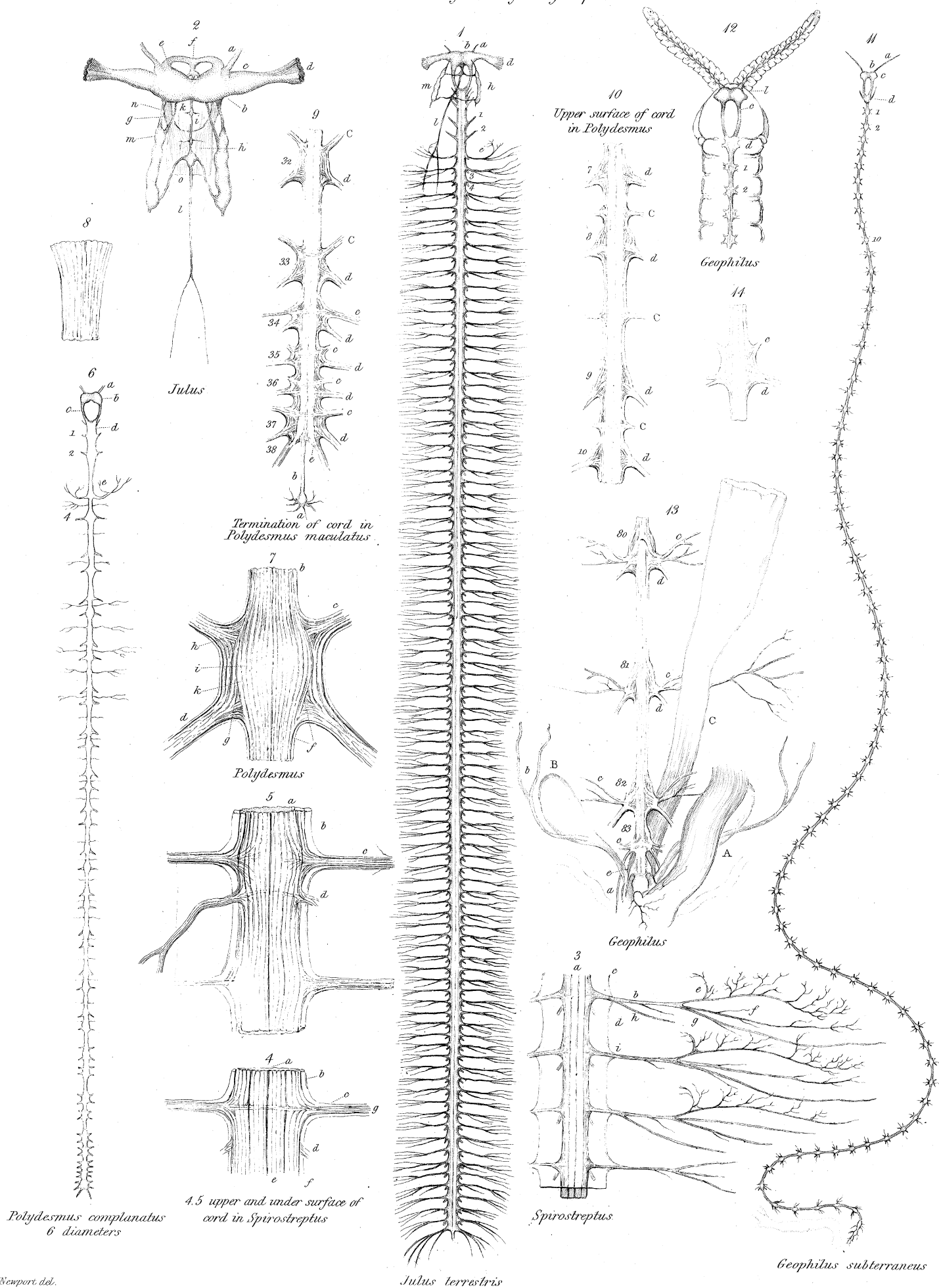
The nervous system of the Myriapoda approaches in the simplicity of its formation nearer to that of the Annelida than to any permanent condition in the higher Articulata, or even to its transitory state in the larvæ of insects. In the lowest types of the

\* Philosophical Transactions, 1834.

orders *Chilopoda* and *Chilognatha*, the great divisions of the Myriapoda, it exhibits two marked conditions. In the *Chilopoda* it has the form of a double cord connected by large ganglia in each segment, as in most of the *Annelida*, *Crustacea*, and *Insecta*; but in the vermiform *Chilognatha*, which former researches\* have proved to me are most nearly connected to the *Annelida*, the two parts of this double cord are so closely united laterally as to appear like a single cord, that gives off a multitude of small nervous trunks at its sides throughout its whole length, but without distinct ganglionic enlargements at their origin. The cord is, nevertheless, composed in each Order of two longitudinal portions, more or less closely approximated, and united at certain distances by ganglia. It is extended along the under surface of the body beneath the alimentary canal, and its ganglia correspond in number to the number of segments, in strict accordance with the character established by CUVIER in his definition of the subkingdom *Articulata*.

In all the *Articulata* two modes of development are in operation in the same animal; first that of *growth*, or simple extension and enlargement of each individual part; next that of *aggregation* of two or more parts to form particular divisions or regions of the body. This latter mode of development is carried to a greater extent in insects than in any other of the *Invertebrata*, and, as is well known, changes the animal from a simple, elongated, worm-like larva, furnished with many pairs of organs of locomotion, and composed of segments almost uniform in size and appearance, to an individual of a totally different character, with its body divided into three distinct regions, differing in size and appearance, and separated from each other, with the number of its organs of locomotion reduced, and those that remain greatly enlarged and altered. Some of these changes in the segments take place also in the *Myriapoda*, but are carried only to a very slight extent. The head is composed of several segments, either consolidated together like the head in true insects, as in the vegetable-feeding *Chilognatha*, or separated, and moveable on each other, to adapt them to the carnivorous habits of the species, as in the rapacious *Chilopoda*. In like manner each moveable division of the body is in reality composed of two distinct segments, originally separate, but anchylosed together at an early period of their formation. Each of these sub-segments ought, therefore, to possess its separate ganglion, and this in reality is the case. The *head* is composed of the elements of at least four segments, and perhaps even of six; and contains ganglia, placed two above and two below the œsophagus, which give nerves to the antennæ, to the eyes, to the maxillæ, and to the mandibles. The two anchylosed portions of each moveable segment of the body have, in like manner, their separate ganglia, as in the *Polydesmidæ*, in which the ganglia remain distinct throughout life in the posterior segments, but have coalesced in the anterior, more especially in those which are nearest to the head. These unions are occasioned by a reduplication inwards of the tegument, as in the aggregation of segments in insects, but this is carried to so slight an extent in the

\* *Op. cit.*, Part II. 1841.



Myriapoda as hardly to affect the general form and appearance of the animal, although influencing every structure in that part of the body in which the change occurs.

*Structure.*—The brain of the Myriapod is formed by the aggregation of separate ganglia\* placed above the œsophagus. The first pair of ganglia are always the smallest, and give origin on their front to the nerves of the antennæ, the anterior prolongations of the nervous cord. The second pair, immediately behind them, constitute, as in insects, the organs of volition, and represent the brain of Vertebrata. They are in reality, as I have elsewhere shown, the analogues of the *corpora quadrigemina*†, and give off nerves at their sides to the organs of special sense,—the eyes. They are always more developed than the ganglia of the antennæ, and continue to increase in importance as we ascend to the most perfectly developed insects. They are of large size, even when those of the antennæ are almost absent, as in the larvæ of lepidopterous insects, and even when the organs of vision are entirely wanting, as in the whole of an extensive family of Chilognatha,—the *Polydesmidae*. They are placed transversely above the œsophagus in the form of a crescent, the side of each lobe being a little in advance of the posterior. They are connected on their under and external surface by two cords of nervous matter, which are prolonged downwards, one on each side of the pharynx, and constitute the *crura cerebri*,—with the united ganglia of the maxillæ and mandibles, which form the analogue of the *medulla oblongata*‡—the commencement of the abdominal cord.

In the *Iulidæ* (Plate XI. figs. 1 and 2) these cerebral lobes (*b*) are convex, both on their upper and posterior surfaces, and their original separation is marked by a median sulcus, which is more or less evident in different individuals. In some it is almost entirely obliterated, and the two lobes are more closely approximated, indicating, perhaps, the greater extent to which this important division of the nervous system has been developed in them than in others in which the union of the lobes is less perfect. Each lobe is connected externally with the *optic ganglion* (*c*), which is of an elongated, oval, and slightly conical form, from which nervous filaments radiate outwards and downwards in a triangular fasciculus to the cornea (*d*). The fibres are extended almost close to the cornea before they are clothed with dark pigment and form the retina, the chamber of each lens being scarcely longer than wide, so that the eyes are fitted only for examining near objects, a condition entirely in accordance with the habits of these animals. The ganglia of the antennæ (*a*) in *Iulus* are very small, and are situated near the junction of the cerebral lobes with the optic ganglia, and each gives off its nerve directly into the antennæ. From the enlargement of each

\* Since this paper was delivered to the Royal Society I have found that, in the embryo of *Necrophleopagus* (*Geophilus*) *longicornis*, LEACH, at the moment of bursting its shell, the brain is composed of *four* double ganglia, the centres of a corresponding number of segments, which are then becoming aggregated together to form the single moveable portion of the head in the perfect animal; so that the brain of the Myriapod, and probably also of all the higher Articulata, is, in reality, composed of at least four pairs of ganglia.—G. N., July 14, 1843.

† Observations on the Anatomy, Habits, and Economy of *Athalia centifolia*. 8vo, 1838, p. 10.

‡ *Op. cit.*



lobe at its junction with the descending crus, a thick trunk of nervous matter (*e*) is extended forwards and transversely across the front of the head, above the palate and mouth, and uniting with its fellow from the opposite side, forms in the middle line a small triangular ganglion (*f*). These nervous trunks are the analogues of the recurrent nerves in insects, from which the visceral nerves (*k*) take their origin. In these Myriapoda the recurrent nerves are more extensively developed than in the other classes, and they seem to decrease in importance as in size, in proportion as the other parts of the nervous system are developed. The small triangular ganglion formed by them above the palate, sends backwards in the middle line a short thick nerve, which terminates immediately before the brain in a more indistinct ganglion that gives off three branches. The middle one of these is much smaller than the lateral, and passes backwards beneath the brain along the pharynx and œsophagus in a small triangular space between the lobes, covered by the median vessel from the heart, that passes between it and the brain and gives vessels to that organ. This median nerve from the recurrent ganglion constitutes the trunk of the proper *vagus nerve* (*l*); while the others from the same ganglion, each of which is more than twice as large as the vagus, after giving off some minute filaments to the pharynx and œsophagus, descend to the sides of the pharynx and pass backward between it and the crura cerebri (*g*) on each side (*h*), to unite at a short distance behind the brain with a series of large visceral ganglia (*m*) collected together, and constituting the analogues of the *anterior lateral ganglia* of insects. This series of ganglia, as in insects, is connected to the brain by two small communicating nerves (*n*), extended backwards from the posterior surface of the lobes, near where they are joined to the optic ganglia. These lateral, visceral ganglia in *Iulus*, are of most extraordinary size, being nearly half as large as the brain itself. There are four on each side of the œsophagus, closely connected in one series, extended along the œsophagus as far as the middle of the first or pro-thoracic segment, giving off branches of nerves to the immense salivary glands, to the œsophagus itself, and to the surrounding structures. They exhibit the appearance of masses of gray nervous matter inclosed in a distinct theca. The last of the series extends a little further backwards than the aortic arches given off from the anterior chamber of the heart. They seem to be the anterior of an extensive series of visceral ganglia, distributed in great part to the salivary glands. They communicate with the vagus by means of a nerve that passes directly from the last of these ganglia, on each side, to a large ganglion formed on the vagus (*o*) at some distance from the brain. The vagus nerve, after passing beneath the brain, forms a minute ganglion (*i*) immediately behind it, which is also connected to the lateral ganglia by a very minute branch on either side. It then passes along the œsophagus and forms the second larger, rounded ganglion, first mentioned as connected to the last of the lateral ganglia. After this it continues its course backwards half way along the œsophagus, and then divides into two branches, which are given, as in insects, to the posterior part of this organ, and to the cardiac extremity of the stomach.

One of the most interesting circumstances connected with the development of the nervous system in *Iulus*, is the relative size of the brain as compared with that of these ganglia of the viscera. In these inferior Myriapoda, in which the power of locomotion is distributed equally to every segment of the body, the brain itself forms but a small proportion of the whole nervous system, and the faculties of sense are less perfect than in insects; while the nerves of organic life, and their ganglia, are nearly equal in volume, as in *Iulus*, to the whole brain, the organ of volition. The very reverse of this is the case in insects. In those in which the faculties of sense, more especially of vision and smell, and the power of voluntary motion are carried to their greatest extent, as in volant insects,—the gregarious Hymenoptera, Neuroptera, and Lepidoptera,—the volume of brain bears a much larger proportion to the rest of the nervous system, and the ganglia of organic life a smaller. This is more especially the case in the perfect insect, in which the volume of brain is not merely relatively, but actually increased in size during the changes from the larva to the perfect state, thus leading to the inference that the importance of the visceral nerves is gradually diminished in proportion as those of volition and active existence become augmented.

Notwithstanding this inferiority of organization in the nervous system of *Iulus*, the brain is inclosed in a proper covering, and is separated from the surrounding structures by a distinct membrane, but this is so delicate as to be detected only with some difficulty. It is completely inclosed in this structure, which also sends off prolongations that form a covering for the œsophagus with its vessels and nerves.

The *nervous cord* is extended from its commencement in the crura of the brain (*g*) and medulla oblongata, or first subœsophageal ganglion (*h*) to the antepenultimate segment of the body, and is almost uniform in size throughout its whole length. It is slightly larger at its anterior, and smaller at its posterior extremity, than in the middle part of its course. In *Iulus terrestris* it has ninety-six very minute ganglionic enlargements, situated entirely on the under surface of the cord, and so closely approximated together as not to be observable, except on very close inspection. Each of these enlargements gives off two pairs of nerves, one of which, on the under surface, is given to the legs, and the other, on the lateral and superior surface, to the sides of the body; so that the whole number of nervous trunks from the cord, including those from the medulla oblongata, is ninety-four pairs to the head and sides of the body, and ninety-two pairs to the legs, making in the whole one hundred and eighty-six pairs, or two hundred and seventy-two nervous trunks from the cord, exclusive of those which belong more immediately to the brain. In *Spirostreptus* (fig. 3.) the ganglia are even smaller and closer together than in *Iulus*, but the cord is larger in proportion to the size of the nerves, the distribution of which is almost precisely the same as in *Iulus*. Each enlargement of the cord (*a*) gives off at its upper and lateral surface a single nervous trunk (*b*), which passes outwards for some distance as a single nerve, but which in reality includes two distinct sets of nerves,

that separate as principal trunks at the inner side of the great longitudinal series of abdominal muscles. The anterior of these trunks (*e*) is the analogue of the respiratory nerves of insects, and passes across the upper layer of these muscles, on their visceral surface, giving off to them many minute branches. The first of these branches turns backwards and inwards, in the direction of the spiracles and principal tracheæ, on the under surface of the segment behind the legs, while the main trunk of the nerve, greatly reduced in size, passes upwards to the muscular appendages of the heart. The other set of nerves is divided into two main trunks, which pass between the layers of longitudinal muscles, the first of them (*f*) giving off branches to the muscles of the inferior and lateral parts of the body, to which it is almost entirely distributed; and the other (*g*), the larger of the two, passing round the sides of the body, is distributed to the dorsal muscles. Besides these regular branches each alternate pair of nerves gives off a branch from its posterior surface (*h*), near its origin from the cord. This branch is given to the muscles that connect the two segments. The second pair of trunks (*d*) from the ganglion, as in *Iulus*, is given directly to the legs, and send off only one small branch to the coxæ before entering them.

*Structure of the cord.*—The formation of the great abdominal cord in the Iulidæ, by the lateral approximation of two distinct portions, is indicated on its upper surface by a slight median sulcus, and on its under surface by a slight longitudinal division between the two approximated ganglia that form each of its enlargements. Each of these lateral divisions of the cord in *Iulus*, as formerly shown in the *Scolopendra* and other *Articulata*, is a compound structure, formed of two distinct longitudinal series or columns of fibres, which, notwithstanding the different explanation that has been given of their function, since I had the honour of first describing them to the Royal Society\*, are quite distinct from each other, although closely approximated together. By the aid of means superior to those formerly employed in my investigations, I now find that the abdominal cord contains other structures besides those already described. In my former communication to the Royal Society, I indicated the existence of fibres that run transversely through the ganglia of the cord in the larva of the common butterfly†, and similar structures have since been shown by Dr. CARPENTER‡ in other *Articulata*, and applied to explain some of the reflex phenomena of the nervous system, in accordance with the theory promulgated by Dr. MARSHALL HALL. But besides these two sets of *longitudinal* fibres, and the series that passes *transversely through the ganglia*, there are other structures in the cord that have hitherto been entirely overlooked. These are fibres that run longitudinally, in part of their course, at the *sides* of the cord, and enter into the composition of all the nerves from the ganglia. These fibres I shall designate the *fibres of reinforcement of the cord*.

The *superior longitudinal* set of fibres of the cord (fig. 4. *e*), which I formerly

\* Philosophical Transactions, 1834, Part II. p. 408.

† *Op. cit.*, p. 412, Plate XVI. fig. 37.

‡ Inaugural Dissertation on the Physiological Inferences to be deduced from the Structure of the Nervous System in the Invertebrated Classes of Animals, by WILLIAM B. CARPENTER, M.D., 1839.

described as the *motor tract*, and to which the function of volition seems still to be accorded by VALENTIN\*, CARPENTER†, and BALY‡, is extended in Iulus, as in other Articulata, as a separate fasciculus along the upper surface of the cord; but in these Myriapoda it is much narrower in proportion to the whole width of the cord than in insects. This fact is interesting in reference to its presumed function. On a cursory inspection it does not appear to give off any branches, but seems to pursue its course uninterruptedly along the whole length of the cord. It does not indeed give off filaments to the nerves from a ganglion immediately opposite to their origin, while passing over that ganglion, but immediately it has passed one ganglion it gives off the filaments that proceed to the nerves from the next ganglion. These filaments seem almost immediately to join with others that belong to the sides of the cord, and pass out with them into the nerve from the next ganglion along its anterior surface. This is almost precisely the manner in which the filaments from this aganglionic column in the Crustacea are united with those from the ganglionic, as formerly shown in my description of the nerves in that class, when the existence of the lateral fibres of the cord was unknown to me.

The *inferior longitudinal*, or *ganglionic* set of fibres (fig. 5. *a*) of the cord, affords many interesting considerations. It is placed, exactly as in insects, on the under surface, but like the upper series it is narrower than the whole cord, of which it forms a part. It is formed of a longitudinal series of fibres, like the upper tract, beneath which it is placed, and from which it is divided by some of the fibres that pass transversely through the cord, and which enter into the composition of the nerves from the ganglion on either side. It appears also to receive filaments from the upper series, and perhaps others are sent from it to the upper, thus decussating each other in the middle substance of the cord, where these two longitudinal series are in close apposition; since it is almost impossible, even in the large nervous cord of Scolopendra, to separate these two tracts from each other, although their distinctness is evinced in their relative size and longitudinal lines of separation. But there is one fact of great interest in regard to this ganglionic series of fibres. Almost the whole of the fibres of which it is composed are traceable, in the Iulidæ, directly through each enlargement of the cord, which they mainly assist to form. At the anterior part of each enlargement the diameter of each fibre, or fasciculus of fibres, appears to be slightly increased, and its structure becomes more softened and delicate. While passing through these ganglionic enlargements, occasioned chiefly by their own increased diameter, the fibres take a slightly curved direction outwards, and then inwards, but are reduced to their original size, and assume the longitudinal direction on again forming the aganglionic portion of this tract of the cord. This structure of the fibres is well seen in the *Iulidæ* and *Polydesmidæ* (fig. 7. *i*), as I shall hereafter

\* De Functionibus Nervorum, Bern. 1839. (Vide BALY'S MÜLLER.)

† *Op. cit.*

‡ MÜLLER'S Elements of Physiology, second edit. vol. i. 1840, p. 771.

again have occasion to refer to, more especially with reference to the true structure of ganglia. The fibres are traceable most distinctly in the Iulidæ.

These are the structures to which I formerly assigned the function of voluntary motion and sensation, and to which I am still inclined to believe they minister, since the fibres of which both are composed are traceable to the crura and brain. Whether these functions are restricted separately to the two structures, as I first imagined, the one to the upper and the other to the inferior series, or whether they are administered to conjointly by both, through an interchange of fibres, it is almost impossible to determine by any decisive experiment on these animals, although the structures themselves are distinct. But in the absence of experimental proof there are circumstances connected with the distribution of the nerves to the extremities which seem to indicate, that these low forms of Articulata are endowed with a power of sensation and feeling far beyond what has of late been adjudged to them by some physiologists. In some of the gigantic *Spirostrepti* and *Spiroboli* the legs are adapted for climbing up the trunks and branches of trees, by the under surface of the first and second basilar joints of the tarsi being developed into a soft cushion or pad, as in some insects; and to these parts of the limbs I have found the nervous fibres more extensively distributed than to any other; a fact most strictly analogous to that of the distribution of nerves in the tactile parts of the limbs of Vertebrata.

Those fibres of the cord which seem to be independent of the sets just described, and which do not appear to have any direct communication with the great seat of sensation and volition—the brain,—are of two kinds, which may justly be regarded as *involuntary* in their functions. The first of these are the *commissural fibres* (figs. 4. 5. 7. g) which pass through the ganglia; and the second are those which have hitherto been undescribed, and form the sides of the cord (*f*) in the interspace between the ganglia, or between certain nerves distributed from them—the *fibres of reinforcement of the cord*.

