

XIX. *On the Nervous System of the Sphinx ligustri*, LINN., (Part II.) *during the latter stages of its Pupa and its Imago state; and on the Means by which its Development is effected.* By GEORGE NEWPORT, Esq. Communicated by P. M. ROGET, M.D. Sec. R.S.

Received March 6,—Read June 19, 1834.

IN a former paper* I have described the anatomy of the nervous system of the *Sphinx ligustri*, LINN., and the changes it undergoes during the larva and the earlier stages of the pupa states. In the paper which I now have the honour of laying before the Society, these changes will be followed through the remaining stages, until the insect has arrived at its full development, and I shall endeavour to show the manner in which they are effected.

I. 1. *Of the Pupa.*

We have seen that the nervous system of this insect, during the larva state, is composed of two cerebral ganglia which lie above the œsophagus and dorsal vessel, and eleven ganglia, connected by intervening cords, disposed along the median line of the body, below the œsophagus and alimentary canal. These ganglia and cords undergo considerable changes, both in number, situation, and form, when the insect has entered its pupa state of existence. After these changes have been carried to a certain extent, they appear to be suspended for several weeks, during which the insect remains in a state of hybernation. At the expiration of that period the changes again proceed, and are continued uninterruptedly until the insect has arrived at the perfect state.

In the month of March, when the pupa is becoming more active, all the ganglia of the body are very distinct, and the optic nerves, which proceed from the supra-œsophageal ganglia, and which are soon to equal them in size, are beginning to be enlarged at their base. [Plate XIII. figg. 1 and 2.] The ganglia of the head and thorax have undergone the most alteration. If the nervous system be closely examined at this period, it will be seen that these ganglia and nerves give evidence of still further change. The nerves which supply the wings, and which, up to this period, are each formed by two roots,—one derived from the cord, and one from the ganglion attached to it, as shown in the larva state in my former paper,—are increasing in size, particularly at their base [fig. 2. B.]; while the anterior pair of nerves from the second ganglion, which unite with the second pair from the same ganglion, now originate from the cords, preparatory to the subsequent change in situation of the ganglion itself.

* Philosophical Transactions, 1832, p. 383.

By the middle of April, great progress has been made in the changes which are taking place in all parts of the pupa. The respiratory organs have undergone much alteration; the tracheæ which ramify among the muscles of the thorax being extended in calibre, while some of those from the spiracles along the sides of the abdomen have been gradually developed into pulmonary sacs, which are now of considerable size. Of these there are four upon each side of the body, the anterior ones being much the largest, while the tracheæ in the succeeding segments are also enlarging. The dorsal vessel [Plate XIV. figg. 11. 12. and 13. (*a, a, a*)] has become a much firmer structure; its valves (*b*), the muscles attached to it, and the many vessels which enter it laterally, and carry the circulatory fluid, are more distinct, and its division into several arterial trunks at its termination, anterior to the cerebral ganglia, [fig. 12. (*f*),] is now more easily traced. The muscles of the thorax are also more developed, and certain processes which at first are soft and delicate, and which during the previous months have been in the progress of formation, have now become hard and of a dark colour, like the exterior of the pupa-case. Four of these processes exist along the under surface of the thorax [Plate XIV. fig. 1. (*t, u, v, x*)]. They are developed, as we shall hereafter see, from the duplicatures, or folds, into which the integuments of the thoracic segments are thrown at the period of assuming the pupa state. The anterior one forms the division between the head and collar; the second, [fig. 1. (*v*),] between the collar and thorax, and is posterior to the first pair of legs; the third traverses the thorax, [fig. 1. (*u*),] and serves as an attachment for some of the principal muscles; and the fourth, [fig. 1. (*t*),] or posterior one, is that which in future will constitute the division between the thorax and abdomen, and even at this period of development, before there has been much deposition of earthy matter to form the covering of the future insect, it is continued around the whole segment, and is of firm but transparent texture. By means of these processes we may clearly indicate the situation of the thoracic ganglia at this stage of development. The second subœsophageal ganglion lies between the first two processes, immediately anterior to the first pair of legs. The third ganglion is opposite to the second pair of legs, and anterior to the third process. The fourth and fifth ganglia lie between the inferior pair of wings (*i*) and third pair of legs (*h*), and constitute one mass, which is situated just behind the third process. The sixth ganglion (*m*) is separated from the fifth only by a short extent of cord, is very much decreased in size, and is altered from a circular to an oval form. It is situated upon or immediately behind the division between the thorax and abdomen. The nerves from this ganglion are still disposed irregularly, as at the period of transformation, and the longitudinal cords, which are continued from it into the abdomen, have the ganglia situated as in the previous stages of the pupa.

By the second week in May the future exterior of the perfect insect begins to be formed beneath the common covering of the pupa-case, and in each segment of the abdomen, along the upper surface, on both sides of the dorsal vessel, there is a little

deposit of gelatinous pink-coloured matter, precisely in the situation of the red bands which encircle the body of the perfect insect; but no distinct traces of organization, in the form of scales, can be detected in it, nor have the black bands as yet begun to make their appearance. The nervous system is now about to undergo its final change. There is an evident alteration in the appearance of the ganglia, although they retain the same situation, both in the thorax and abdomen, as in the month of April. The second ganglion is much decreased in size, has become of an oval