The *fibres of reinforcement of the cord* form the lateral portions of the whole nervous cord of the body, and enter into the composition of all the nerves. They constitute, as it were, circles of nervous communication between two nerves that originate from the cord at a greater or less distance; and form part of the cord in the interval between these nerves, and bear the same relation to the segments, individually, which the cord itself does to the whole body. They form a part of the nervous trunks which come off from its upper, or aganglionic tract, as well as of those which proceed from the ganglionic enlargements in the lower, and in each instance they bound the posterior side of one nerve and the anterior of another, to which they proceed along the sides of the cord, forming, in the interspace, a part of its structure. Each fibre may thus be traced from its peripheral distribution, in the structures of the external surface of the body, inwards, along the course of the nerves, on their posterior surface, to the cord, where its direction is altered from that of the nerve

transversely inwards, to that of the cord on which it is reflected, and passes longitudinally backward; thus forming a part of its external surface until it arrives at the root of the nerve to which it is to be distributed, and along which it again passes transversely outwards, bounding the anterior side of the nerve to its distribution on the lateral surface of the body. These fibres of reinforcement form a large proportion of the whole cord, and enter into the composition of the upper, anterior, and part of the inferior surface of the root of every nerve, in their course inwards to the cord; and of its posterior and inferior surface on their again proceeding outwards. In this manner these fibres of reinforcement connect all the nerves of the cord on one side of the body, as the corresponding fibres do those on the opposite side. They form, as it were, double, treble, or quadruple circles, one within the other. Thus the fibres that pass inwards along one nerve may proceed along the cord to pass outwards again on the front of a second, a third, or a fourth, thus linking the segments in one continued series of nervous communications, independent of the brain. But these communications exist only between nerves on the same side of the body, and not between those on the opposite. The *commissural* nerves connect the opposite sides of each individual segment, as those of *reinforcement* do the same sides of two separate segments.

Every nerve from a ganglionic enlargement of the cord is thus composed of *four sets* of fibres, an upper and an under one, which communicate with the cephalic ganglia; a transverse or *commissural*, that communicate only with corresponding nerves on the opposite side of the body; and a lateral set that communicate only with nerves from a ganglionic enlargement on the same side of the body, and form part of the cord in the interspace between the roots of the nerves. It is by the successive addition of these lateral portions of the cord that its size is maintained almost uniformly throughout its whole length in the elongated bodies of the Myriapoda. On examining the cord very closely, I have reason to believe that the upper and inferior sets of longitudinal fibres, the ganglionic and the aganglionic, are somewhat smaller at their posterior than at their anterior extremity, a circumstance readily understood in the fact that successive series of filaments are given off from them at each distribution of nerves from the ganglionic enlargements, while the relative size of the lateral portions of the cord appears to be greater in the posterior than in the anterior. On this account I have named these lateral fibres, *fibres of reinforcement of the cord*.

In regard to the identification of these fibres, it may be well further to state, that their separate existence is indicated chiefly at the postero-lateral margin of the ganglia, (fig. 7. *f*) where they are seen to form part of the nerves and cord without passing upwards to the brain. In other parts of their course they are not distinguishable by colour, and very rarely by any longitudinal line of separation from the fibres which form the inferior longitudinal series, or portion of the cord, to which they are approximated; but from which they are believed to be distinct from the fact, that they do not ascend with them to the brain. Their function must be regarded only as



*reflex*; entirely independent of sensation, but capable of being excited into action by external causes.

The existence of these lateral fibres in the cord may now fully explain the reflected movement of parts anterior or posterior to an irritated limb on the same side of the body, as the commissural ones do the movement of parts on the side opposite to that which is irritated. The presence of these fibres in the cord of insects I had long suspected, from the curved direction of the fibres that bound the ganglia, and from that of the origins of the nerves from the aganglionic tract, as figured in my former paper\*; and although I had communicated this opinion to a friend several years ago, I have never until recently been able to satisfy myself of its correctness.

This uncertainty of the existence of any structure in the cord that seemed sufficient to explain the reflected movements on the same side of the body, independent of the brain and the nerves of volition and sensation, long obliged me to withhold my assent to the doctrines now received respecting these phenomena. Although the fibres that pass transversely through ganglia might explain the effect produced on one side of the body, by the irritation of a corresponding part on the other, there seemed no anatomical structure to account for the movements of distant parts, anterior or posterior to a given point, on the same side, if the doctrine long received, that each fibre is endowed with but one special function, were correct. Now, therefore, that we find an anatomical structure in the cord that seems to account for these phenomena, I ought, in justice, to state, that Dr. HALL, to whom is due the high credit of collecting, comparing and arranging in one system numerous facts connected with the reflected movements of animals, as observed by WHYTT, BLANE and others, and also by himself,—adopting the principle established by our distinguished physiologist, Sir CHARLES BELL, that every nervous fibre is continued unbroken from its origin to its termination, and is capable of ministering only to one special function,—conceived the necessity for the existence of special nerves for the reflected movements; and that, at the period when I was engaged with Dr. HALL in his experiments on this subject, in 1833, he requested me to examine the cord in the Hedgehog to ascertain the correctness of his opinions. This examination was not made, because at that period I differed from him in attributing the reflected movements to the agency of another part of the nervous system. Now that the views of Dr. HALL seem proved to be correct, I am desirous of adding this testimony of the acuteness and perception of one who has done much for physiological science.

In the *Polydesmidæ* (Plate XI. fig. 6.) the nervous system corresponds with that of *Iulus* in regard to the nerves given to the generative outlets, but the ganglia of the cord are larger and situated at much greater distances. Those of the first two pairs of legs have united with the first subœsophageal ganglion (*d*), and the whole form one elongated large nervous mass, similar to the short nervous cord of the *Ostracion* and some other fishes. This great elongated ganglion is situated anterior to the

\* Philosophical Transactions, 1834, Plate XVII. fig. 40–42, *g*.

outlets of the female organs of generation, and consequently anterior to the third segment of the thorax. From its posterior extremity the cord is continued backwards, in the middle line, between the female organs, immediately behind which it gives off a pair of nerves to these organs, apparently from the structure of the cord itself, but in reality from an atrophied ganglion (*e*), which has almost entirely disappeared from this part of the cord, precisely as similar ganglia disappear in the changes of insects; thus showing the constant tendency of the gangliated portions of the nervous cord to become united.

The number of segments in *Polydesmus complanatus*, LEACH (Plate XI. fig. 6.), is twenty-two, including the head and anal segment. The number of ganglia in the cord, separate and distinct from each other, is thirty-four, each of which supplies one pair of organs of locomotion. Besides these there are the united ganglia (*d*. 1, 2.) which supply the manducatory organs and the first and second pairs of legs. The nerves from the atrophied fourth ganglion (*e*) above alluded to are given to the two ovipositors of the female, the analogues of a pair of organs of locomotion; and the thirty-eighth (37, 38.) is itself a double ganglion that supplies nerves to the apodal antepenultimate, penultimate, and anal segments.

*The brain* (*b*) in this family affords some interesting considerations. The two lobes are very small, pear-shaped, and developed on their under surface into very long and slender crura, which join beneath the œsophagus with the great aggregation of ganglia. Each of these lobes is rounded on the external side; and the optic nerves and ganglia are entirely absent, there being externally no organ of vision. On the front of each lobe there is a small elongated ganglion for the antennal nerve, which passes directly into each of those organs (*a*). This is a remarkable condition of the brain in these Myriapodes, and a similar one has been described by TREVIRANUS\* in *Geophilus*, although in that genus, as I shall presently show, the optic nerves are not entirely absent, as in the Polydesmidae. This fact is especially interesting in reference to the analogy that is believed to exist between these lobes of the brain and optic ganglia, and the corpora quadrigemina of Vertebrata, and seems to show that their office is more important than that of simple ganglia of any individual organ; and that the ganglia of the optic nerves themselves are those by which impressions are received from the retina and transmitted to the middle supra-œsophageal ganglia, the brain, the common sensorium of the whole nervous system.

The distribution of the ganglia and nerves of the cord deserve particular attention. On entering the fourth segment the cord is somewhat elongated and passes between the double outlets of the female organs, immediately behind which it gives off the nerves to those organs from the atrophied ganglion. These nerves are exceedingly large, and ramify extensively over the muscles and distal portions of those retractile structures. Behind this atrophied ganglion the cord itself gives off a pair of nerves, which are distributed to the sides of the segment; after which it almost immediately

\* Vermischte Schriften Anatomischen und Physiologischen inhalts. Bremen, 1817.

forms the next ganglion (4.) which gives nerves to the third pair of legs, the posterior of the two pairs of organs of the segment, the female outlets being the analogues of the first pair. In the male the organs are situated further backwards behind the seventh pair of legs. Posterior to the fourth segment of the female, and the seventh in the male, the cord is extended backwards nearly in a uniform manner throughout the remaining segments, as far as the thirty-second ganglion, when it becomes less uniform. In this first part of its course it forms two ganglia in each segment, as we have seen in the double segments of *Iulus*. These ganglia are separated only by a short interspace of cord (fig. 10. *d d*), but there is more than twice the length of cord between the last ganglion of one segment (8.) and the first of that next beyond it (9.). In the interspaces between these ganglia the cord gives off a pair of nervous trunks (*c*), which are distributed to the muscles and sides of the segments; and each ganglion gives off a single pair of nerves to the organs of locomotion (*d*). The nerves from the anterior ganglion in each segment are always directed backwards into the first pair of legs, since the ganglion is situated a little anterior to the coxæ, and is more elongated in form than the second ganglion, the nerves from which enter the legs in a more transverse direction. But in proceeding backwards along the cord the distance between the ganglia is gradually lessened, until in the posterior segments the ganglia are found to follow each other very closely, and almost to unite. So again in regard to the nerves. Those which, in the anterior part of the cord, are given from it at equal distances between the ganglia, are found nearer and nearer to the ganglion next behind, until they at length cease to come from the cord, but are derived directly from the ganglia, each of which then gives off two pairs of nerves, instead of the single pair to the legs, as in the anterior segments. But although the ganglia are thus closely collected together, this is not the result of aggregation in this part of the body, but is consequent on the non-completion of changes which take place in the formation of new ganglionic centres and nerves in this part of the cord, during the successive periodic formation and addition of new segments to the body in these animals, as I have heretofore shown in the *Iulidæ*\*. These formations always take place in all the Myriapoda between the penultimate and antepenultimate segments, and in that part of the cord the new ganglia are produced to those segments. This leads us to some important facts in reference to the means by which the nervous cord itself is developed by extension and elongation of its fibres during the growth of the whole body, and the development of the new segments; and it shows that an elongation takes place in the longitudinal fibres of the cord in the new segments, and that ganglia are developed in its structure while commissural and lateral fibres of reinforcement are in the course of formation. But the distribution of the nerves from these ganglia, and the structure of the ganglia themselves, seem to lead us to the facts. In *Polydesmus maculatus* (fig. 9.), Nob., each of the six posterior ganglia gives off two pairs of nerves. In no instance in these posterior seg-

\* Philosophical Transactions, 1841, Part II.

ments of the body do the nerves come directly from intervening portions of cord, or from spaces between the ganglia. The anterior pair from each ganglion are always given to the sides of the segment, like the nerves from the intervening cords in the anterior segments; and the posterior, to the legs. In the last-formed of these ganglia (36.) the ganglion is very short, the nerves (*c*, *d*) being given off from it almost transversely; and the whole corresponds to the diminutive extent of the posterior of these newly-formed and incomplete segments. The ganglion (35.) immediately preceding this is larger, and is separated from the one next before it (34.) by a more constricted portion of cord; and it gives off its anterior pair of nerves (*c*) in a diagonal direction forwards. So again the next ganglion (34.) is still more complete, corresponding to the greater length and more perfect condition of the segment, and is separated from its fellow (33.) anterior to it in the same segment, by a short portion of cord. These two ganglia still give off their anterior pair of nerves, but there are no nerves given off from the cord. The form of the ganglia is now changing, the anterior one is becoming elongated, and its anterior pair of nerves are given off from it in a direction more diagonally forwards and outwards. The length of cord between this ganglion, and that in the segment immediately before it, is now greatly increased, but still no nerves are yet given off from this portion of cord; they remain in connexion with the ganglion on which they have been formed. The ganglion (32.), anterior to this elongated portion of cord, also gives off both pairs of nerves, but the first pair are now at the very front of the ganglion, and are directed still more forwards, and appear as if exerting much traction upon it, while the ganglion is narrowed and greatly elongated, and seems as if it were about to separate. This separation between the nerve and ganglion actually takes place in the next segment, in which the ganglion gives off but one pair of nerves, while the anterior pair comes from the cord, in close approximation to the ganglion. In this way the interspace between the ganglia is increased from behind forwards in each segment, and is greater in proportion to its distance from the terminal ganglion. The cord is elongated in the ganglia, by extension, or growth longitudinally; and those nerves, which are given to the sides of the segments, and to the respiratory structures, and which originally are formed on the ganglia, or in immediate connexion with them, are gradually separated from them, and are afterwards attached only to the interspaces of the cord, so that they are removed to a greater distance from the ganglia in proportion to the earlier development and more complete state of the segment to which they belong. This elongation of the cord commences in the posterior ganglion, at the front of which, apparently by separation of part of its own structure, the new ganglion of each last-formed rudimentary segment is always produced. Hence the ganglia must be regarded as performing a most important office in the nervous system, that of being centres of growth and nutrition to the cord and nerves. The *structure* of the ganglia confirms these conclusions, and shows that not only are these parts centres in which the reflected motions of the limbs are effected, but that they are even of more importance,

being those in which the structures themselves are nourished. The vessels distributed over the ganglia penetrate into their substance, and are more abundantly supplied to them than to any other parts of the nervous system, as will hereafter be seen in the *Scolopendra*.

The *structure* of the ganglia in *Polydesmus complanatus* is well seen after the cord has remained for some time in spirit. When examined in the recent state it is far less distinct, but the nuclei, which enter largely into the composition of the ganglia, are well observed on the under surface. In specimens which have remained in spirit the whole of the fibres of the cord are rendered apparent, although the ganglia themselves are more opaque. In *P. maculatus* the aganglionic tract passes in a direct line over the ganglia (figs. 9, 10.), as in other Articulata, and gives off its branches as in *Iulus*, at some distance anterior to the ganglion. The fibres of the inferior or ganglionic tract (fig. 7. i), on arriving at a ganglion, are softened and somewhat enlarged in diameter, and take a slightly curved direction outwards, as far as the middle of the ganglion, and then are gradually reduced in size and again directed inwards, until they are about to leave it, when they again assume the longitudinal course and form the under surface of the cords. This curved direction of the fibres is owing in part to their own enlarged structure, and in part also to the presence of numerous gray nucleated cells, which assist to form the ganglion. Between these two series of longitudinal fibres are placed the commissural ones (*g*), which pass transversely through the ganglia for the posterior pair of nerves (*d*). The fibres of reinforcement which form the sides of the cord are distinctly seen at the sides of each ganglion beneath the transparent covering of the cord (*b*), bounding the sides of the ganglion in the interspace of two nerves (*f*), and also at the posterior surface of the nerve where they join the cord, having between themselves and the commissural fibres, and fibres of the cord, a slight interspace, which is occupied by nucleated cells. Those fibres which belong to the anterior pair of nerves, which have been seen to be afterwards removed from the ganglia, have communications both with the anterior and posterior nerves, thus combining in action the nerves which are distributed to the muscles (*c*) and sides of the segment with those which are given to the legs (*d*). This fact is interesting from the circumstance that the commissural fibres which enter into the composition of these anterior nerves are placed above the superior aganglionic tract of the cord, and this will in great measure account for the removal of these nerves from above the ganglion, with which they are thus shown to be in connexion during the growth and elongation of the cord itself. It is also further worthy of notice, that this is a condition in these nerves of *Polydesmus* precisely analogous to that which exists in the respiratory nerves in the larva state of insects, in which, as I formerly\* showed, there are commissural fibres running transversely across the segments and lying loosely above the aganglionic tract of the cord. In regard to the enlargement of the fibres of the cord, it may be remarked, that the ganglia are always softer and far more

\* Philosophical Transactions, 1836, Part II. p. 544.

readily miscible in water, and more easily destroyed than the fibre of the cord itself; and that they usually break off (fig. 8.) on injury at their junction with the longitudinal portion of the cords, thus further leading to the inference, that in these parts the nervous substance is less consolidated, and that the growth of the structure is effected at these places. This view of the gangliated portions of the cord in Articulata may perhaps be extended to those of the cord in Vertebrata, seeing that in both there is an accumulation of gray nucleated cells in each enlargement. May not the office of these cells be to supply means of growth for the cord itself, and also for the large nerves distributed from the cord in those regions?

The *Geophilidæ* (fig. 11.) present a condition of the nervous system similar to that of the *Polydesmidæ*, in the size and distinct form of the ganglia, but they approach also to that of the *Iulidæ* in the uniformity of distance of the ganglia from each other, and in their great multiplicity. Their number varies much in different species and subgenera. In some instances, in *Mecistocephalus*, NEWPORT (*Geophili maxillares*, GÉRAVIS), there are not more than forty-six, but in *Geophilus subterraneus*, LEACH, there are eighty-six, besides those of the brain; and in a new genus, *Gonibregmatus*, NEWPORT\*, there are even so many as one hundred and sixty. In the higher forms of Chilopoda, as in *Scolopendra*, there are only twenty-three; and in *Lithobius* and *Scutigera* fifteen, besides the brain and medulla.

In *Geophilus subterraneus* (fig. 11, 12.) the brain (*b*) exhibits a condition similar to that of *Polydesmus*, in the almost entire absence of optic nerves. But it differs in the fact that the optic ganglia (*c*) are slightly developed at its sides, and that these give off a very minute filament to the single ocellus, which exists on the under side of the head, behind the antenna. TREVIRANUS† has described the brain in *Geophilus longicornis*, LEACH, as entirely without organs of vision; but from the existence of an ocellus in that species also, on each side behind the antenna, he has probably overlooked its minute nerve. The brain itself is large, as compared with the size of the head, and the ganglia of the antennæ (*a*) have almost completely coalesced with it. The nerves of the antennæ are also exceedingly large, and, as in *Polydesmus*, seem to compensate for the imperfection of vision, by appreciating the condition and proximity of surrounding objects by the sense of touch. Each nerve appears to have a small gangliform enlargement of its structure in every joint, from which branches pass off directly to the muscles. This is a condition of the antennal nerve not before met with in the Myriapoda. The crura which pass down from the brain are long and slender, and the medulla (*d*) with which they are joined is considerably larger than any of the other ganglia, the first fifteen or twenty of which are much closer together than in the middle portion of the animal; thus further showing the constant tendency of those ganglia, and parts of the cord that have acquired their full dimensions, again to approximate and unite. The form of these anterior ganglia is slightly different from that of the posterior. They are rounded, and give off one pair of nerves at their front;

\* Proceedings of Zoological Society, Dec. 1842.

† *Loc. cit.* tab. vii. fig. 5.



in the posterior region of the body they are elongated, and somewhat oval. TREVIRANUS has correctly described and delineated them as giving off each three pairs of nerves, but he has not identified these with the nerves of *Scolopendra*, or of insects. It has been seen in *Iulus* and *Polydesmus* that each moveable segment of the body is originally composed of two others that have become united, and that each of these contains a ganglion. In *Polydesmus* the ganglia of each segment are nearer together than those of two separate segments, and notwithstanding the manner in which the intervening cords are developed, there is a tendency in the ganglia to unite. In *Geophilus* each segment is also composed of two parts, but one of these is much smaller than the other, and is fast disappearing. Hence the ganglion in each of these segments may be regarded as formed of the elements of two ganglia. Three pairs of nerves are given off from this ganglion in close approximation, at its posterior lateral surface, in the posterior half of the cord, but these are separated from each other in the anterior, in a manner similar to what we have already seen in *Polydesmus*. The posterior pair of nerves from each ganglion (fig. 13.81. *d*) are supplied to the pair of feet. Immediately anterior to these, and coming as it were from the same origin, the proper muscular nerves passes outwards to the sides of the segment. These nerves, as is the case with the corresponding muscular nerves in the larvæ of insects, pass on the outside of the longitudinal layers of muscles, between them and the diagonal muscles, to the sides and upper part of the segments, and thus are enabled to give off branches in their course to both layers. The third or anterior pair of nerves (*c*) are analogous to the respiratory nerves of insects. They pass off from above the ganglion on the upper surface of the cord, and after crossing the longitudinal layer of muscles, on their inner side, to which they give filaments, are distributed to the spiracles and muscles connected with them. These nerves vary a little in their mode of passing off from the ganglia, owing to the changes which take place in the ganglia, as already seen in *Polydesmus*. They are composed of fibres derived, as in that genus, both from the ganglion and sides of the cord, and its superior tract, above which they are formed by the union of these with a series of commissural fibres. In the posterior part of the cord (81. 82.) these nerves pass off in the same trunk with, but immediately anterior to, the second or muscular pair, but in the middle of the cord they pass off more anteriorly (fig. 14. *c*), while in the anterior segments, in which all the ganglia are slightly enlarged and rounded (fig. 12.), they pass off directly from the front of the ganglion. This pair of nerves is of great interest in the anatomy of the nervous system, since these are the analogues of nerves which exist in the Crustacea and in Insects, and in the latter, as in *Geophilus*, they are always given to the organs of respiration. They have the same relations to the other nerves and layers of muscles in all, but in *Geophilus* they lie on the superior longitudinal tract of the cord, in actual contact with a ganglion, deriving part of their structure from the ganglion, from the fibres of reinforcement, and from the aganglionic tract; and they also contain commissural fibres, precisely as in the respiratory nerves of insects. They exist in all the families of Chilopoda, but with this difference, that

in *Scolopendra*, *Lithobius*, and *Scutigera*, they appear to come off behind the ganglion, from the superior tract of the cord, to which they have been closely joined in these more perfect forms of the nervous system. This difference of position is readily explained by the changes which have been seen to take place in *Polydesmus*, and which are also in operation in *Geophilus*. In the posterior part of the cord, which is the part last formed during the gradual and successive changes of these animals, there is but a short space between these nerves, which lie above the aganglionic tract of the cord, and the commissural fibres of the nerves from the ganglia. But in the course of the development of the segments of the body by elongation, a corresponding elongation of the nervous cord itself takes place in the substance of the ganglia, and these nerves become further and further removed from each other in that part which lies on the cord above the middle of the ganglion, while they still remain attached to the other nerves at its sides, and thus form a kind of triangle (fig. 13. 80. c) above the aganglionic tract, as it passes over the ganglion. This elongation of the cords in the ganglion goes on, as in *Polydesmus*, until in the middle portion of the body these nerves have become released from those at the sides of the ganglion, and pass off from its anterior part. In the anterior third of the body they are directed forwards, but are still kept in contact with the ganglion by means of the lateral fibres of reinforcement, and also by a delicate set of fibres derived from the ganglion itself (fig. 14. c). These facts seem further to show that the ganglia are the centres in which the growth and elongation of the cord always take place, and also that the nerves of the cord are usually first formed in connexion with ganglia, although they may be afterwards removed from them by further growth and changes.

The compound structure of the cord is distinctly seen in *Geophilus*. The superior aganglionic tract is more clearly seen along the whole length of the cord, even while passing over a ganglion, than in any other genus. It is scarcely more than one-half of the width of the whole cord. The lateral fibres are also distinct, and may be readily seen bounding the roots of the nerves.

The disposition of the terminal nerves of the cord is curious. Each ganglion gives its pedal nerves backwards to the legs in the next segment, so that the penultimate pair of legs are supplied from the ganglion of the antepenultimate segment, and the terminal styles, or anal appendages, are supplied by nerves from the preceding segment. By this arrangement it is proved that the anal styles are not supplied by the terminal portion of the cord, as is usually the case, since there are three ganglia, much smaller than these, posterior to them (figs. 13 and 14. 83. e a). The anterior of these *caudal ganglia* (c) supplies the anal valves and segments, and may be regarded as the *anal ganglion*. The next (e), which also gives nerves to the anus, is partly supplied to the rectum, and part to the outlets of the female organs, which in Chilopoda are always placed in the same relation to each other as in insects. The terminal ganglion (a) is situated in the middle line of the junction of the *receptaculi seminis*, between these and the rectum, and corresponds in situation to a ganglion on the

junction of the oviducts in *Gryllus*. It always gives nerves to the terminal portion of the oviducts, as the preceding ganglion does to the rectum.

The nervous cord attains its maximum development in the Myriapoda, in the *Scolopendridæ* and *Scutigridæ*. Each ganglion now gives off four pairs of nerves, the first and third of which are distributed to the muscles, and the second to the feet, while the fourth pair, the analogue of the respiratory nerves, lies above the ganglion at its posterior margin, but derives from it, as in *Geophilus*, part of its structure. It is closely joined to the side of the superior tract of the cord, from which at first it seems to be derived, as I formerly\* believed when describing this structure. Its distribution to the spiracles in *Scolopendra* was subsequently shown in the Plates of Mr. SWAN†, and its analogy to the respiratory nerves of insects has since been pointed out by Professor OWEN‡. The existence of commissural fibres passing through the ganglia in *Scolopendra*, one to each nerve, was also made known by Dr. CARPENTER§, but the presence of the lateral fibres of the cord has not heretofore been ascertained. These lateral fibres exist in the *Scolopendra*, as already described in the other Myriapoda, but are less readily observed than in *Polydesmus* and *Geophilus*, in consequence of the more perfect structure and approximation of all the parts of the cord. The ganglia of the anterior segments have approached nearer to each other than in *Geophilus*, more especially the first five, which are separated only by a short portion of cord. In *Lithobius* this approach of the ganglia is carried still further, and in the *Scutigridæ*, in which the first seven ganglia are very closely approximated, it has reached its maximum. In these latter instances also, the brain has acquired a greater development, the optic nerves and ganglia are enlarged, and the separate organs of vision are greatly multiplied. The caudal ganglia are united into a separate larger ganglion in *Scolopendra*, and in *Lithobius* (Plate XIII. figs. 23 and 24, 17. 18.) form an elongated caudal appendage to the last great ganglion of the cord.

In the *Scorpionidæ* the nervous system exhibits two opposite conditions in the same animal; that of concentration of structures in the anterior part of the body and extension in the posterior, thus reminding us of the pseudo changes which are taking place in the anterior segments of the *Iulus*, while growth and elongation of others are taking place in the posterior. In the anterior part of the *Scorpion* the aggregation of segments has been carried to its greatest extent, the cephalothorax being formed of at least six segments that can be identified, and doubtless of still more; and not only have the ganglia of these segments been collected into one mass, but they have been joined by others from the segments of the abdomen, as in perfect insects and Crustacea. But instead of the nervous cord terminating in the abdomen, as in the most perfect of those classes, it is extended backwards and forms a series of ganglia in the tail, a condition which marks a close affinity to the macrourous Crustacea and

\* Philosophical Transactions, 1834, Part II., p. 408.

† Comparative Anatomy of the Nervous System, 1835, Part I., Plate V. fig. 1.

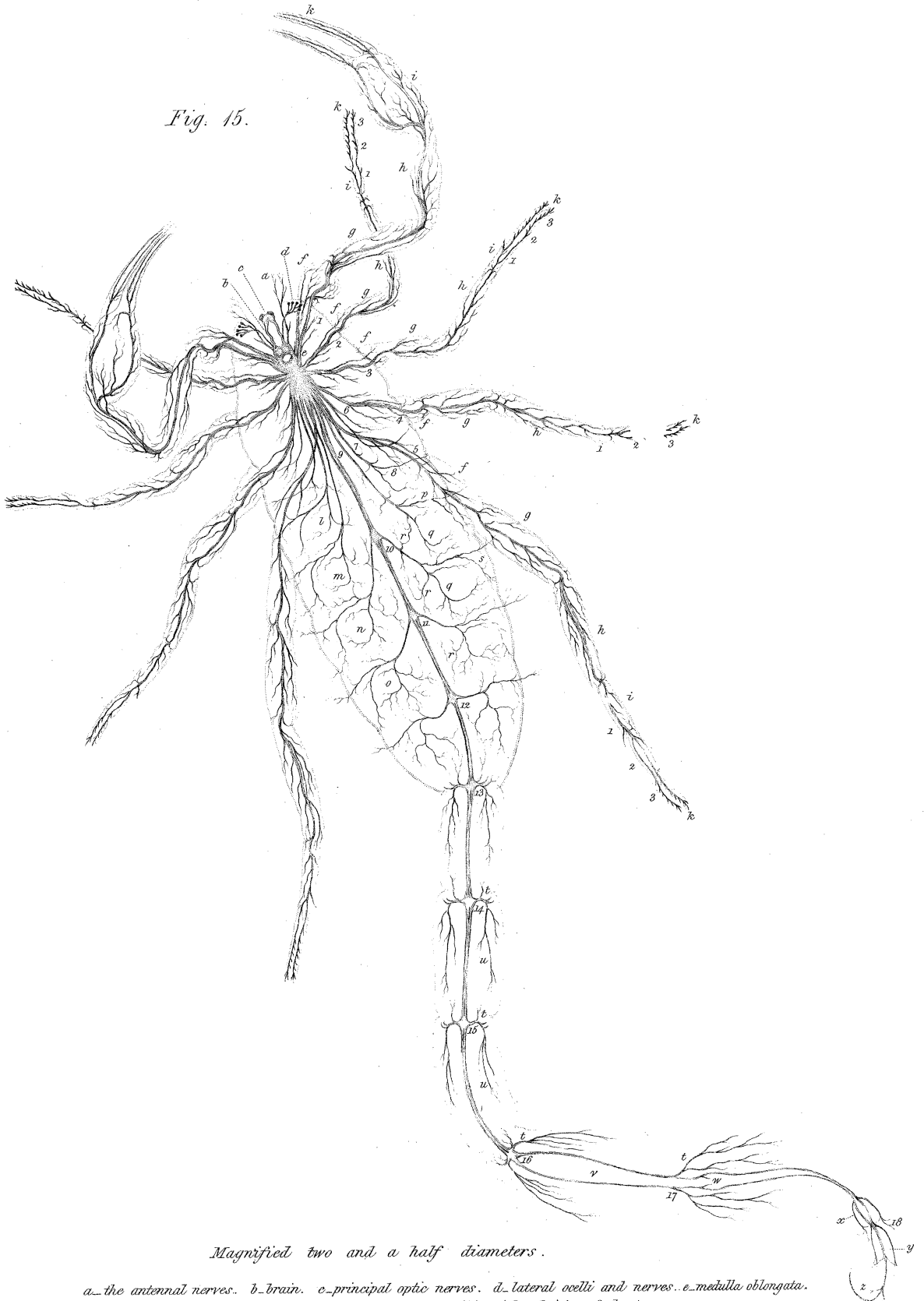
‡ Hunterian Lectures, 1842.

§ Inaugural Thesis, 1839.

*Nervous System of Arachnida.*

*The Scorpion. (Androctonus)*

*Fig. 15.*



*Magnified two and a half diameters.*

*a*—the antennal nerves. *b*—brain. *c*—principal optic nerves. *d*—lateral ocelli and nerves. *e*—medulla oblongata.  
*f*—coxa or basal joint of the limb. *g*—the femur. *h*—the tibia. *i*—basal joint of the tarsus.  
*2, 3*—the second and third joints. *k*—the terminal nerves to the double claw. *l* to *o*—abdominal branchiæ.  
*p, q, r, s*—distribution of the nerves of the segments. *t, u*—nerves of the ganglia in the tail. *v*—terminal nerves.  
*w*—fifth joint. *x*—anal collar. *y, z*—termination of the cord in the extremity of the sting.

18

22

21

20

16

17

Polydesmus.

24

19

18

19

20

21

23

25

22 A

Heart of Scolopendra.

Termination of the  
Supra spinal artery  
in Lithobius.

Heart and vessels in Scolopendra  
showing the chambers & muscles f. valvular orifices g.  
Systemic arteries h. distributed on the Hepatic vessels l.n.  
and the aortic arches of the heart p.p.  
A. cephalic segment. B. vasilar segment. C. mandibles, or foot-jaws.

Chambers of heart in  
Scutigera.

Supra spinal vessel y.y.  
in Scolopendra.  
Termination of the heart  
in the aortic arches s.p.

to the Myriapoda, more especially to the latter, in the number of ganglia that enter into its composition. Thus there are six ganglia which belong to the head and thorax, and four of the seven that belong to the segments of the abdomen, which enter into the composition of the great nervous mass in the cephalothorax, while three remain in the abdomen and four in the caudal region, making seventeen sub-œsophageal ganglia, a number equal to that of some of the Myriapoda, and more than is ever found in any hexapod insect.

*The brain* in the Scorpion (Plate XII. fig. 15. *b*) is exceedingly small. It is composed of two rounded, closely united ganglia, from the sides of which proceed directly upwards two small trunks, the optic nerves, which are given to the large median eyes (*c*) of the cephalothorax. At the base of these nerves, on the front of the brain, and arising from the same part, two other small trunks pass forwards and inwards to the middle line, around the muscles of the prehensile organs on the front of the head, and while passing outwards, on the upper surface, each is divided into separate branches for the lateral ocelli (*d*). These vary in number in different species. In *Buthus*, LEACH, there are three on each side; in *Androctonus*, KOCH, there are five, but in *Scorpius*, EHRENBERG, only two. Immediately beneath the nerves to the eyes a large nervous trunk passes forwards, from the front of the brain on each side, to the small prehensile organs (*a*), which, in the Scorpions, are modified antennæ. From the inner side of the front of each lobe of the brain, beneath these nerves to the antennæ, a small recurrent nerve passes forwards, and joins with its fellow on the opposite side to form a minute ganglion, from which a very small median trunk, the vagus\*, passes backwards beneath the brain for a short distance along the alimentary canal, but I have not yet been able to detect lateral ganglia connected with this trunk, as in the Myriapodes. The brain is connected with the medulla oblongata (*e*) by very short and thick crura, so that it scarcely appears distinct from the great nervous mass in the cephalothorax. The *medulla oblongata* (*e*) forms the first portion of this great mass, from which it is distinguished by a slight constriction, although closely approximated to it. It is spread out beneath the brain into a large concave ganglion, which gives off at its sides one very large pair of nerves, which are distributed to the great prehensile organs (1.), and which, from their origin, must be regarded as the analogues of the mandibles of insects, and of those of the forcipated foot jaws in the Chilopoda. These organs, as already shown by SAVIGNY in other classes, are themselves the analogues of those of locomotion, as is well exemplified in the anatomy of these organs in the Scorpions. The nervous mass behind this first ganglion gives off four pairs of large nerves (2. 3. 4. 5.) to the organs of locomotion, and four pairs of smaller ones (6. 7. 8. 9.) to supply the abdominal segments, to which the trunks of these nerves pass backwards on each side of the cord, their ganglia being united with those of the thorax. The remaining ganglia of the abdomen (10. 11. 12.) are

\* This vagus nerve is very small, and has been omitted on the drawing of the nervous system of the Scorpion, Plate XII., to avoid confusion.



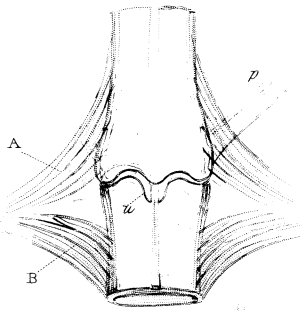
situated at a great distance backwards in the cord, but not in the segments to which their nerves are distributed. These ganglia also have moved forward, and each is in a segment anterior to that which they supply with nerves. This shifting of the ganglia has also extended to those in the caudal region (13. 14. 15. 16.), each of which has moved forwards and is situated near the articulations of the joints of the tail, one in each of the first four basilar joints.

The distribution of the nerves to the legs affords an interesting illustration of the uniformity of plan in the distribution and use of similar structures in all animals. The great claw (*i*) of the Scorpion is formed by an arrest of development of the three tarsal joints (1. 2. 3.) that have coalesced into one large hand; but the finger-like digitations of this hand (*k*), which exist in the true organs of locomotion as minute claws, have become excessively developed, to form the two powerful fingers of the claw, as is proved by the manner in which the nerves are distributed. The great nerve of the limb in the other extremities is always divided into two branches immediately before or after it has entered the second joint of the tarsus (2.), and these are given separately along each side of the under surface of the tarsus to the two minute claws, exactly as the nerves are distributed to the digitations of the hands and feet of Vertebrata; and it is precisely in the same way that the nerves are distributed to these great claws in the Scorpion. But further evidence of the beautiful uniformity of design is afforded in the distribution of these nerves to the tarsi. As each division of the nerve is passing along the under surface of the last joint of the tarsus it gives off a distinct nerve to each of five spines (3.), which are arranged in a series on each side of the under surface of this joint of the foot, on which joint the animal usually rests. Can it be doubted that these nerves are to supply the rigid spines with sensation and a power of feeling, as this part of the foot is so constantly employed in touching and examining the objects over which it passes? The extremities of the two divisions of the nerves to the tarsus are extended into the minute claws (*k*) and terminate at the base of the nail, having first given off, on each side of the claw, a small branch to the muscles.

The nerves that pass backwards from the thorax into the abdomen continue distinct, and are given separately (6.7.8.9.) to the respective segments. Immediately each nerve enters its proper segment it divides into two branches (*p*, *q*); one of these (*p*) passes outwards in the anterior part of the segment, across the front of the branchia, and near the margin of the ventral plates this also is divided into two branches, one of which ascends to the dorsal surface of the segment, while the other passing backwards in front of the branchia (*s*) is given to the sides. The second branch (*q*) of the main trunk passes backwards in the segment behind the branchia, and gives off some ramifications to the muscles (*r*) on the ventral surface, and some are distributed over the branchia (*l*, *m*, *n*, *o*). This second branch of the great trunk is itself a separate nerve, the analogue of the respiratory nerve which exists so distinctly in all the Myriapoda, more especially in the *Scolopendra* and *Lithobius*. The aggregation of origi-

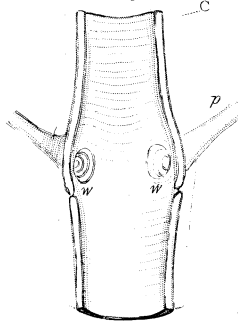
34

Superior external surface.



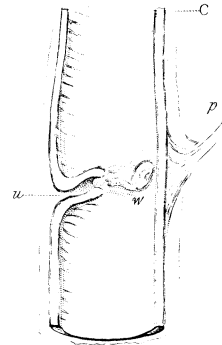
35

Internal inferior.



36

Anterior lateral.



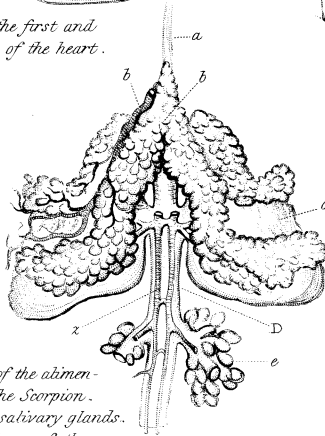
37

Superior interior.

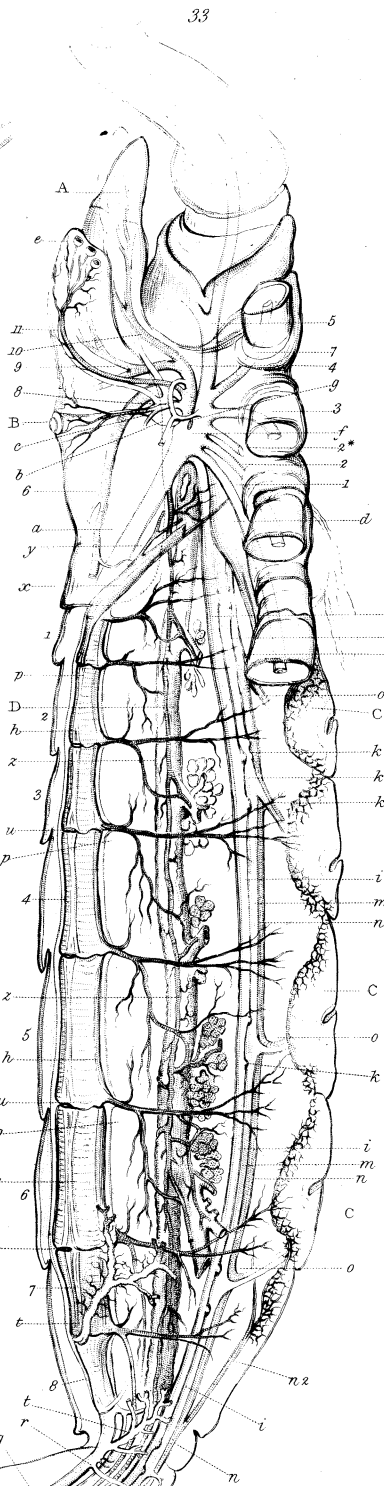
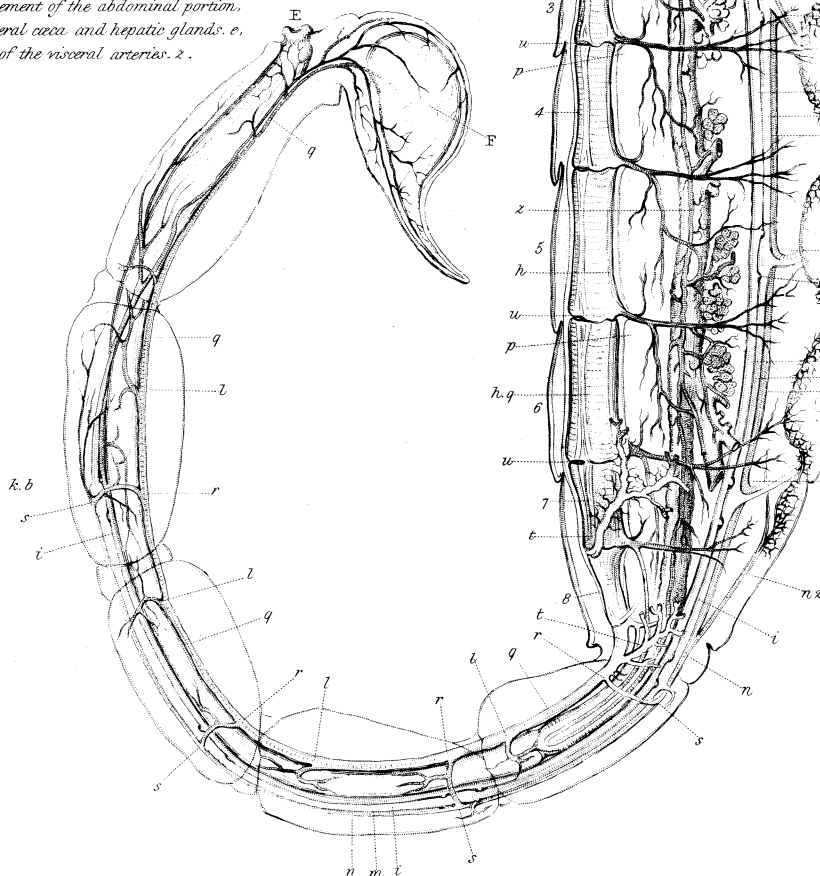


34 to 37, part of the first and second chambers of the heart.

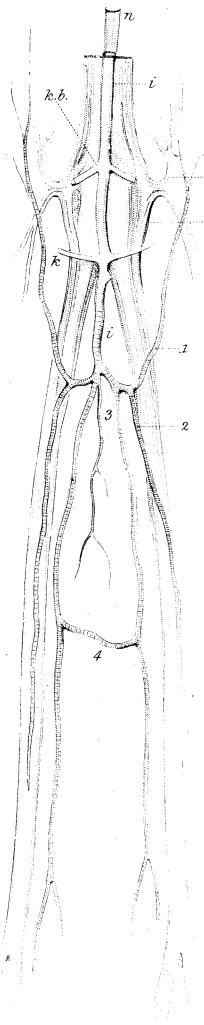
39



Anterior portion of the alimentary canal in the scorpion. a. esophagus. b. salivary glands. c. lateral appendages of the thoracic portion of the canal (? gizzard ?) D. commencement of the abdominal portion, with the lateral caeca and hepatic glands. e. and origin of the visceral arteries. z.



38



Termination of the supra-spinal artery of the last caudal ganglion in the scorpion. (Buthus.)

Diagram of the Circulatory, Alimentary, Nervous and Respiratory systems in *Buthus*, as seen on the right side of the body, magnified 2 diameters. h.g. the heart and caudal artery. p. systemic arteries. a. the aorta. i. supra spinal artery. m. nervous cord. n.o. sub-spinal vessel. A. antennal claws. B. e. the eyes. C. the pulmono branchiae. D. the alimentary canal. F. the anal orifice. F. the poison glands.

nally distinct parts, which has been carried to so great an extent in the ganglia of the cephalothorax of the Scorpion, has also taken place in the development of the ganglia and cord of each segment of the abdomen, in the union of all the primary trunks of nerves into a single pair in each segment; so that throughout the whole body each ganglion appears to give off only one set of nerves; and this condition exists even in the ganglia of the tail.

The cord in the tail has four distinct ganglia, one at the commencement of each of the first four joints. The terminal ganglion gives off two pairs of nerves. The first pair (*t*), are the proper nerves of the joint, and the second, the terminal nerves (*v*), are the continuations backwards of the two halves of the cord. One of these main trunks passes backwards on each side of the colon, and the two ascending, one on each side, and winding inwards, meet above it in the middle line of the dorsal surface, at the posterior part of the fourth caudal joint. On entering the fifth joint each trunk gives off a large branch to the muscles (17.), and then passes backwards, one on each side of the strong tendons of the flexor muscles of the dorsal surface. On entering the fifth segment these trunks again give off a pair of branches (*w*), but do not form ganglia. The two trunks, now reduced to small nerves, pass backwards in the middle line, side by side, and give off a few lateral branches to the muscles of the sixth joint, the *aculeated joint* of the tail, through which they pass parallel to each (*y*) other along the dorsal surface to the extremity of the poison duct (*z*) and point of the sting. At the termination of the fifth segment they send a branch on each side of the anus, which is thus inclosed between them (*x*) as in an elongated nervous collar, and immediately behind it (18.) they give off the branches to the base of the sting without forming a ganglion.

The nervous cord is narrowed and rounded in the abdomen, but in the tail it is thin and flattened, and spread out like a riband, and is larger in proportion to the size of the nerves, than in any other part of the body. Throughout its whole length the two halves of the cord are closely approximated, excepting immediately anterior and posterior to each ganglion, where the blood-vessels pass downwards from the supra-spinal artery to join the sub-spinal structures. The pair of nerves given off from each ganglion in the tail are divided into two sets of branches, and these are again subdivided. The anterior set (*t*) is the smallest, and is directed forwards and downwards to the muscles of the under surface of the joint. The posterior set (*u*) is divided into four trunks, which pass upwards and backwards, and are given, like the lateral branches from the terminal ganglion, to the great flexor muscles, which pass downwards on each side from their strong tendinous attachments in the preceding joint. The ganglia of the tail are oval, flat, and thin, like the cords, but those of the abdomen are thick and elongated, oval or spindle-shaped, but flattened on the upper surface. The two nerves, which are united into a single trunk at the side of each ganglion, are derived, one from its anterior, and the other from its posterior border. The anterior one (Pl. XV. fig. 38. *a*) passes backwards until it meets with the pos-

terior (*b*), which passes forwards to join with it, and these two approximated nerves, forming one trunk, have between their roots and the margin of the ganglion a very minute interspace, which is filled up with cellular tissue. Each of these approximated nerves contains distinct commissural fibres. Those of the anterior nerves are on the front of the ganglion, and are distinctly traced from side to side. Those of the posterior traverse the posterior part of the ganglion, and passing forwards on each side join with the lateral or *reflex* fibres of the cord, which ascend along the sides of the cord at the posterior part of the ganglion, or, as before described, if traced from the peripheral surface of the segment, pass inwards from the nerve to form part of the sides of the cord. The existence of the longitudinal tracts of the cord is also distinct. The fibres of the inferior series have a large proportion of gray nucleated cells interspersed between them in each ganglion, and these are more especially abundant and distinct at its sides. The caudal ganglia exhibit the different structures of the cord better than the abdominal ones, above which the superior aganglionic tract of the cord is less distinct, and is less easily observed in consequence of the greater opacity and thickness of the ganglia. I ought also to state that the structure of the cord and ganglia of the Scorpion, owing to their greater thickness and more compact and united condition, can only be satisfactorily seen in the very small specimens, or in the very early condition of the animal, and after being preserved for some time in strong spirit. This remark also applies to the Myriapoda and other Articulata.

*Functions of the Brain and Nervous Cord.*

Although I have now pointed out the existence of fibres in the nervous cord of Myriapoda and Arachnida, which lead us to the conclusion that the doctrine of the individuality, or special function, of each fibre is correct; that there are fibres in every nerve derived from two distinct portions of the cord, which from their direct communication with the brain, from one end of the body to the other, are believed to minister to volition and to sensation; and that other fibres also exist in the same nerves, that have no communication whatever with that organ;—and further, that some of these, which are extended transversely across the body, influence both sides of those individual segments to which they are distributed, and those only; while others combine in action two or more contiguous segments, but only by direct influence on one side of the body;—it yet remains to be shown by experiment, whether the assignment of certain functions to these parts of the nervous system, in these inferior animals, is correct;—whether the results of experiments on these worm-like beings agree in principle with the experiments already made by many physiologists on the vertebrated classes, and with those which the pathology of disease has afforded in Man himself;—whether, as leading to these important results, they coincide with the first experiment made on one of the Crustacea, conjointly by Dr. MARSHALL HALL and myself\*, in the spring of 1834, and with others subsequently performed by

\* Lectures, *Lancet*, Feb. 3, 1838, p. 650. *Memoirs on the Nervous System*, p. 67.

VALENTIN\* on the same animal, and afterwards repeated by Dr. BALY and myself in 1840†; and lastly, whether the seat of sensation and volition is confined entirely to the supra-œsophageal ganglia, the brain, in these Articulata.

No experiments have yet been made on any of the Myriapoda with reference to these inquiries, save only one, imperfectly described by DUGÉS‡; hence it has become especially necessary that, with this object, our inquiries should be extended to these lower forms of life, so far removed from those on which experiments have already been made, and in which, from their low organization, the phenomena may be well studied.

With this object I have made experiments on one of the lowest of the Chilognatha, *Iulus terrestris*, and on one of the highest of the Chilopoda, *Lithobius forficatus*.

The questions that seemed necessary to be examined, were—

1st. Whether sensation and volition are confined to the supra-œsophageal ganglia, the brain, or whether they exist also in the first subœsophageal ganglion, or in the other ganglia of the cord?

2nd. Whether these functions are destroyed by partial destruction of the brain?

3rd. Whether there is any direct evidence of sensation in a portion of the cord that is insulated from the brain?

4. Whether the movements in these animals, when deprived of the brain, are identical with those of the Crustacea and Vertebrata?

#### *Iulus terrestris.*

*Experiment 1.*—The front of the head, antennæ, eyes, and brain were at once removed with a pair of scissors from an active adult specimen. While held between my fingers there were powerful contortions of the whole body of the animal, and when placed on a table it moved rapidly forwards, as in the usual mode of locomotion, and continued to do so for a few minutes, but the motions gradually became slower and slower, and at last were so feeble that onward progression was suspended, although the legs were still feebly moved, as in walking, for nearly half an hour, when their motions entirely ceased. There was no evidence whatever of sensation or volition, although the subœsophageal ganglion and cord were uninjured. During locomotion the body moved in a direct line, and always *forwards*. When it met with a slight obstacle it climbed over it, or when too high to pass over, the body stood directly opposed to it, with the mutilated portion of the head in contact with the obstacle, and the locomotive actions of the limbs gradually increased, apparently by the excitement of contact with a foreign body against the lacerated surface of the head. When the movements of the limbs ceased, the body was maintained in its natural position upon them for several hours, until fresh mechanical excitement was applied to it, when the locomotive actions were repeated.

\* De Function. Nervorum, Bern. 1839. (*Vide* BALY's MÜLLER.)

† MÜLLER's Physiology by Dr. BALY, second edition, vol. i. 1840, p. 771.

‡ Traité de Physiologie Comparée, tom. i. p. 162.

*Experiment 2.*—The head was removed from the body in the *third* segment, the second of the trunk, and acts of locomotion were performed by the body precisely as in the last instance, and were always re-excited in the same manner. When turned on its back the body was instantly excited to violent contortions, until it had regained its proper position, and stood supported on the legs, which were extended, and slowly moved as in locomotion, after it had continued to walk for four minutes. When the anterior cut extremity of the cord was irritated with a needle, locomotion forwards was again induced. Pressure on the anterior segment excited it most readily. Motions of the legs were instantly excited by simple contact with any foreign body, and those on both sides, anterior and posterior, were moved, but insufficiently for locomotion. Violent contortions were always induced when the body was placed on its back, until its proper position was regained; but the motions of the legs were not excited by a current of air directed on them from a blowpipe, until after the lapse of a few seconds; but there was always a slight convulsive motion of the body after each *sudden* current. The legs were less excited during the first few hours after decapitation by pressure on the posterior than on the anterior segments.

*Experiment 3.*—The body was divided in the *seventh* segment while the animal was running briskly. It continued to move forwards for a few minutes, but the motions gradually became slower and slower, as in the preceding experiments. They were actively *re-excited* by a brisk shake of the table, but soon became quiet with slow but very gradual motions of the legs. Progression was always quickly reinduced by pressure on the anterior segments, and this was more active than when applied to the posterior. It was always reinduced when the cut extremity of the cord was irritated slightly with the point of a needle. At the expiration of an hour from the making of these experiments, the atmosphere continuing at about the same temperature, 56° FAHR., the excised heads of No. 2 and 3. were still living, and exhibited acts of volition, and that of the latter, with the segments and legs attached to it, made attempts to walk. Both of these moved the antennæ briskly, and touched objects that were near to them, as if to *feel* and appreciate.

*Experiment 4.*—The body was divided at the *fourteenth* segment, while running. The anterior part exhibited all the voluntary actions of the perfect animal, those of touching, avoiding, or seeking an object, and also of locomotion, but its movements were slow and were made with difficulty. This arose from want of proper counterpoise of the body, since when that was supplied by the proximity of the individual to the upright surface of any object, locomotion was well performed. The remaining portion of the body was then divided into two parts, both of which were instantly excited to movements of the legs when irritated, but without any power of locomotion, or ability of either part to support itself in its proper position. The motions of the legs were readily induced by a current of air, or when the segments were compressed, or the cut end of the cord touched with the point of a needle. At the expiration of *nine* hours the anterior division of the body with the head was dead, and not the



slightest voluntary or reflex action could be excited in it by any means. But the middle division of the same individual was readily excited to reflex actions of the legs, and contractions of the segments, by compression of the segments, by irritation of the cord with a needle, and by brisk currents of air from a blowpipe. These reflected actions were much stronger in the third or posterior division of the segments, and were all induced by similar means. After *twelve* hours they were feebler in the middle division of the segments, but were even more readily excited in the posterior. After *eighteen* hours they were scarcely perceptible in the middle division on the application of the needle, and not at all on compression; but they were still easily induced in the posterior, and continued to be so in the four or five posterior pair of legs, even at the expiration of *twenty-four* hours. The temperature during the interval was not higher than  $64^{\circ}$  FAHR.

*Experiment 5.*—The cord alone was divided in the *fourteenth* and also the *twentieth* segment, and the intervening portion was destroyed by breaking it down with a needle. The animal exhibited in the anterior part of its body all the evidences of perfect volition. It moved actively along, turning itself back on either side repeatedly, as if to examine the anterior wounded portion, which it felt again and again with its antennæ, and when attempting to escape, frequently turned back as if in pain and aware of some hindrance to its movements, but it seemed perfectly unconscious of the existence of the posterior part of its body, behind the first incision. In those segments in which the cord was destroyed, the legs were motionless, while those of the posterior division, behind the second incision, were in constant, but involuntary motion, the movements being similar to those of walking or running, uniformly continued, but without any consentaneous action with those of the anterior part, by which locomotion was performed, dragging the posterior divisions of the body after them. When the animal was held by the posterior segments, reflex actions were excited in the legs, and powerful contractions and gyrations of the whole animal were performed in those segments; but these movements appeared to be entirely the result of reflex actions of the muscles, since exactly similar ones took place in the whole body in decapitated specimens. At the expiration of *twelve* hours the most perfectly voluntary acts were performed by the head and anterior division of the body, such as locomotion forwards or to either side, avoidance of any obstacle, touching it with the antennæ, which were in rapid action as in an uninjured animal, and attempting to reach and to climb up an object presented to it, but not in immediate contact with it. But reflex movements alone existed in the posterior division, in which the legs were very slowly moved, even when the animal was not progressing. Brisk actions were now more easily excited in them than at first, either by contact with the segments, by irritation of one or two of the legs themselves, or by a sudden current of air. By these means, when the animal was lying still, actions were immediately excited in all the legs of the posterior part of the body anterior and posterior to those which were irritated, and these actions were induced in those of both sides of the body, but ap-

peared to commence on the opposite side, in the legs corresponding to those which were first irritated. In *eighteen* hours the anterior part of the body was quite dead, no motions whatever could be excited on it, either voluntary or reflex; but reflex actions were then readily excited in the posterior, and also slightly so by mechanical irritation, even at *twenty-four* hours.

Other experiments were now made on the brain itself without detaching the head of the animal from the body.

*Experiment 6.*—The brain was completely divided longitudinally in the centre by a fine pair of scissors. All power of recognising objects was immediately lost. The antennæ were perfectly motionless, and the animal at first moved directly forwards, as in the first and second experiments, dragging the antennæ along with it at the sides of the head. It passed on with the head and first segment elevated, and climbed over every slight obstacle, and when opposed did not turn to the right or to the left, but passed forwards with the legs moving rapidly as in the act of running. At the expiration of half an hour it had regained a little power in the left antenna, and then constantly moved in a circle to the left side. When either antenna was pinched a sudden convulsive movement was induced in the whole body, but the antennæ were not retracted when touched, as they always are by the uninjured animal. At the expiration of an hour, slight motion was regained in *both* antennæ, but the movements to the left side were still continued. The brain was now entirely destroyed with a needle. All power of volition, which seemed to have been partly restored, as well as the use of the antennæ, were instantly lost, and the movements of the legs and body were precisely similar to those already seen in the decapitated specimens. Pinching the antennæ did not occasion the slightest convulsion of the body, or reflected movements of the legs, but slight pressure on the segments immediately induced them, and also violent contortions of the whole body, especially when applied to the anterior segments. In this specimen the reflected movements were excited at the expiration of eighteen hours, but mostly so, at that time, at the posterior extremity of the body.

*Experiment 7.*—The brain was divided in the middle, and one lateral half with the antennal ganglion and optic nerve were removed. Some of the motions of the antenna of the uninjured side seemed to indicate the remains of volition. The animal coiled itself up and remained quiet as in health, but the posterior legs of the body were in constant motion. The power of recognizing objects appeared almost entirely destroyed. When the remaining lobe of the brain was irritated with the point of a needle, the body was again extended and excited to slow progression forwards, exactly as in the preceding experiments, but the power of moving was very feeble. At the expiration of two hours, the specimen having remained undisturbed in the interval, slow progressive movements *in a circle* were induced by pressure on the segments, and always in the direction of the *injured* side, the left in this specimen.

*Experiment 8.*—The lobe on the right side of the brain was removed, and the

results were precisely similar to those of experiments 6 and 7, and the movements were to the *right*, the side injured in this specimen.

*Experiment 9.*—The right eye and optic ganglion were both destroyed by puncturing with a fine needle. The antenna of that side of the head became completely motionless, and perception of objects was destroyed; but the animal still retained its voluntary powers, and was able to recognise objects on the left side, on which the antenna and eye were uninjured, and seemed to a great degree to retain their usual powers.

*Experiment 10.*—Both antennæ were cut off close to the head, leaving the brain uninjured. All the powers of the animal continued perfectly voluntary, and it sought or avoided objects as usual, but by means of the palpi and vision, with not the slightest indication of reflex movements. When the point of a needle was passed in at the antennæ, the animal gave indications of great pain by its movements, but these were not reflex. When placed on the table it again sought objects, and carefully avoided falling over, by changing its course when it arrived at the edge. The brain was then destroyed through the insertion of the antennæ, and the movements immediately became reflex, and soon ceased, except when they were artificially re-excited.

*Experiment 11.*—The eyes on both sides of the head were removed without injuring the brain or antennæ. Volition continued perfect, but the movements of the animal were slower, and all objects were very carefully explored with the antennæ; and it avoided nothing except when in direct contact with it, or when its presence had been ascertained by means of these organs. But immediately the needle was passed into the brain all the motions became reflex and precisely similar to those already detailed.

These experiments on *Iulus* sufficiently prove that the seat of sensation and volition is in the cerebral ganglia, and that when these are destroyed, or greatly injured, all consciousness ceases and the movements of the body are reflex, and not voluntary. But it seemed necessary to confirm these conclusions by similar experiments in a higher form of Myriapoda, in which, from the peculiar structure of the head, the cerebral ganglia could be removed from the body without removing the medulla oblongata, from which the nerves are given to the parts of the mouth; and further, that the experiments should be made on an animal in which the ganglia of the cord are large and quite distinct, and are removed from each other, and thus afford a better comparison with experiments made on the large Crustacea, in which the experiments on the brain cannot be so satisfactorily performed. The subject selected for this purpose was *Lithobius forficatus*.

*Experiment 12.*—The front of the head and the brain were removed at once by the scissors. All volition instantly ceased, and reflex movements were induced. The mandibles were in constant action as in manducation, and the body performed onward progressive movements, which gradually ceased, as in *Iulus*, but there were no attempts to escape. When placed on its back the body instantly regained its

position and remained with its legs widely extended. When quiet, progressive motions were instantly induced by touching the cut end of the cord, or by pressure on the anterior segment. When pressure was made over the posterior caudal ganglion, violent contortions of the whole body were induced, as in *Iulus*. The antennæ were completely paralyzed and dragged along the sides, and compression of them produced no retraction, or any movements of the body or legs. But contortions of the whole body were produced by compression of the mandibles, or of the posterior pairs of legs. When a brisk current of air was passed from a blowpipe along the sides of the body on the stigmata, no motions were induced in the legs until after a few seconds, and then they were regular but slight. A brisk knock on the table always re-excited the movements. At the expiration of half an hour the antennal subsegment was removed, leaving the medulla *in situ*. Progression was again induced, but more feebly than before. When pressure was applied on any of the segments the reflected movements were as violent as at first. The mandibles were now fixed, but contortions of the whole body were induced when these were pinched. These contortions were most violent when pressure was applied over the great subœsophageal ganglion, the medulla, but occurred also when the cut extremities of the crura were irritated with a needle.

*Experiment 13.*—The left antenna and side of the brain were removed together. The results were very similar to those in *Iulus* (experiments 6 and 7). The volition of the animal was greatly impaired, but when the remaining antenna was touched the animal gave full evidence of sensation by instantly retracting it, and when it was pinched the whole body was violently contorted. It was also frequently drawn between the closed mandibles, as if to cleanse it from anything adhering to it, as is the usual habit of this species. This was evidently the result of sensation, but not perhaps an act of volition, since in all other respects the movements most certainly were reflex. The movements were usually to the left, or injured side, but not invariably. At the expiration of half an hour the cord was divided between the fourth and fifth pairs of legs. Excessively violent movements were now induced, but when placed on its back the animal did not regain its natural position. Pressure on any of the segments produced motions of the jaws, as in the act of biting, but without any direction, consequently these were reflex. The cord was then divided between the seventh and eighth pairs of legs. The reflex movements of progression were now more imperfect, but continued longest in the *anterior* portion of the body. Powerful contortions were as readily excited in the posterior part as before, but these contortions were confined to the posterior half; since none were excited in the insulated portion of cord between the fifth and ninth pairs of legs, except on firm pressure of the ganglia. When the animal was placed on its back the motions to recover its position were feeble and ineffectual, and almost entirely ceased without the body recovering its natural position. But motions were instantly re-excited when pressure was made over any of the ganglia; and the limbs, both anterior and posterior to the ganglion pressed on, were thrown into violent actions on both sides of the body, exactly as in the original

experiment on the Lobster. Pressure on the cut extremity of the nervous cord, in the posterior half of the body, induced scarcely any movements. When the anterior portion of the body, with three or four pairs of legs attached, was separated from the posterior, there were acts of progression as in *Iulus*. But the most striking fact was, that when that portion of brain which had been removed from the head in connexion with the antennal ganglion and antenna was irritated, contractions were immediately excited in the joints of the antenna. How difficult to understand is the influence of that power which resides in this mysterious centre of all the animal movements!

*Experiment 14.*—The body was divided at a stroke between the second and third pairs of legs. Sensation was perfect in the head and two pairs of legs, with which there were voluntary attempts at locomotion. But volition and sensation were sooner lost than in *Iulus*, and this also was the case with the reflected movements, all which had ceased in less than three hours. In each of these experiments on *Lithobius* sensation and volition ceased in the anterior portion of the body in a few minutes, and sooner in proportion to the fewer legs connected with the head. Reflex actions continued to be manifested longest in the posterior portion of the body in *Lithobius* as well as in *Iulus*, and usually were most readily excited in those regions.

These experiments seem to lead to the conclusion that the seat of volition is solely in the supra-oesophageal ganglia or brain of these animals, since all direction of purpose, all avoidance of danger, all control over the movements of the body, either of speed or change of direction, are lost when these are much injured or removed. Volition ceases quickly when they are severely wounded, and is greatly diminished even when one only is slightly affected. This latter fact is indicated by the loss or diminution of purpose, and by the gyratory movements of the body. The experiments seem also to show that sensation may remain after the injury or removal of one lobe of the brain, as was proved by the retraction of the antenna when slightly touched on the uninjured side of the head, and by the cleansing and excited act of drawing it constantly through the mandibles; and further, that pain is felt when the cerebral lobes are injured, as when the needle was applied to them after the antennæ had been removed. They lead also to the conclusion, that all the phenomena which occur in the posterior parts of the body after the brain and cord have been separated are reflex or excited, and that these are most intense at the two extremities of the cord—the medulla oblongata, and the terminal ganglion; and further, that the reflex phenomena are always excited and do not occur spontaneously, and that their intensity is greater in proportion to the stimulus applied, and gradually diminishes until they entirely cease, or are re-excited, precisely as already shown by Dr. HALL in the Vertebrata.

The experiments both on the *Iulus* and *Lithobius* seem further to show, that the reflected movements cease first in the anterior part of the cord and its ganglia, and that they are retained longest in the posterior; that the movements are most powerful and continue longest when the cord is entire, the brain alone being separated from it; and that they entirely cease sooner in proportion to the greater number of

parts into which the cord is separated: further also, that the reflex phenomena are less readily excited in the anterior part of the cord, while it is still in connexion with the brain, and that they cease entirely soon after the cessation of volition in that organ; as in those experiments in which only a very short portion of cord was removed with it from the body.

Many of the phenomena are precisely similar to those which have heretofore been observed in the Crustacea. They agree in the circumstance that violent contractions of the segments and limbs, both anterior and posterior to a ganglion, are induced by irritation of that ganglion, both when connected with the brain and when insulated from it, thus proving these movements, in the latter instance, to be reflex; but there is as yet no direct *proof* that sensation does not also exist in these ganglia.

The general results of these experiments tend to confirm the belief that the fibres now pointed out in the composition of the cord and ganglia, and which cannot be traced to the brain, are those by which these movements are executed independently of that organ; and further also; that the reflex phenomena are most intense, most easily induced, and are of longest duration in those animals of low organization in which the volume of brain bears the smallest proportion to that of the whole nervous system, in which also volition and sensation are of small amount, and which have the body formed of the greatest number of similar uniform parts or segments\*.

## 2. THE CIRCULATORY SYSTEM.

The existence of a motion of the fluids in the Articulata has long been known to the microscopic observer. So long ago as the middle of the last century it was seen by BAKER† in the limbs of some insects. But notwithstanding this, and the evidence of a distinct pulsatory action of the great dorsal vessel, as seen through the tegument in the larvæ of insects, the existence of a true circulation of the fluids in them and some of the neighbouring classes was doubted until the fact was demonstrated by CARUS‡, and afterwards by WAGNER§. Yet the means by which this circulation is

\* While this paper has been passing through the press, I have repeated these experiments, on the functions of the brain and cord, with still more conclusive results on the Coleoptera, Orthoptera, Hymenoptera, Neuroptera, Diptera, and other hexapod insects. The cord was divided between the first and second pair of legs. The two posterior pairs of legs were immediately deprived of volition, and exhibited only reflex actions, while the anterior pair gave marked indications of being as completely under the influence of volition and sensation as in the uninjured animal. The cord was then divided between the first pair of legs and medulla oblongata, when these legs also were deprived of volition, and exhibited only reflex actions like the posterior.

Other experiments made on the brain itself, by removing that organ, or by simply separating it from the medulla oblongata and cord, without decapitating the insect, fully confirmed the experiments on the Myriapoda, in proving that the supra-œsophageal ganglia have the functions of a true brain, and are the sole seat of sensation and volition; and that although, when this organ is removed or is insulated from the cord, a regular, combined, and consentaneous series of muscular actions can be excited in the limbs, and locomotion induced, these acts are then entirely automatic, and are performed without the intervention of sensation or volition.

August 29th, 1843.—G. N.

† On the Microscope, vol. i. p. 130.

‡ Nova Acta Nat. Cur. t. xv. p. 2.

§ Isis, 1832.

carried on, whether in vessels with distinct parietes, or in sinuses bounded by the other structures of the body, is still a matter of inquiry, and the existence of vessels in insects has recently been denied by no less an authority than LEON DUFOUR. LYONET\* himself, in his admirable work on the Anatomy of the Cossus, states that he could discover no vessels connected with the great dorsal vessel, which he believed to be closed, and to contain a fluid. This also was the opinion of MARCEL DE SERRES†, who regarded it as a structure for the secretion of fat. CUVIER also believed that this organ was entirely closed, and in consequence supposed that nutrition in insects is effected by simple imbibition. But so early as the year 1812, TREVIRANUS, in his account of the anatomy of the Arachnida, pointed out the existence of vessels connected with the sides of the dorsal vessel in the Scorpions and Spiders; but stated that he was unable to determine whether they are arterial or venous‡. In a subsequent work in 1816§, he has stated that no vessels exist in the Tracheary Arachnida, a remark which LATREILLE§ repeated in 1831; and in 1817|| TREVIRANUS stated, that none exist in the Myriapoda. But in 1825 STRAUS DURCKHEIM¶ discovered the existence of distinct chambers and valves, with lateral orifices in the dorsal vessel of insects, all which had been overlooked by TREVIRANUS in the Arachnida, but he was unable to discover any vessels connected with, or proceeding from, the dorsal vessel in insects. In the Myriapoda, he found the anterior portion of this structure in the Scolopendra divided into three branches, which are distributed to the head, and that the middle one of these gave off other branches, the course of which he was unable to trace. In 1828 CARUS published his discovery of a circulation in insects; and WAGNER in 1832, Mr. BOWERBANK in 1833\*\*, and Mr. TYRREL†† in 1835, added some new facts. But our own countryman HUNTER, long before this period, seems to have been acquainted with the course of the circulatory fluids in insects, and with the existence of the lateral canals described by WAGNER, which he regarded as veins. Professor MÜLLER‡‡ also, in 1824 had traced a connexion between the dorsal vessel of insects and the ovaries, which he described as vascular, although that opinion was controverted by CARUS, TREVIRANUS, BURMEISTER and WAGNER. Some unpublished observations made by myself in 1829§§ on these structures, several years before I was acquainted with the observations of MÜLLER, led me also to regard them as vascular, and this opinion has since been strengthened by my recent discovery of

\* *Traité Anatomique de la Chenille qui range le bois du Saule.* À la Haye, 1760, p. 427.

† *Der Arachniden*, 1812; and *Vermischte Schriften Anatomischen und Physiologischen inhalts.* Göttingen, 1816 (*Die Spinne*), p. 5.

‡ *Op. cit.* (*Die Afterspinne*), p. 32.

§ *Cours d'Entomologie, &c.* 8vo. Paris, 1831, p. 170–176.

|| *Op. cit.* Bremen 1817 (*Die Scolopender*), p. 31.

¶ *Considérations Générales sur l'Anatomie comparée des Animaux Articulés.* 4to. Paris, 1828.

\*\* *Entomological Magazine*, vol. i. April 1833.

†† *Proceedings of the Royal Society for January 15, 1835.*

‡‡ *Nova Acta Nat.* xii. 2.

§§ *Cyclopædia of Practical and Comparative Anatomy*, Article "Insecta," vol. ii. No. 18. p. 979, Oct. 1839. See also Dr. ROBERT'S *Bridge-water Treatise*, vol. ii. p. 245, 1834.

vessels in Myriapoda and in insects. The bifurcation and distribution of the aortal portion of the dorsal vessel in insects was noticed in the first paper which I had the honour of submitting to the Royal Society\*, and was also figured in a subsequent one†, in which I described a structure that had previously been seen by TREVIRANUS in the Scorpion, who believed it to be part of the nervous system, and by MÜLLER, who thought it was a ligament. This was also described by myself as a nervous structure, although subsequent examinations led me to suspect it was vascular, a suspicion which afterwards was found to be correct, by the discovery by Mr. LORD‡ that this structure in the Scolopendra has a direct communication with the anterior part of the dorsal vessel, by means of two lateral vascular arches, the continuations of the two lateral divisions of the dorsal vessel observed by STRAUS in the head of Scolopendra. These arches, descending one on each side of the œsophagus, and meeting in the middle line beneath it, form this single median vascular trunk, which is extended backwards above the abdominal nervous cord. The facts ascertained by Mr. LORD were immediately confirmed by my own observations, and the corresponding structure in the Scorpion was also shown to belong to the vascular system§, and to form in like manner a vascular collar around the anterior part of the alimentary canal. In addition to this vessel lying above the nervous cord, I then first described another system of vessels extended beneath it, the chief of which, placed immediately beneath the cord, communicates with the upper vessel, both anterior and posterior to each ganglion, by means of very short branches, while the inferior one is also connected with a system of vessels that ramify in the inferior part of the abdominal segments. I also noticed the existence of a large vascular trunk that is extended along the abdominal cord in perfect Lepidopterous insects, so that distinct vascular trunks were thus shown to exist in Myriapoda, Arachnida, and Insecta, similar to those already known in the Crustacea. Since that period I have succeeded in tracing other vessels in these classes, the distribution of which, and their connexion with the nervous system, I will now attempt to describe.

*Structure.*—The most rudimentary condition of the circulatory system in Myriapoda exists in the Iulidæ, the family most nearly connected by its mode of growth, as well as by the whole of its structure, with the Annelida. In the lowest genera of this family, the *Spirostrepti* and *Spiroboli*, BRANDT, the structure of the heart is exceedingly delicate, and its separate chambers are very numerous. Their number is almost equal to that of the segments of the body, being only two less than that of the whole number of segments, there being none in the head, or in the anal segment. The number of segments varies considerably in the different species, being in some of the *Spirostrepti* not more than forty-four, but in others so many as seventy-two, and in *Spirobolus* even seventy-five, so that in the latter there are sometimes as many as seventy-two or three distinct chambers to the heart. This structure is ex-

\* Philosophical Transactions, 1832, Part II. p. 385.

† *Op. cit.* Part II. 1834. Plate XIV. fig. 12 k.

‡ Medical Gazette, March 3, 1838, p. 893.

§ *Op. cit.* March 17, 1838, p. 971.



tended along the middle line of the dorsal surface of the body beneath the muscles of the segments, and immediately above the alimentary canal, from which it is separated, in the Chilognatha, only by a very delicate peritoneal membrane. It is attached on the upper surface to the median line of the segments, by means of delicate suspensory muscles, one pair in each segment, as in the larvæ of insects. At its sides it has broad triangular muscles, which are collected into narrow fasciculi, and attached to the sides of the body, like the corresponding muscles, the *alæ cordis* already well known in insects. These muscles are formed of two sets of fibres attached to the sides and termination of each chamber. The *anterior set* is much the largest, and proceeds from the sides of the anterior half of each chamber, along which its fibres are extended, and intermingled with those of the external tunic of the organ. These fibres are gradually collected into fasciculi, on each side, which pass forwards, and are attached to the anterior lateral margin of the segment. These muscles assist to dilate the chamber, and to draw it forwards in the segment, while the ventricular, or contractile action is performed by the structure of the organ itself in the segment next behind it. The *second set* of muscles originates from the posterior lateral part of each chamber. This fasciculus of fibres is smaller than the first, and passes backwards and outwards, and is also attached to the margin of the segment, and seems to be the first to act in dilating the chamber. These structures exist in the whole of the Myriapoda, Arachnida, and Insects, and mainly effect the auricular, or dilating action of the heart, which, in these classes, is not a simple passive act, or the result solely of a relaxation of its own structure. The contractile, or ventricular action of the organ, is performed entirely by its own fibres, the structure and arrangement of which I shall describe in the Chilopoda.

The chambers of the heart are separated from each other by constrictions, or reduplications of the muscular tunics, as shown by STRAUS in insects, but these constrictions are only partial, and far less perfect than in insects, or in the Chilopoda, the most perfect Myriapods. Their rudimentary condition very much resembles that of the chambers of the heart in some of the lowest forms of the larvæ of Dipterous and Hymenopterous insects, in which the heart is scarcely more than an elongated vessel, very slightly constricted in each segment, and almost as simple as the dorsal vessel of some of the Annelida.

At each constriction of the heart in the Iulidæ (Pl. XIII. fig. 16. *f*), between two chambers, there are two transverse lateral orifices, as in insects, through which the blood enters the organ. Whether these orifices in the Iulidæ are the terminations of delicate veins, as I shall hereafter have occasion to show in the Arachnida, or whether they are simple apertures, that admit the blood from venous sinuses in the body, I am not certain. Most of my observations lead me to believe that they are the inlets of the venous trunks that bring back the blood to the heart. The vessels which I have already indicated in *Iulus*\* and *Spirostreptus*, as passing round the sides of the

\* Philosophical Transactions, 1841, p. 103.

body in each segment, are given off near these orifices. The heart is inclosed in a delicate membrane, which excludes it from the surrounding structures. This covering ought certainly to be regarded as a *pericardium*, and not as an auricle, as supposed by STRAUS. The anterior chamber of the heart (*f*) is situated in the second segment (1.), and descends on the œsophagus at the junction of that part of the alimentary canal with the cardiac extremity of the stomach. It is there divided into three trunks of nearly equal size (*p, q*). Two of these pass, one on each side (*p*), around the œsophagus, and unite beneath it; thus forming a vascular collar around this part of the alimentary canal, as was first seen by Mr. LORD in the *Scolopendra*; while the other proceeds for a short distance and then gives off a second pair (*u*) of vessels, and afterwards a third (*v*), all which inclose the œsophagus, thus forming three vascular collars around this structure, very similar to those which encircle the alimentary canal in some of the *Annelida*.

The first of these lateral arches is of great importance in regard to the development of the vascular system. I propose therefore to call them the *aortic arches*. In *Spirostreptus* these are divided into two branches, the posterior of which surrounds the œsophagus to form the great median vessel of the abdomen, while the anterior passes forwards and downwards by the side of the œsophagus to the large mandibles, giving off at the same time a large branch that enters the head, and seems to be given to the inferior labium. The other two branches which surround the œsophagus give vessels to the maxillæ, and the middle trunk is carried forwards to the brain, beneath which it passes and terminates in the antennæ.

In all the *Iulidæ* the heart gives off in each moveable segment of the body two pairs of arterial branches, which have not hitherto been demonstrated in *Myriapoda*. These vessels, which I regard as the *systemic arteries*, I shall describe more particularly in *Scolopendra* (figs. 18 and 19. *h*). They proceed from the under surface of the posterior part of each chamber, and passing outwards in the course of the lateral muscles, as noticed in a former paper, distribute themselves to the sides of the body, to the viscera and to the organs of generation, thus indicating the existence of a complete system of arterial vessels, even in these low forms of the *Myriapoda*.

In this general structure of the circulatory organs in these vermiform *Articulata*, we perceive a shadowing out of the great circulatory organs of the higher animals. The ventricular heart, with its aortic arches and great descending aorta, is rudely sketched in this many-chambered great dorsal vessel or heart of the *Myriapod*, with its lateral arches uniting below the œsophagus to form the great channel for the blood to the organs of locomotion and sides of the body, a structure of which the type of formation is continued uninterruptedly, but gradually increasing in complication and importance as we ascend through this and the other classes of the *Articulata* to the lower forms of vertebrated animals.

In the observations already detailed on the nervous system of these animals, I have shown that each moveable segment of the body is double, and is formed originally of

two segments, which are anchylosed together from a very early period of growth; and that as the segments in the anterior part of the body become more and more nearly approximated, the gangliated portions of the nervous cord in those segments also become more closely united. Now what occurs in this respect in the nervous system takes place also in the vascular. Each double segment of the body in the Iulidæ contains, at an early period of growth, two distinct chambers of the heart, each giving off its pair of arterial vessels, and furnished also with its two pairs of lateral muscles. I have found these chambers distinct, and still separated in *Iulus terrestris*, so late in life as that which I shall hereafter have occasion to describe as the *ninth period of development*, when the individual possesses forty-four moveable segments. After that period the two chambers in each double segment unite and form but one chamber, while the reduplication of the muscular tunics, which form the boundaries of each double chamber, and in which are situated the auricular openings, becomes more complete. Each chamber of the heart, in the adult Iulidæ, has therefore two pairs of systemic arteries, and four pairs of lateral muscles. The union of the two chambers seems to be occasioned by the growth and changes induced in the external coverings of the body, at the period when the animal undergoes its semi-metamorphosis, or change of tegument.

The abdominal portion of the vascular system is less perfectly developed in the Chilognatha than the dorsal. The great ventral vessel, formed by the union of the aortic arches, is a wide dilated structure, that covers the upper surface of the nervous cord, and also the roots of the nerves to some distance from the sides of the cord (Pl. XI. fig. 3. c). Certain processes are extended along the nerves to a short distance, and then appear to separate, and to form for them a vascular sheath (*i*); but this, in reality, is only on their upper surface, since I have distinctly observed vessels passing off from these structures, which I have traced to a great distance along the trunks of the nerves, as will presently be shown in the Chilopoda. I have seen these vessels very distinctly in the *Spirostrepti*. The upper surface of the cord in these families is thus covered by a vascular structure, at least three times as broad as the cord itself and its ganglions. I have reason to think that this structure is in reality formed by two vessels, one on each side of the cord, but connected transversely by a membrane that covers the cord; and that, consequently, in these families the blood is sent backwards in a double stream, from the sides of which vessels pass off to the sides of the body in the form of a vast number of minute trunks, and not in two or three principal trunks, as we shall find in the Chilopoda. This condition of the abdominal vessels, closely resembling that of the Annelida, is indicative of the principle on which all large vascular trunks are originally developed, by the formation, first of numerous minute branches, which anastomose, and are aggregated together in pairs, to form larger vessels. It is precisely similar in principle to the approximation of the ganglia of the cord to form enlarged portions of that structure, and to the lateral approximation of small branches of nerves in the formation of the principal nervous trunks of the body.

In the next family, the *Polydesmidæ* (fig. 17), the circulatory system closely resembles that of the *Iulidæ*. Thus there are the same divisions of the heart into chambers, which distribute systemic arteries, and the aortic arches are given off a little behind the head. But the development of most of the structures is more complete. There are fewer segments to the body, and chambers to the heart, and the latter are more muscular and distinct. The spinal vessel now forms a single large canal above the nervous cord, giving off fewer branches, but it still exhibits the remains of its original formation from aggregations of nucleated cells, which are distinct in its texture, but less so than in the corresponding structure in *Iulus*.

In the *Glomeridæ* the development is still more complete, and approaches in its general condition to that of the Crustacea.

In the *Geophilidæ*, the lowest of the Chilopoda, which still retain the general vermiform type of the Chilognatha, the segments of the body and the chambers of the heart are more numerous even than in the *Iulidæ*. But the whole organization of this family is greatly in advance of the *Iulus*. The heart presents a greater number of segments than in any other Myriapodes. In some species, as in *Mecistocephalus maxillaris*, GERVAIS\*, there are only forty-six chambers, but in others, as in *Gonibregmatus*, NEWPORT, there are more than three times that number, or at least one hundred and sixty. Yet notwithstanding this multitude of parts and segments, the whole organ and its vessels are further developed than in the Chilopoda. The chambers are divided by more distinct valves, and give off each but one pair of vessels. The aortic arches are a single pair, as in Scolopendra, and the supra-spinal artery is not so large as the nervous cords, but is a distinct vessel that gives off a few lateral branches, as we shall find in the next family.

In the *Scolopendridæ* there is a still more perfect development of the whole of these structures. The heart (figs. 18, 19, 20, 21, 22) is inclosed in a distinct membranous covering, which may be regarded as a true pericardium. It is also separated from the great mass of fatty omentum by which it is surrounded, and from the organs of generation, and the alimentary canal, which are situated beneath it, by a distinct, thick peritoneum, which entirely invests the alimentary canal, and in which a great number of circulatory vessels ramify and anastomose. The pericardium that incloses the heart is a loose, delicate membrane, between which and the sides of each chamber there is a slight interspace. It was regarded by STRAUS DURCKHEIM as an auricle. It is attached to each chamber along the median line, both on the upper and under surface of the organ. At its sides it is reflected downwards and outwards, and has lateral prolongations that pass between the *ala cordis*, and seem to inclose vessels that return the blood to the heart. The number of chambers (1 to 21) is reduced in the heart of the *Scolopendra* to twenty-one, the anterior (1.) and posterior (21.) of which are the shortest and smallest. This number is uniform throughout the whole of the species, and the structure and distribution of the parts in all are very similar. In *Scolopendra alternans*, LEACH, and *S. Hardwickei*, Nob., there are two short and

\* This authority refers only to the specific name.

small chambers of the heart in the last dorsal, or preanal segment of the body (20, 21), but one only in each of the other segments. The posterior of these is of a pear-shaped form, and has four minute vessels at its extremity. The two middle ones are given to the posterior pair of legs, and the two outer pass backwards and upwards to the sides of the segment. The second chamber is short, and scarcely longer than broad. The other chambers are equal in length to that of their respective segments. The two posterior chambers, perfectly distinct from each other, but located in the same segment, are analogous to the two chambers which exist in each segment in the earlier periods of development, as we have already seen in the Iulidæ. The *general form* of each chamber of the heart (figs. 20. 21.) is very peculiar. It is dilated, and somewhat lobular and rounded at its posterior extremity (*b*), but is narrowed towards its middle portion, and again enlarged at its anterior (*f*), but is very narrow and constricted at its junction with the next chamber (*e*). This constriction in the young animal, in which I have most carefully examined these structures, is only in the external tunic of the organ, and is not extended to the interior. The *auricular orifices* (*d*) through which the blood enters, are situated at the point of junction of this part with the next chamber. They are two somewhat elongated oval apertures (fig. 21. *d*), in the external muscular coat of the organ, placed a little diagonally on each side of the median line, on its dorsal surface, and are divided only by a thin muscular partition. They are bounded externally by a series of curved fibres (*e*), the continuations of those which connect the posterior of one chamber to the anterior of the one next behind it. These orifices, when examined in specimens that have remained long in spirits, often appear bag-shaped and dilated, and the fibres that bound their external margin are then very distinct. They seem very much to resemble the apertures in the heart of Crustacea, and are, I believe, in their natural state continuous with the parietes of some exceedingly delicate venous trunks, that convey the blood to the heart. At the posterior part of each chamber, in the median line, on the dorsal surface, and extended backwards to the commencement of these orifices, there are a pair of suspensory muscles that pass diagonally upwards and backwards to their attachment in the next segment. These muscles still exist in the larvæ of insects, and appear to have considerable influence on the auricular action of the chambers, and the admission of the blood. At a corresponding part of each chamber, on its under and lateral surface, there are two large arterial trunks (*b*, *c*), which have already been mentioned in the Iulidæ as the *systemic arteries*. The distribution of these, which supply most of the blood to the viscera and sides of the body, I shall presently describe. The *alæ cordis* (figs. 18, 19. *f*) resemble those of *Iulus*.

The *minute anatomy of the heart* (fig. 22.) is exceedingly interesting. This organ is composed of two distinct contractile tunics, an external (*a*) and an internal one (*e*), each covered by its proper serous membrane. The *external tunic* is covered by the membrane that forms the inner layer of the pericardium. It is a very thick, muscular

structure, the fibres of which are loosely interwoven with each other. It completely incloses the second, or inner tunic, the proper ventricular structure, from which it may be separated without difficulty; and it also forms the external covering of the systemic arteries (*c*) at their origin, and may be traced along them to some distance from each chamber. The action of its fibres seems to be chiefly in the longitudinal direction, and thus to assist mainly in shortening the vessel. The *inner tunic* is formed of two sets of muscular fibres. The inner one of these, covered by a delicate membrane, lining the ventricle, consists of longitudinal fibres, which are most perfectly developed on its upper and under surfaces, and which are extended throughout its entire length, from the posterior segment to the head. The other set (*e*), which is external to this, is formed of numerous short, broad, transverse muscular bands, very much resembling in appearance the cartilaginous rings of the trachea in vertebrated animals. These transverse muscular bands are thicker and stronger than the longitudinal fibres, and form the sides of this tunic. They do not completely encircle the longitudinal ones, but pass only half-way round, on each side, having a space between those of the two sides, both on the upper and under surface. This space is occupied by the principal longitudinal fibres, to the sides of which the extremities of these transverse bands are approximated. They are not, however, all arranged in one parallel longitudinal series, but are placed alternately nearer to, or more distant from the median line. This arrangement of the transverse fibres may perhaps be of great importance in the action of the vessel, since the inequality and the necessarily varied direction of the forces of the successive contractions of these fibres must occasion a spiral or peristaltic motion of the whole organ, which may be necessary to propel the blood onwards. Physiologically considered, it may be of still more importance than is at first apparent, with reference to the structure of arterial vessels in the Vertebrata, and their function of conveying the blood; since not only does this arrangement exist in the heart of the Scolopendra, but also in the systemic arteries, given off from it in each chamber; and consequently, by the analogies of comparative anatomy, we may reasonably expect to find a similar arrangement, mode of action, and function of fibres in the arteries of all animals. The passages into the systemic arteries in the Scolopendra are free circular openings (*d*), bounded by these transverse fibres, the existence of which I have traced in the inner tunic of the arteries to a considerable distance from their origin. These openings are in the infero-lateral surface of the enlarged posterior part of each chamber of the great auriculo-ventricular cavity, into which the blood is poured, through the auricular orifices, on the dorsal surface. The auricular orifices pass close together through the internal tunic on its dorsal surface, a little posterior to the outlets of the systemic arteries on the under surface. From their postero-lateral margin a series of oblique fibres passes diagonally forwards, in the interior of the chamber, until meeting in the middle line they form a double valve, with its apex directed forwards, very similar in appearance to the tricuspid valve in the heart of Mammalia. This valve is extended forwards from the

upper surface of each chamber a little beyond the outlets of the systemic arteries, and prevents the return of the blood from the anterior of the chamber. I am not certain whether these valves are extended around the whole of the interior of the chamber, but believe that they exist chiefly at its upper and lateral surfaces, and are almost absent on the under.

The *systemic arteries* (figs. 18 and 19. *h*) given off from each chamber of the heart supply nearly the whole of the blood to the viscera and sides of each segment. They are each divided into two branches (*i*) at a short distance from their origin, and pass diagonally forwards in the segments, giving off numerous ramifications in their course. One of the main branches always passes backwards and outwards, and the other forwards and downwards among the viscera. The latter of these gives branches to the alimentary canal and to the ovaries, which are situated between it and the dorsal vessel, or heart. The posterior pair of these arteries, which belong to the second chamber (20), in the last segment of the body are of small dimensions, and seem to be given chiefly to the rectum and the terminations of the organs of generation. Their place is in a great measure supplied by the arteries of the third and fourth chambers, the largest and most extensively distributed of the whole series. These arteries I have examined more minutely than any of the others. Those which belong to the fourth chamber (18. *h*), in the nineteenth segment, pass almost directly outwards to the hepatic vessels (*n*) and divide immediately into two great trunks (*i*, *k*). One of these passes (*m*) backwards and downwards to the anterior of the twentieth segment, first giving off a secondary branch that distributes some minute ramifications to the coats of the hepatic vessels in its course; and then, turning inwards, it gives some branches to the investing peritoneal coat of the tracheal vessels in the twentieth segment; and then passes downwards (*o*) into the segment and divides into three branches, which are given in part to the colon and in part to the pyloric extremity of the stomach. The other branch (*l*), the principal division of this great artery, passes forwards in the course of, and very close to the hepatic vessel. Soon after it has separated from the posterior branch it gives off some small vessels that go to the great hepatic vessel and ramify in its texture; and others that pass downwards to the interior of the segment. It then accompanies the hepatic vessel (*n*) as far as the middle of the segment, where it meets with a large tracheal vessel (*p*) that is passing inwards to be distributed to the organs of reproduction. At that point it gives off another branch, which also passes downwards in the segment, and is given to the muscles and fatty structures. The main branch then winds round the trachea that passes between it and the hepatic vessel, and gives off some small ramifications that pass inwards with the trachea to their distribution. The main trunk of the artery (*q*) then pursues its course along the hepatic vessel as far as the seventeenth segment, where it forms some anastomoses with the systemic arteries of the fifth chamber. Throughout the whole of its course along the hepatic vessels, to which this branch of the artery is chiefly distributed, it gives off numerous small vessels that ramify in its coats, and other

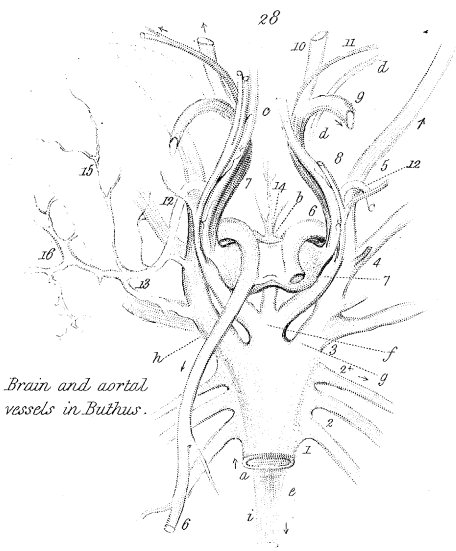
larger ones that pass upwards to the dorsal surface of the body. This is the general distribution of the systemic arteries, their anterior branches (*k*) are given chiefly to the viscera, and their posterior (*i*) to the sides of the segments and dorsal surface.

*The vascular collar* (fig. 18. *p, q, r*) around the œsophagus is formed by the anterior pair of systemic arteries. These pass off from the front of the small anterior chamber of the heart (1.) at its termination in the basilar segment of the head (B), where this organ becomes divided into three trunks, as I have already shown in the Chilognatha, and have distinguished them from the other systemic arteries, as the *aortic arches*, from the great analogy which they bear to the connexions between the heart and its aorta in many of the inferior Vertebrata. They are found in all the Myriapoda in the same segment, not only in the Scolopendra, but also, as we have already seen, in the *Iulidæ* and *Polydesmidæ*, and in the higher genera of the Chilopoda *Lithobius* and *Scutigera*. In Scolopendra they pass a little forwards and outwards before they bend downwards to surround the œsophagus at its junction with the cardiac extremity of the stomach, and unite beneath it to form the great *supra-spinal artery*. While passing round the œsophagus each of these arteries gives off on its front a large branch (*s*), which, as shown by Mr. LORD, is supplied to the muscles of the great mandibles, or foot-jaws (*c*). This branch, however, like the other systemic arteries, is divided into two (*s, t*), one of which is given to the muscles of the foot-jaws, while the other passes into the first, or cephalic segment (A), and is distributed to the muscles of the pharynx and œsophagus, and anterior parts of the head. In *S. alternans*, LEACH, there are two branches from each arch, the posterior of which is supplied to the salivary glands. In all the species there are minute branches given off from the great branch of the arch to the upper and under surface of the œsophagus and cardiac portion of the alimentary canal. The small median trunk (*q*), given off from the heart on the œsophagus with the lateral arches, passes forwards along the œsophagus to the cephalic segment, in which it gives off two pairs of minute *secondary arches* (*u, v*), and then, becoming very much smaller, the main trunk is divided behind the brain (*b*) into some minute ramifications, which are given to that organ, to the eyes (*d*), and to the antennæ (*a*). The *secondary arches* give off a pair of branches to the maxillæ and internal parts of the mouth, and then unite beneath the œsophagus to form a small trunk (*w*) that passes backwards to the junction of the great aortic arches with the supra-spinal artery. This junction of the arches beneath the œsophagus takes place immediately above the second subœsophageal ganglion, where the supra-spinal artery commences.

*The supra-spinal artery*.—This vessel (fig. 22. A. *w, x, y*), which has become a matter of much interest in our examinations of the vascular system, both in Myriapoda and Arachnida, is extended along the middle line of the body, immediately above the nervous cords, as far as the terminal ganglion in the last segment. At its commencement it is nearly equal in size to the great nervous cords along which it



*Circulatory System in Myriapoda & Arachnida.*

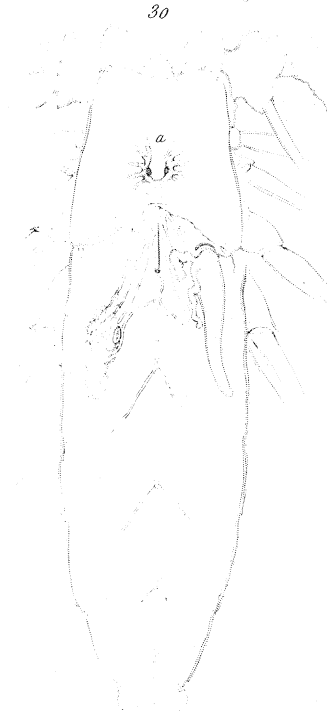
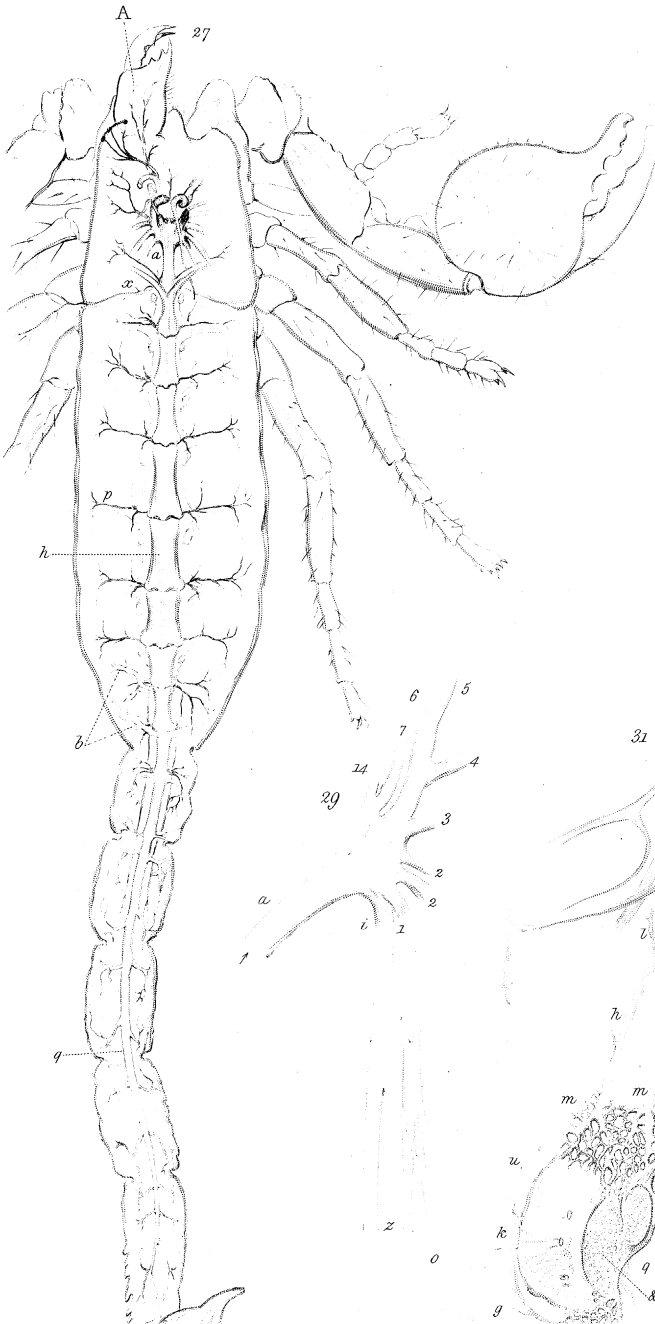


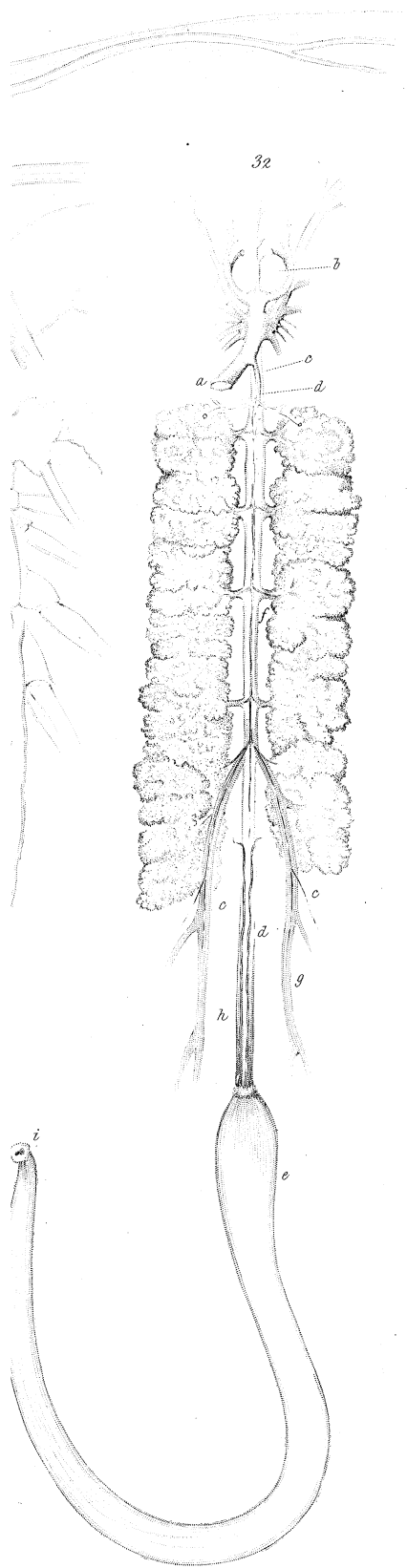
*Brain and aortal vessels in Butkus.*

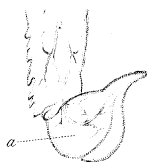


*Distribution of the supra spinal artery on the cord and a*

*Supra spinal artery ganglion of Scolopendra.*



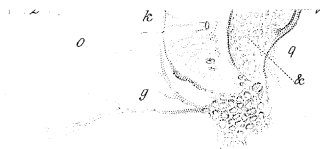




The heart with caudal artery, visceral arteries and distribution  
in cephalo thorax of *Buthus Afer*? natural size.

a. poison gland of the sting.

G. Newport del. 1841. 43.



Portal System in *Buthus Afer*?  
magnified 3 diameters.



Digestive app.  
gastric caeca /  
visceral arteri  
m.



*digestive apparatus (without the salivary glands and  
 astric caeca) with distribution of the aortic and  
 visceral arteries in Androctonus .  
 magnified 2½ diameters .*

*J. Basire sc.*

is extended, becoming gradually smaller as it approaches the posterior segments of the body. The situation of this interesting structure, relatively to that of the nervous cord, the alimentary canal, and the other organs of the body, its connexion by vascular arches with the last ventricle of the heart, and the course of the blood which it distributes, all strongly remind us of its similarity to the great aorta of Vertebrata, and of the analogies which the whole of the vascular structures in these worm-like Articulata bear to those of Fishes and Amphibia, and the earlier condition of the foetus in the higher animals. As it passes backwards along the cord, this spinal artery (Plate XIV. fig. 26. *a*) gives off a pair of branches (*b*) above the anterior part of each ganglion. These branches pass diagonally backwards and outwards, and on reaching the base of the first pair of nerves from the ganglion each gives off a large vessel (*c*) that takes the course of the nerve, and is distributed with it to the muscular and other structures. It then proceeds to the origin of the second, or principal nerve from the ganglion, and gives off a still larger branch (*d*). This, like the first, pursues the course of the nerve which is given to the great muscles of the legs, and is distributed with it to those structures. After this it turns a little backwards and gives off its third branch (*e*), which accompanies the corresponding nerve from the ganglion, and is given with it to the sides of the body. It is then greatly reduced in size, and gives off its fourth and smallest branch (*f*), which accompanies the fourth and smallest nerve, that is given exclusively to the tracheal vessels and parts concerned in respiration. From the origin of this branch to the fourth nerve, a very minute branch (*g*), the continuation of the trunk, proceeds diagonally backwards and inwards to the median line above the ganglion, to become united again with the great spinal vessel (*h*), and thus forms a channel back again into the great trunk for any residual small quantity of blood that is not passed into the other branches: the two principal vessels on each side thus form a complete vascular circle above each ganglion. Besides these principal branches each lateral trunk gives off on its inner side a small branch to supply the ganglion itself (*i*), and other minute vessels are given from the sides of the great artery to the cord. This is the distribution of the vessels from the spinal artery on each ganglion until it has reached the last segment of the body, in which it is scarcely more than one-third of its diameter at its origin in the third segment. Immediately above the last ganglion the artery itself is divided into two principal branches, with only a very minute median one between them. These branches take the course of the terminal nerves of the cord, and are distributed with them to the last pair of legs and the surrounding structures. These are the distributions of the arterial structures in the Myriapoda; some further idea of the extensiveness of which may be formed from the circumstance that the structure of the heart itself is extensively supplied with nutrient branches (fig. 18. *z*). A small artery passes along the median line of the heart, on its dorsal surface, included between the median suspensory muscles. This vessel gives off a pair of branches in each segment, about the middle of each chamber, and these are ramified on its upper surface. Some of the

minute ramifications of this vessel are extended backwards and outwards to the sides of the pericardium. In the peritoneum also there is an extensive ramification of circulatory and tracheal vessels, intermingled with each other in the most complex manner. Some of these vessels run parallel with the tracheal vessels, others are distributed to the structures covered by the peritoneum, and others pass through the peritoneal coverings and are distributed to the organs inclosed by them.

In the genus *Lithobius* the number of chambers to the heart, and of leg-bearing segments to the body, is reduced to fifteen. The form of the chambers and the general distribution of the systemic arteries closely resemble those of *Scolopendra*, but there are some peculiarities that deserve notice. The anterior chamber (fig. 23. 1. *p*) gives off three trunks, as in *Scolopendra*, but the two lateral ones, instead of passing forwards and then arching backwards, as in that genus, pass directly outwards, transversely to the chamber, and give off a single large trunk from their sides directly into the basilar joint of the great mandibles (*c*), at the posterior part of the short basilar segment of the head (*b*); and then unite beneath the œsophagus (*r*) in the same transverse manner, above the great subœsophageal ganglion to form the supra-spinal artery (*y*), which commences in this union without receiving a small median trunk from the inferior surface of the head, as in the *Scolopendra*. This artery passes backwards, in the middle line above, and between the two separated nervous cords (*y, y*), and gives off a pair of branches on the ganglions almost precisely the same as in that genus. It appears also to form some unions, both anterior and posterior to the ganglions, as in the *Scorpions*, with vessels that exist below the nervous cord, and which seem to belong to a portal system. All the blood sent through the aortic arches is returned along the under surface of the body in the spinal artery, from which it is sent off to the sides of each segment through the lateral trunks, the divisions of which take the course of the nerves to the muscles, to the legs, and to the respiratory organs. Posterior to the fourteenth pair of ganglia in the nervous cords the spinal artery (fig. 24.) is divided into two branches (15.) which pass backwards, side by side, as far as the anterior margin of the terminal ganglion, at the front of which (*z*) each gives off a branch that passes laterally backwards and outwards, and the main trunk then pursues its course over the ganglion on which it gives off a second branch (*x*) which accompanies the great nerves from this ganglion to the posterior pair of legs. The remaining portion of each division of the spinal artery then divides into several small branches, which accompany the nerves from the *caudal ganglia* (17, 18.) to the external organs of generation and the rectum. The supra-spinal vessel in *Lithobius* is accompanied on each side by ramifications of tracheal vessels, distributed along the sides of the cords. From these vessels numerous ramifications are sent to the ganglia, as in insects, and are distributed through their structure. When a tracheal vessel is given off behind a ganglion, it sends a branch forwards beneath the lateral vessels from the great spinal artery, and it is then divided on the upper surface of the ganglion into very minute ramusculi, some of which

penetrate the substance of the ganglion accompanied by the arteries given to it from the lateral branches from the spinal artery.

The small median cephalic artery (fig. 23. A. *q*), given off from the heart with the aortic arches to the head, passes along the œsophagus to the posterior pair of muscles of the pharynx, behind which it gives off its second pair of branches. These pass downwards to the maxillæ and internal parts of the mouth and unite beneath the pharynx, but do not send any vessel backwards to join the great spinal artery at its commencement and junction with the aortic arches, as in the *Scolopendra*. The small median trunk then passes beneath the brain, and is divided on the front of it into two pairs of branches, one of which passes laterally to the organs of vision, and the other proceeds forwards on the inner side of the great nervous trunk to the antenna. I have not yet ascertained to what distance this vessel is extended in the antenna of the perfect individual, whether throughout the greater part of the organ, forming a series of loops in the joints, or whether the whole trunk is returned backwards across the third joint of the antenna, in the course of the current of the blood seen in this part of the head in the young *Lithobius*. It is quite certain that the course of the blood backwards in the antennæ and head is in a vessel on the external side of the antenna, both in *Lithobius* and *Scolopendra*. The existence of this vessel I have repeatedly traced in *Scolopendra*, backwards from the antennæ, beneath the optic ganglia, to its union with a small median trunk beneath the œsophagus that passes backwards between the nervous cords to the junction of the aortic arches and spinal vessel. The course of the blood in the antenna in the young *Lithobius* is always forwards on the inner side, and backwards on the outer side of the organ.

In the *Scutigridæ* the circulatory system affords a still further proof of the principles already advanced, that the complete development of every structure is by the union of two or more original parts. In the *Iulidæ* we have already seen this very principle illustrated in the same animal, in different stages of its growth, in the union of two chambers of the heart in each moveable double segment; and there is a further illustration of it in the permanent structure of the heart of the *Scutigridæ*. In this family the number of chambers is still fifteen, as in *Lithobius*, but every alternate chamber (fig. 25.) is reduced both in size and extent. This reduction of length had already begun to take place in *Lithobius*, in which the dorsal plates of the body are alternately longer and shorter in the different segments, to the respective lengths of which the chambers of the heart were begun to be reduced. This is a condition preparatory to the union in pairs, first of the dorsal plates, and afterwards of the chambers of the heart. In the *Scutigridæ* the dorsal plates are already united, and form but eight moveable coverings, one to each pair of segments, which still remain distinct on the ventral surface of the body. But although there are still sixteen chambers to the heart, the changes commenced in *Lithobius* are carried still further in this genus, and each alternate chamber is very much smaller and shorter than the one next before it, and covered by the same dorsal plate. But although the

union of the chambers has actually commenced, it is yet very imperfect, and the original divisions between them are still evident, and the systemic arteries pass off from their sides as in their imperfect state of development. But very little blood enters at the auricular orifices, which still exist in these unions. The chief part now enters through the large auricular orifices of the chambers in the middle of each dorsal plate. These are very distinct, but are placed more transversely to the heart than in *Scolopendra*, corresponding to the more obtuse form of each chamber, and the more compact general form of the whole heart. Here then in the gradual reduction of the number of the chambers, their compact form, and the shortening of the organ, we trace the stages of the formation of the heart in insects, in which there are seldom more than eight chambers.

The minute anatomy of the heart exhibits also a more perfect state of development than in any of the other Myriapoda. The two tunics of which it is composed are united more firmly together, the longitudinal fibres are less distinct than the transverse, which are very strong and powerful, and distinctly marked in the external tunic. The great contractile power of the heart seems to exist chiefly in the transverse fibres, the longitudinal contractions being greatly influenced by the suspensory muscles and the *alæ cordis*.

The distribution of the vessels in *Scutigera* closely resembles that of *Lithobius*; three principal trunks being given off from the anterior chamber of the heart, immediately behind the head, which has assumed in this family the compact form of true insects, the great basilar segment, to which the mandibles or foot-jaws are attached in *Scolopendra*, and the other genera, reduced to a very narrow short segment in *Lithobius*, being now united to the chief portion of the head in this genus. The aortal arches, in consequence of the union of these segments, pass around the œsophagus to unite beneath it, immediately behind the occipital portion of the head, while the small median trunk is situated entirely within this region of the body, thus affording further proof of a higher grade of development than that which we have already seen in the *Chilognatha*.

*The circulatory system in Arachnida* has already engaged the attention of several anatomists, but hitherto has been only very imperfectly understood. TREVIRANUS in 1812 described it vaguely, and first noticed the structure, now described as the supra-spinal artery, as part of the nervous system, and considered it a peculiarity of the nervous system of the Scorpion. MÜLLER, as before stated, noticed the same structure in 1828, but regarded it as a ligament. Both these anatomists entirely overlooked the extensive distribution of vessels from the anterior extremity of the heart in the cephalothorax.

*The Heart.*—*The heart* (Pl. XIV. and XV. figs. 27 and 33. *h*) of the Scorpion is a strong muscular organ, extended along the middle of the back, from its continuation with the great caudal artery (*q*), in the last segment of the abdomen, to the commencement of the aorta (*a*) at the diaphragm (*x*), that divides the abdomen from the



cephalothorax. The aorta descends obliquely forwards and downwards, between the muscles, to the œsophagus, on which it is spread out, behind the brain, into several large vessels, the two posterior of which are united beneath the œsophagus, and give origin to the great spinal artery (*i*)—the structure above noticed. In the dorsal part of its course the heart is divided into eight separate chambers, which are wider and stronger in proportion to their length than in the highest of the Myriapoda—the *Scutigæridæ*. They are more muscular and compact in proportion to the greater quantity of blood to be transmitted through them, and the force with which it is necessary to be propelled. The form of each chamber (Pl. XV. fig. 34.) is somewhat heart-shaped, being slightly contracted in its middle portion, and enlarged at its posterior. Each chamber has two auricular openings (*u*) for the passage of the blood, placed very close to the median line of the heart on its dorsal surface; and it gives off at its inferior lateral angles a pair of large arterial vessels (*p*), the systemic arteries, which distribute the blood downwards to the viscera, and to the dorsal and lateral surfaces of the body. These are the vessels imperfectly noticed by TREVIRANUS. Each chamber is also provided at its sides, as in the Myriapoda and insects, with two sets of muscles, the *alæ cordis*. The anterior and largest pair of muscles are attached to the anterior part of each segment, and pass diagonally forwards, and the posterior, the proper retractor muscles of the chamber, to its posterior angle, and are directed backwards, leaving between the two sets of muscles a passage for the vessels. Of the eight chambers that form the heart in the Scorpion, the posterior two are the smallest, and are situated in the seventh, or last segment of the abdomen. The eighth chamber is very imperfect, and is continuous with the caudal artery, which passes backwards to the post-abdomen, or tail (*q. q.*). The sixth chamber is the largest and most powerful of the whole organ, and seems to correspond to the two chambers in the nineteenth and twentieth segments of the Scolopendra, and which, in that animal also, are the largest. Each succeeding chamber, from the sixth to the anterior one (*t*), at the termination of the heart in the aorta, as it enters the thorax, is shorter, and narrower than the one next behind it, and the systemic arteries (*p p*) are smaller than those of the posterior. The structure of the chambers internally differs considerably from that of the chambers in the Melolontha, as described by STRAUS DURCKHEIM. Each valve or division between them is formed by a reduplication (fig. 36. *u*) of the whole muscular structure of the dorsal surface of the organ. This reduplication, which is chiefly on the upper and lateral surfaces, is very imperfect on the under, and in some of the chambers is entirely absent on the under surface. It is extended about midway into the interior, which it divides more completely than in its less perfect state of development in the young Myriapoda. It is most complete in the sixth abdominal segment, between the largest chambers of the heart. In the middle ones it is extended inwards and forwards, in the form of a broad nipple-shaped protuberance, the orifice of which is opened behind in the middle line. This protuberance (fig. 37.) is situated above, and a little behind, the two large outlets of the systemic

arteries (*w*), through which the blood is transmitted to the sides of the segments. The reason for this imperfect structure of the valves may perhaps be explained by the fact that the blood is distributed from the heart in the Scorpion in opposite directions, partly backwards to the tail, but chiefly forwards and outwards to the head and sides, as in the Myriapoda, and hence it may be necessary that a reflux of the blood should not be entirely prevented, as may be required in those instances in which the whole current is in one direction. This also may be the reason for the valves being formed more transversely, and less completely than in insects. The structure of the organ is exceeding thick, opaque, and muscular. It is formed of two layers of fibres, longitudinal and circular in each layer, the most powerful of which are the latter. On its internal surface it is smooth, and lined by an exceedingly delicate membrane, through which the strong circular fibres are distinctly marked. It is by means of these that its most powerful contractions are effected, the auricular action being chiefly the result of the relaxation of these fibres, assisted by the reactions of the lateral muscles.

At the junction of the heart with the aorta (figs. 27. 33. *t*), as it enters the thorax, the last pair of lateral muscles descend forwards, on each side, into that region, and thus confine it above the diaphragm (*x*). Immediately anterior to the origin of these muscles, close to its junction with the aorta, the heart gives off its anterior pair of systemic arteries (*y*), which ramify on the diaphragm and in the posterior parts of the thorax.

*Distribution of the Aorta.*—The *aorta* is short, thick, and smooth on its external surface, without lateral muscles, or internal divisions into chambers, but there are indications of an obliterated chamber at its commencement. It descends obliquely forwards and downwards, and after passing beyond the great median arch of the thorax, to which many of the muscles of this region of the body are attached, it is widened, and rests on the upper surface of the œsophagus, and gives off the vessels to the head, to the organs of locomotion, and to form the great spinal artery; at this part of its course its distribution is exceedingly interesting. I have already attempted to show the remarkable uniformity of principles on which the nervous and circulatory systems are developed. In no instance is this uniformity more curiously illustrated than in the distribution of the aorta to the limbs and to the head in the aggregation of segments that constitute the cephalothorax. We have seen that vessels are given off from corresponding parts of the chambers of the heart both in the Myriapoda and the Scorpion, and that these vessels, *the systemic arteries*, are given to precisely similar parts in both. In the Myriapoda the anterior pair of these vessels form a vascular collar around the œsophagus in the posterior region of the head, and this also is the case in the Scorpion. The median continuation of the vessel beyond this collar in the Myriapoda is given to the head, to the brain, optic nerves, antennæ and internal parts of the mouth; while the external parts of the manducatory organs, the great foot-jaws or mandibles, are supplied from the vascular collar, or from parts immediately connected with it. Now, notwithstanding the aggregation of all these parts

together, as well as the proper organs of locomotion, the trunks of the arteries still preserve their original distinctness, and enable us to identify the organs and parts of the head in the Scorpion with corresponding structures that exist under other forms, although endowed with similar functions, in the more distinctly developed head of the Myriapodes and insects.

When the aorta (figs. 27. 28. 29. 33.) has descended on the alimentary canal, at a short distance behind the brain, it gives off its second great trunk backwards (1.) to the posterior pair of legs. The first trunk (*i*) having passed downwards, unites with its fellow of the opposite side below the œsophagus to form the supra-spinal artery, the great systemic continuation of the aorta backwards, into the abdomen, the distribution of which I shall presently describe. The third trunk (2.) is given to the penultimate pair of legs, and the fourth (2\*), which is smaller than the others, is specially distributed to the middle portion of the thorax. Opposite to this pair the aorta is considerably widened, and is separated into three great divisions (*f*, *g*, *h*). The middle one of these (*f*), which also is divided into three branches, still preserves its original distinctness, and constitutes the cephalic artery and arterial vessels of the head above the œsophagus, while the two great lateral divisions of the aorta are given at the sides and below the œsophagus to the two remaining pairs of legs (3, 4.), and the great prehensile claws (5.), the analogues of the foot-jaws in Scolopendra, and the mandibles of Iulus and of insects. In this mode of origin and distribution, we obtain a clue to the identity of the special organs of the head in the Scorpion with those of the more perfect Articulata, and also with those of the mouth in the Chilopoda, the foot-jaws, which many naturalists have regarded as not forming part of the organs of manducation. The size of these prehensile organs in the Scorpion requires that an immense volume of blood should be supplied to them in the least difficult manner, and this is effected by the trunk of the great artery being extended into them at an angle very little diverging from the direct line of action of the heart and aorta, so that the blood is necessarily propelled onwards through their extensive ramifications of vessels, with as little resistance as it is passed into those of the head. Before the great lateral artery enters the prehensile organs, which it always does on the inner side of the great nervous trunk, it gives off a large branch that ascends in front of the brain (6.), and forms a transverse anastomosis with the middle cephalic artery (14.), and also with its fellow on the opposite side; and then passing upwards, it is distributed to the large salivary glands (fig. 39.), to the muscles on the upper surface of the thorax, to the diaphragm, and to the anterior parts of the dorsal surface of the abdomen\*. This then we may regard as the proper distribution of the supræœsophageal blood-vessels of the thorax.

*Cerebral Arteries.*—In the distribution of the *cerebral arteries* we find that the cephalic artery (Plate XIV. fig. 28. *f*), which we saw in the Myriapoda divided into three

\* These two vessels are often united into a single trunk on the front of the brain, and are then divided again and distributed as described.

branches, which are given to the brain and the organs of sense, is distributed in the same manner in the Scorpion. The middle branch (14.)\* goes forward to the brain (*b*), to which it gives some very fine vessels, and then passes beneath it, to be distributed above the palate, on the anterior part of the head, where it is again divided into three small trunks (14.), above the small origin of the vagus nerve. It also forms an anastomosis, as already stated, with the divisions from the great lateral artery from the prehensile organs, and thus assists to complete a vascular circle around the brain (*b*), the centre of the animal functions. The two lateral branches of the cephalic artery (7.) pass, one on each side of the brain, giving off a large vessel (8.) to the great optic nerve (*c*), with which it ascends to the surface of the head, divided into many minute ramifications, that supply both the tegument and the chief organs of vision (*b*). After this the lateral cephalic artery bends inwards on the front of the nerves, to the middle line, on the inside of the flexor muscles of the small prehensile organs (*a*), the analogues of the antennæ, and it is then divided into two principal branches (9. 10.), having first given off one (12.) that, passing backwards and outwards, forms two anastomoses with branches from the great subœsophageal division of the artery (13.), from which other branches are distributed. Some of these ascend to the tegument that covers the muscles of the second pair of legs, while others (16.) pass downwards among the muscles of the thorax. The largest division (9.) of the lateral cephalic artery then passes upwards, and is given to the great muscles of the antenna on the dorsal surface, while the other enters the basal joint of the antenna on its inner side, and is again divided into two branches which are given to the two prehensile divisions of this organ (*a*). Besides these there is a third and smaller branch (11.) given off very near to that (8.) which goes to the principal eyes. This branch in like manner passes upwards and inwards with the nerves of the smaller lateral eyes (*d*), which arise by a single trunk from the same part of the brain as those which are placed on the middle of the cephalothorax (*c*).

Thus then in the origin, and in the uniformity of distribution of the vessels and nerves of the head, we are enabled to identify the small prehensile organs on the front as the analogues of the antennæ of insects, and which, although so remarkably altered in form from a simple, elongated, many-jointed organ, to one of a prehensile character, still retain the same primary function, that of touching and feeling as in their less complicated structure.

This arrangement and identification of the structures in the Scorpion serves still farther to illustrate that admirable uniformity of design on which all organized bodies are constructed. The distribution of the blood-vessels in these Invertebrata is as uniform in its plans, and as precise in its character, as in the blood-vessels in the higher animals. The large arterial trunks always accompany the principal trunks of the nerves, especially at their origin from the brain and cord. So likewise the arterial vessels invariably exhibit a strong fibrous texture, more especially those which

\* This branch is very frequently absent in the Scorpion.

carry out the chief currents of the blood from the heart itself, the systemic arteries, and the aortic branches; while on the contrary, like the veins of the Vertebrata, those which bring back the blood in the principal organs do not always pursue the course of the nerves, nor are of the same dense elastic texture. They are usually exceedingly delicate, membranous and transparent; and this is more especially the case with those which, covered by the peritoneum, bring back the blood round the sides of the body to the heart. An exception however must be made to a system of vessels in the Scorpion, which, although performing the function of veins in collecting the blood that has been distributed through the system by the arteries, partake also of the character of arteries in their texture as well as in their function of propelling the collected blood into the branchiæ for the purposes of respiration. This, which may be regarded as a *Portal System* of vessels, is in close connexion with the sub-œsophageal distribution of the arteries which pass backwards into the abdomen from the vascular collar formed by the aorta around the œsophagus.

*Arterial Vessels of the Abdomen.*—The *vascular collar* which surrounds the œsophagus analogous to the *aortic arches* in the Myriapoda, forms the great *supra-spinal artery* (fig. 31. *a. i.*), which may be regarded as the *aorta descendens*. This great vessel is formed by it immediately anterior to the middle bony arch (*b*) of the cephalothorax, and passes backwards above the nervous cord (*s*), in the median line, beneath the arch, to which it is slightly adherent by fibrous tissue. It was this circumstance, probably, which led Professor MÜLLER, who observed it in 1828, to regard it as a ligament. It is extended backwards (Plate XV. fig. 33. *i. i. i.*) along the whole nervous cord (*m. m. m*) to the terminal ganglion of the fourth segment of the tail, gradually lessening in diameter, and giving off on its under surface a single short trunk (*k*), both anterior and posterior to each ganglion. These short trunks pass downwards between the nervous cords (*m*), and unite with the system of portal vessels which extends beneath them (*n*). The supra-spinal artery does not give off any other branches in its course through the abdomen until it arrives at the terminal ganglion; so that these azygos branches, which seem to distribute very minute vessels to the ganglion itself, and to the two nervous cords as they pass between them, may be regarded as analogous to those which we have seen given off from the supra-spinal artery on the ganglia in the Myriapoda; while their continuation with the vessels of the portal system beneath, with which they pass outwards, may represent those which are also continued outwards along the nerves in the same class. When the artery has reached the terminal ganglion in the tail (Plate XV. fig. 38.), it gives a descending branch usual to unite with the subspinal vessel (*n*) beneath it, and then becomes a little expanded, and produces on each side a small branch on the front of the ganglion (*k. b*), precisely similar to the first of the terminal branches in the Myriapoda. This accompanies the lateral pair of nerves outwards to their distribution in the lateral muscles and the surrounding structures. The trunk of the artery then passes over the ganglion and immediately gives off another pair of branches (*b*), which seem first to form an

union (*k*) at the roots of the nerves with the subspinal vessel beneath, and then pass outwards to the sides of the segments. Immediately after this a second median branch is united behind the ganglion with the subspinal vessel, and the main trunk passes on for a short distance between the terminal nerves of the ganglion, and is then divided into two branches which take the course of the terminal nerves. Each of these divisions of the artery gives off a branch which is distributed in part forwards (1.) to the under surface of the colon, and part backwards to the same structure (2.). The two terminal divisions of the artery (3.) then pass backwards with the terminal nerves and anastomose by a short transverse trunk (4.), and each again divides into two branches immediately before the nerves also are divided, at the posterior part of the fourth segment. They then accompany the nerves to their ultimate distribution, and are always divided immediately before any division takes place in the nerves. This is invariably the manner in which the arterial vessels accompany, and are divided with, the nerves, and proceed with them to their ultimate distribution.

Having traced the distribution of the arterial vessels from the anterior extremity of the heart, it remains now to follow those of the posterior, which afford some curious peculiarities. The last two chambers of the heart which are situated in the seventh segment of the abdomen, are greatly reduced in size, and constitute the origin of the caudal artery, and seem to be the means by which part of the current of blood is directed backwards to the tail. Each of these chambers receives its venous trunks (figs. 27.*b*. 33.*t*.) in a direction more transversely backwards than the other chambers, so that the influx of the received blood is directed backwards. The vessels which convey it ascend between the muscles and the peritoneum, as well as around the sides of the segments. The visceral arteries from these chambers (*p*) are also altered in their direction. Instead of passing laterally and forwards, they give off only a small trunk forwards and to the sides of the segments, while their principal trunks are directed backwards. Those from the seventh chamber proceed as far as the posterior part of the first caudal segment, at the sides of the colon, and are specially distributed to the terminal alimentary cæca, while the eighth chamber (*p, q*) sends off only a single artery on its under surface. This is divided into three branches, two of which pass, one on each side, to the terminal cæca, while the third proceeds in the middle line, beneath the caudal artery, as far as the middle of the second segment, where it is divided into branches which are given to the muscular structure of the colon. When the caudal artery has entered the first segment of the tail it gives off on each side a plexus of four vessels, two of which are distributed forwards and laterally; the third backwards, to the great flexor muscles on the dorso-lateral surface of the segment; and the fourth (*r*), passing round the sides, between the peritoneum that covers the muscular structures and the colon, meets with the nerves that are passing upwards from the ganglion of the cord, and pursuing their course downwards unites beneath the ganglion (*s*) with the caudal portion of the subspinal vessel (*n*) that is passing inwards to the abdomen. At the commencement of each segment of the tail a pair of vessels

passes in this manner from the artery, on the dorsal surface around the colon, to unite beneath a ganglion of the cord with the subspinal vessel on the ventral surface; thus forming a series of four vascular collars (*r. r. r. r.*) around this portion of the alimentary canal, one in each segment, at its commencement nearest the abdomen. At the distal end of each segment a second set of vessels is given off, but these are given solely to the muscular and other structures, and do not form any anastomoses with the subspinal vessel.

Besides the arteries already described, there are others which deserve to be regarded as proper *visceral arteries*. These originate from the inferior surface of the aorta before it spreads out on the œsophagus into great branches. They come off from the under surface of the aorta, either in pairs, as in the genus *Buthus*, LEACH (fig. 33. *z*), or as a single trunk, as in *Androctonus*, KOCH (fig. 32. *c, d*), as we have seen in the caudal vessels. They are given specially to the alimentary canal and the liver, to which they give off a branch on each side (*f*), opposite to each junction of this viscus with the alimentary canal (*d*). They also anastomose extensively along the whole of the abdomen with branches from the proper systemic arteries, and are continuous with branches which pass forwards on the alimentary canal from the trunks of the systemic arteries from the great chamber of the heart in the sixth abdominal segment. The beautiful uniformity of the principles of development is thus further illustrated in these vessels. Like the great divisions of the aorta these also are modifications of the systemic arteries, the primary vessels of the segments, and are specially given to the alimentary canal at its anterior extremity, as the systemic arteries in the Myriapoda are to the hepatic appendages of the same structure at its sides and posterior extremity.

The *portal system of vessels* (figs. 30, 31.) is situated chiefly below the nervous cord on the ventral surface of the body, and is the means by which the blood is collected and conveyed to the branchiæ, from which it seems to be returned to the system, after circulating through the organs, by means of a large sinus or vessel at their posterior superior angles. Behind the bony arch of the thorax (fig. 31. *b*) there is a hollow fibrous structure (*d*) that closely surrounds the cord and nerves, as in a sheath, but the precise nature of which I have not fully ascertained. It seems to form a kind of sinus, from the posterior part of which a small vessel passes backwards, which, joined by anastomoses from the supra-spinal artery, forms the commencement of the subspinal vessel (*g*); and it gives off two pairs of vessels at its sides. The first (*h*) and second (*e*) pair of these efferent vessels, covered by the thick peritoneal lining of the abdomen (*n*), send the blood in a diagonal direction backwards to the first pair of abdominal branchiæ (*k*). The first pair of these vessels originate close to the folds of the diaphragm (*x*). They pass backwards and outwards into the abdomen, and are joined in their course by numerous small vessels (*l*) from the sides of the segments; and immediately anterior to the first pair of abdominal branchiæ are each divided into two branches (*m*), which are again divided and subdivided into

a multitude of anastomosing vessels before they are distributed on the branchiæ. These branchiæ also receive the second pair of efferent vessels (*e*), which, like the first, pass diagonally backwards from the fibrous structure to the inner side of the branchiæ, on approaching which they are divided, like the other pair, into two branches (*m*), which are subdivided and anastomose with the divisions of the first pair. The whole form a most intricate web of anastomosing pulmonic capillary vessels before they are distributed on the anterior part of the branchiæ. We have thus a complete distribution of the blood to the pulmono-branchiæ in the anterior part of the abdomen. There is a similar but less perfect distribution in the posterior. Besides the vessels from the sides of this fibrous structure, which in reality may be regarded as a great *vena cava*, there is also the single vessel extended backwards (*g*) from its posterior extremity in the median line beneath the nervous cords (*f*) into the abdomen. This vessel was formerly described by me\*, before I had traced its origin, as the *sub-spinal vessel*. It is extended backwards beneath the nervous cord and receives a small vessel from the supra-spinal artery above it, both anterior and posterior to each ganglion. Immediately after it has entered the abdomen it gives off a single trunk (*o*), which, joined by a minute vessel from the supra-spinal artery (fig. 29. *z*), passes outwards and downwards on the right side of the cord and a little backwards, lying loosely in the under surface of the segment, and at length becomes slightly enlarged (*o*) and is divided into two branches, which also are enlarged at their origin; and the whole form between them in the middle line a triangular dilatation or *small vena cava* (*w*), in which the blood may be accumulated. These branches then pass diagonally outwards and are given one on each side to the anterior part of the second pair of branchiæ, each being first divided into numerous anastomosing capillary vessels, as in those already described. But before this division takes place each branch receives the double trunk of two other venous branches (*r, s*) that convey the blood backwards and outwards from the middle inferior surface of the abdomen. These unite with the first branch on the inner side of the great vertical muscles (*v*) that mainly assist in the respiratory action of each segment; after which the branch passes backwards to its distribution, accompanying the great nerve of the segment (*p*). When the sub-spinal vessel has given off this first pulmonic trunk it passes onward, and opposite the middle of the first pair of branchiæ gives off a second, which, like the first, is extended backwards for a short distance, lying loosely in the segment. This second trunk is then dilated and divided into two lateral branches like the first, and these, after receiving other vessels from the inferior surface of the segments, are given to the second pair of abdominal branchiæ. At a little distance further on, when it has arrived at the second ganglion of the abdominal cord, the sub-spinal vessel is itself a little dilated, and is divided into two lateral branches which pass outwards in close approximation with the nerves from the ganglion; and having received an accession of venous trunks as before, these branches are given to the third pair of branchiæ. After this the sub-

\* Medical Gazette, March 10, 1838, p. 971.



spinal vessel becomes very much smaller, and about midway between the second and third abdominal ganglia sends off a pair of smaller branches, which are given in like manner to the posterior part of the same branchiæ. It then continues its course as a very minute trunk to the third ganglion. At this point the direction of the lateral vessels given off from it is altered (fig. 33. *n.* 1). Instead of passing laterally backwards they are now directed outwards and forwards, to distribute the blood to the anterior part of the fourth pair of branchiæ. This altered direction of the vessels is necessary in order to convey inwards to the body the blood that is passing forwards along the subspinal vessel in the tail to be aerated in the posterior branchiæ of the abdomen before it is again transmitted to the heart. That this is the case is proved by the fact, that a single median trunk (*n.* 2.) is given off from the under surface of the subspinal vessel beneath the ganglion in the first caudal segment. This trunk is directed forwards into the seventh or terminal segment of the abdomen, lying loosely like those which are directed backwards in the anterior segments. When opposite to the posterior part of the fourth pair of abdominal branchiæ it is dilated and divided into two branches, which together form a dilatation like the anterior ones before they are directed outwards and are joined by other venous trunks and distributed over the branchiæ. This is the mode of distribution of these vessels in the great Scorpion, *Buthus afer*, LEACH, but a slight variation is found in some other species. Thus in the specimen formerly\* examined, *Buthus costimanus*, KOCH, or a species nearly allied to it, instead of a pair of branches given off from the subspinal vessel midway between the second and third abdominal ganglia, I found an azygos vessel given off beneath the latter, and which having passed forwards, midway between these ganglia, was then divided into lateral branches like those at the anterior part of the body.

This peculiar distribution of the subspinal vessel in the abdomen enables us to understand a fact that seems at first very difficult of explanation; viz. that the branches from the caudal artery on the dorsal surface of the tail do not anastomose with the spinal artery (*i*) that lies above the cord, and in which the course of the blood, as we have already seen, is from before backwards, but with the subspinal vessel beneath it (*n*), in which the course of the blood is inwards to the abdomen, precisely that of the dorsal artery; so that the unemployed blood from this structure, and that which has become venous, is collected as it returns from the tissues by the subspinal vessel, and intermingled together before it is transmitted to the branchiæ.

*Structure of the Pulmono-branchiæ.*—Professor MÜLLER† has already accurately described the pulmono-branchiæ as formed of a multitude of closely approximated, thin, double lamellæ, which communicate by a small orifice in each with the external air admitted into a common cavity through the spiracle on the surface of the body. The blood distributed through these lamellæ is brought into contact with the air in their interior through their membranous structure. The minute anatomy of these lamellæ, and the manner in which they are permeated by the blood, afford some

\* *Loc. cit.*

† MECKEL's Archiv, 1828.

points of interest. Each side of these double lamellæ is formed of an exceedingly delicate and apparently structureless double membrane, which include within it a parenchymatous tissue, formed of single vesicles or cells, in which I have been unable to detect any nuclei. These cells exhibit the appearance of simple bodies, from which it might well be conceived that vessels might be formed. In some places these vesicles are arranged more in distinct series, and are also slightly elongated. The whole parenchymatous tissue of the lamina is made up of these cells, which are larger and more elongated, and assume a slightly conical appearance near where the air enters at the base of each plate, in which part these cells are nearly uniformly distributed within the double membrane. But in the upper or more convex portion of each lamina, numbers of these minute cells are aggregated together in numerous, irregular, rounded patches, which thus produce a tuberculated or glandular appearance in the lamina. These aggregations of cells are more thickly interspersed through the structure of the lamina the nearer they are to its convex margin, where I have sometimes seen what I believe to be delicate but exceedingly indistinct vessels penetrating the lamina, but which could be followed only for a very short distance into it among the cells. The convex margin of each lamina is however bounded by a delicate but distinct vessel, which seems to form the means of intercommunication between the anastomosing net-work of vessels distributed over the branchiæ and the structure of the lamina, since the delicate evanescent vessels traced into the lamina are derived from those which bound their convex margin. I have also observed vessels extended from these marginal vessels on the lamina, which I regard as the anastomoses between these and those which cover the whole branchiæ, and distribute the blood from the portal branches.

It has already been stated, that at the posterior part of the inner side of the branchiæ, on their superior internal margin, where the lamina are covered by the thick membrane and peritoneum that covers the common cavity of the branchiæ, there are several small orifices (fig. 31. *t*), the commencement of vessels which afterwards, when collected together, form the larger channels that convey back the blood to the heart. At the superior angle of each lamina of the branchial plates there is a small sinus that opens into a larger one, formed on this border of the common cavity by the whole of the lamina, which from its direction backwards appears to communicate with the orifices. From these facts it would appear that the blood permeates the nucleated parenchymatous tissue of each double lamella, and is brought into contact with the air, when the branchiæ are inflated during respiration, by endosmosis through the membranes, and then, collected in the sinuses at their base, it passes out again through the orifices and vessels at their superior border, to be returned again to the heart. These vessels form delicate vascular trunks or sinuses which pass around the sides of the body in the posterior part of each segment, and gradually enlarged by communicating with other vessels in their progress, pour their contents into the heart at the auricular orifices (*u*) on its dorsal surface.

The orifices in the common cavity of the branchiæ (fig. 31. 8), which communicate with the interior of the lamellæ, are largest in the anterior and smallest in the posterior ones. The cavities of all the branchiæ communicate directly with each other by a short narrow passage, so that the whole on one side of the abdomen forms one common cavity or lung-like organ, like the large tracheal vesicles in the abdomen of perfect insects, and thus ensures an uniformity of function at each act of inspiration throughout the whole body.

*Nutrition of the Branchiæ.*—Besides the vessels already described, the branchiæ are supplied with *arterial branches* apparently for the nourishment of their tissues. The first arterial vessel is derived from the supra-spinal artery while passing over the *vena cava*. This vessel (*p*) accompanies the nerve (*q*) that is passing backwards to the fourth abdominal segment, behind the first branchia, to which it is distributed after supplying the trunk of the nerve in its course. The other vessels (*u*) are derived from branches of the systemic arteries. TREVIRANUS\* long ago described vessels in the Scorpion distributed on the branchiæ; but he acknowledged, in his description of similar vessels in the Spiders, that he was unable to determine whether they are arterial or venous. He seems to have thought that they carry back the blood to the heart. But this is not the case. They are derived from the great systemic arteries, along with which I have traced them upwards to their origin in each chamber. These then are the structures of the pulmonary organs in the Scorpions, a system as perfect as in any of the Articulata, and which will lead us clearly to understand the course of the circulation in these animals.

*Course of the Circulation.*—The blood received by the veins from the branchiæ is conveyed to the heart round the sides of the segments receiving accessions from other vessels in the segments in its course, and enters the heart at the posterior part of each chamber on its dorsal surface through the orifices of STRAUS. The auriculo-ventricular cavity, dilated by the influx of blood, begins first to contract by the action of the circular fibres at the posterior part of each chamber. By this contraction part of the blood is at once propelled laterally through the systemic arteries to the interior and sides of the body; while the remaining and chief portion is forced onwards through the valves and body of the chamber by the successive contraction of the circular fibres into the next chamber. A fresh accession of blood enters the heart at the auricular orifices in the short interval of time that elapses between the contractile actions of the two chambers, which interval is probably occasioned by the reaction of the lateral muscular appendages of the organ. These contractions, commencing in the principal chamber in the sixth abdominal segment, are carried gradually onwards through the whole of the succeeding segments; so that ere a third chamber has contracted the first is again filled and ready to be emptied, thus occasioning by their alternate movements those pulsatory motions observed in all instances in which the heart is formed of a longitudinal series of chambers and valves, motions which are

\* Vermischte Schriften, Anatomischen und Physiologischen Inhalts, vol. i. Gottingen, 1816.

so well known in insects. The blood, propelled by these successive contractions through the aorta, is distributed to the organs in the head and thorax, and the organs of locomotion. Part of it also is sent round the *aortic arches*, through the supra-spinal artery, backwards into the abdomen, giving off its minute currents for the nourishment of the cord, while another portion intermingled with that collected in the portal vessels is sent to the branchiæ. But its principal current still flows in the spinal artery, along the upper surface of the cord to the terminal ganglion of the tail, where it is divided into four streams, two of which go out at the sides of the ganglion to nourish the segment, while the other two, now greatly reduced in size, proceed backwards along the terminal nerves of the cord, and becoming more and more subdivided in the last segment of the tail are diffused through the surrounding structures. These form minute anastomoses with numerous small vessels, which, gradually collecting in separate trunks on the under surface of the last segment, form the origin of the caudal portion of the subspinal vessel, which conveys the returning blood forwards from the tail to the abdomen to be aerated in the branchiæ before it is again transmitted to the heart. In like manner the blood that has already circulated through the organs of locomotion, the cephalothorax and abdomen, appears to be collected in the *venæ cavæ* which transmit it to the branchiæ before it is again employed in the circulation. Throughout the whole of its course along the artery in the tail the blood is passed in small currents, both anterior and posterior to each ganglion, into the subspinal vessel; thus intermingling the venous and arterial blood precisely as occurs in the abdomen. But the circulation in the caudal prolongation of the heart yet remains to be explained. We have already seen that the great dorsal artery in the tail, above the colon, forms direct vascular anastomoses around its sides with the subspinal vessel on the ventral surface, in which the course of the blood is *forwards* to the abdomen. It is certain, therefore, that the action of the great chamber of the heart must impel the blood at once in every direction, chiefly forwards and laterally, but also in part *backwards* through the caudal artery, otherwise it would be impossible for this structure to form its anastomoses with the subspinal vein without occasioning two opposing currents in the same vessel, and this diversion of the current may perhaps be effected through the interposition of the two imperfect chambers of the heart in the last abdominal segment.

#### *Recapitulation and Conclusion.*

Although I propose to continue these investigations of the anatomy and development of the nervous and circulatory systems in the other classes of Articulata, it may be well briefly to recapitulate the principal statements contained in this paper.

1. First, in regard to the nervous system, which has already so deeply engaged the attention of physiologists, certain facts appear, nevertheless, to have been overlooked or imperfectly examined. The double nervous cord is composed in all the Articulata of a superior and inferior series of longitudinal fibres, superimposed one on the other,

as I formerly had the honour of stating to the Royal Society. Both these series may be traced along the whole cord upwards to the cerebral ganglia, and hence may fairly be inferred to minister to volition and sensation, either separately, or, as there seems reason to believe, conjointly, through a mutual, partial interchange of fibres; although it appears almost impossible to demonstrate, with certainty, by any experiment on these structures, the precise individual function of either series. The inferior series is swelled out in each half of the cord, in every segment, into ganglia, from which nervous trunks are given off; while the superior series passes longitudinally over the ganglia, without becoming perceptibly enlarged, or entering into the composition of these ganglia. These enlargements of the cord are produced, in part, by a slight enlargement of the longitudinal fibres themselves, and in part also by the interposition between them of nucleated cells, which are chiefly collected in the middle portion of each ganglion. The ganglia are traversed transversely by fasciculi of commissural fibres, which form part of each nerve given off from the ganglia, as shown by Dr. CARPENTER, myself, and others. Those fasciculi of fibres which pass through the ganglia are equal in number to the nerves given off from them, and enter into corresponding nerves on either side. They form no direct connexion with the brain, nor with any nerves anterior or posterior to them in the cord, but only with the corresponding nerves on the opposite side of the ganglia. Their function may therefore be regarded as *commissural* and *reflex*; combining in action the two opposite sides of that segment of the body to which they are distributed. But there are other fibres that form part of the sides of the cord which combine distant parts and segments on the same side, and which, although extending longitudinally in the cord, in part of their course, have no direct connexion with the brain, nor are traceable to that organ. Hence the function of these also, which have not before been pointed out by anatomists, must be regarded as *reflex*, and as combining distant organs or segments on the same side of the body, as the commissural fibres do parts on the opposite side in the same segment. These fibres form the exterior of the nerves and cord. Tracing them from their peripheral extremities, on the surface of the body, they pass inwards to the spinal cord in the course of the nerves, bounding the posterior surface of the root of each as it comes from the ganglion. They are then reflected backwards, and form the postero-lateral surface of the cord, into the composition of which they enter, and along which they are extended backwards until they arrive at the ganglion. They then again pass outwards on the ganglion, forming its antero-lateral surface, to the root of a nerve, along the anterior of which they pass to their peripheral distribution on the surface of the body. Some of these fibres, after joining the cord, seem to pass beyond the next ganglion to be given to nerves from one more distant, so as to form, as it were, a series of circles one within the other. These fibres are joined with all the nerves of the body, both those which pass directly from the ganglia, and those which seem to come from the upper or aganglionic portion of the cord. Now since these fibres have no direct communication with the brain, as may

be shown from the manner in which they bound the posterior roots of the nerves, their influence can only be regarded as reflex, and not as voluntary or sensitive. Consequently, they tend to explain the cause of movements of parts on the same side of the body, excited by irritation of the nervous fibres connected with those parts in distant segments, in accordance with the theory of the reflex movements, as promulgated by Dr. MARSHALL HALL. The uniform size of the nervous cord, into the structure of which these fibres enter, in the interspaces between the ganglia, is a further reason for inferring their separate existence from those of the longitudinal series, which are traceable to the brain; although they exhibit no structural differences from those series, and their separate existence is not distinctly marked, excepting where they bound the posterior surface of each nerve and ganglion, while passing inwards to form part of the cord. In other respects they closely resemble the fibres of the inferior longitudinal series, to which they are approximated. It is on account of the separate additions of these fibres to the cord, in the interspaces between the ganglia, that I have designated them *fibres of reinforcement of the cord*. According to these views, each nerve is formed of *four sets* of fibres, two of which, derived from the primary structures of the cord, the ganglionic and the aganglionic, which are traceable to the brain, are supposed to minister to volition and sensation: the other two, the fibres of reflected action, are the *commissural*, which communicate with those on the opposite side of the body, and those of *reinforcement*, which, independent of the brain, connect distant parts on the same side of the body. The ganglia of the cord are regarded not only as analogous, anatomically, to the enlarged portions of the cord in Vertebrata, but physiologically as centres of reflexion, agreeably to the views of Dr. CARPENTER; and they also possess a still more important character and function in the nervous system, that of being the centres of growth and nutrition to the cord and nerves, the nuclei contained in them being perhaps the sources of supply and nourishment. This is shown from the fact that, in these parts, the fibres of the cord are softer and larger than in the rest of their course; and are elongated during the growth of the body, and the development of new segments; as is seen in the *Polydesmidæ* and *Geophilidæ*, families from the two divisions of Myriapoda. These additional facts fully accord with the already ascertained mode of development *by extension*, or simple growth of the segments.

2. The examination of the circulatory system has afforded many facts, which appear equally new and important. In the whole of the Myriapoda and Arachnida a distinct circulation of the blood is carried on in vessels; and such also is the case in insects and other Articulata. These structures are less perfect in the earliest condition or larva state of the animal in each of these classes, in which many of the structures are still in the course of formation, more especially in those species which undergo a true metamorphosis, as in insects. A distinct system of arterial and venous structures exists in the Myriapoda and Arachnida. The first of these are in the original course of the fluids from the central organ, in the formation of the embryo. The *systemic*

*arteries* are now first pointed out in the Myriapoda, and their analogues shown in vessels, which heretofore have been imperfectly traced by TREVIRANUS in the Arachnida. The course of the blood to the heart has hitherto been regarded as simply intercellular; but the conclusion now arrived at, from a careful examination, is, that in the perfect state of the animal the blood always flows in vessels, the parietes of which are usually quite distinct, although in some parts of their course they have rather the character of sinuses. These vessels empty themselves at the valvular orifices of STRAUS, with which they appear to be in direct communication, and surround the orifices as delicate membranous structures. They convey back the blood from the branchiæ in the Arachnida around the sides of the body, and are joined by other vessels in their course, and form numerous connexions with the adipose tissues; so that some intermixture of venous and of recently aerated blood from the branchiæ takes place in the course of the fluids to the heart.

The *structure* of the heart and vessels is particularly examined in the Myriapoda and Arachnida, and the vascular collar in each, formed by the *aortic arches*, at the anterior extremity of the aorta, is shown to be a modified condition of the systemic arteries. The distribution of vessels from these arches, both in the Myriapoda and Arachnida, is minutely traced, and the analogies pointed out between the seemingly confused and aggregated distribution in the Arachnida, with corresponding portions of the same structures in the more distinctly developed parts in the Myriapoda. This identification of parts of an intricate distribution of vessels in one animal, and their comparison with those well ascertained in another, exemplifies the uniformity of plan of creation, and the utility of comparative examinations of structure, even in the lowest forms of animals. The course of the *supra-spinal artery*, formed by union of the aortic arches around the œsophagus, is followed into the abdomen, to the extremity of the body in the Myriapoda, and to that of the caudal region in the Scorpion: and the distribution of its branches in these classes is traced outwards along the course of the nerves from the ganglia. Branches from the systemic arteries are traced to their ramifications on the coats of the hepatic vessels, in the first of these animals; and others from those of the visceral systemic arteries to the alimentary canal and liver in the latter; facts which I regard as new demonstrations of the existence of circulatory vessels distributed to the internal organs in Articulata.

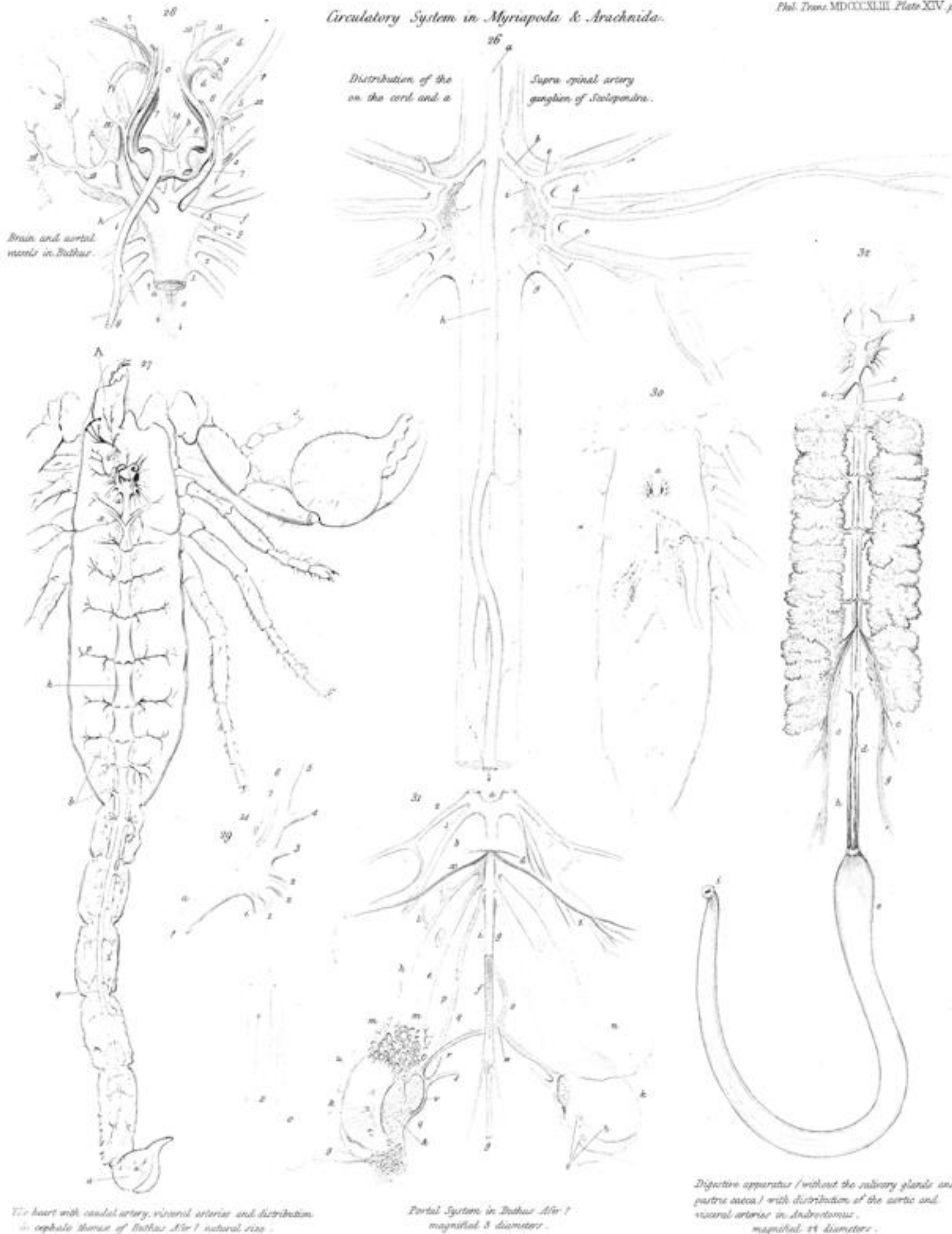
A set of vessels which I formerly described as portal vessels are also further examined, and are traced to their terminations in extensive anastomoses and web-like capillary distributions on the branchiæ. The *structure* of the *branchiæ*, and the manner in which the blood seems to permeate their delicate laminae, and is afterwards collected in sinuses at their base, and again returned to vessels that convey it back to the heart, are also investigated; and the vessels specially given for the nourishment of the branchial structures are noticed. The course of the circulation is traced from the heart, through the systemic arteries, laterally, to the sides of the segments; and forwards, through the chambers and the aortic arches into the cephalothorax

and limbs; and backwards, through the spinal artery into the tail; the returning blood being collected by the portal vessels and sent to the branchiæ, from whence it is again transmitted to the heart. This is the general course of the circulation in the macrourous Arachnida, so that in these there is a current backwards along the great dorsal artery, and the heart propels its fluid in every direction by the successive actions of its chambers.

3. The development of the nervous and circulatory systems is shown to be effected by two modes; first that of growth, *extension*, or enlargement of individual parts; of which mode the elongation of the cord in its gangliated portions is evidence; next, that of *aggregation* of two, or more parts, of the same general structure, to form particular regions, or divisions of that structure. Of this latter mode, to which the term *development* has usually been restricted, the union of two or more originally separate segments of the body, as in the changes of insects, of two chambers of the heart, to form a single chamber, as in the Iulidæ, and the coalescence into one mass of two ganglia and their cords, in which the first mode of development, by simple growth, has been completed, are examples, as in the pseudo-changes of the Myriapoda, and the complete metamorphoses of insects. This latter mode of development usually takes place when the former has been carried to its fullest extent, and is induced by changes in the external structures of the body, being entirely peripheral in its origin. It is not restricted to those animals which undergo a complete metamorphosis, but also takes place, to a greater or less extent, in those in which changes are scarcely perceptible, and in which the first mode of development chiefly prevails. It is also in operation in the first-formed parts of the body, while that of extension is predominant in the latter; as in those beings in which the body is formed of a multitude of similar structures successively produced; as in the Myriapoda, in which it is least predominant in the lowest forms, the Iulidæ, but is carried to its greatest extent in this class in the highest, the *Scutigeridæ*; while in another class, the Arachnida, it has attained its maximum in the earliest conditions of the animal, even before it has escaped from the ovum.



Circulatory System in Myriapoda & Arachnida.



Brain and aortic vessels in Bathtur.

Distribution of the on the cord and a

Supra spinal artery ganglion of Scolopendra.

The heart with caudal artery, visceral arteries and distribution.  
 a cephalic thorax of Bathtur &c? natural size.  
 a poison gland of the sting.

Portal System in Bathtur After?  
 magnified 5 diameters.

Digestive apparatus (without the salivary glands and partur aeca) with distribution of the aortic and visceral arteries in Androctonus.  
 magnified 24 diameters.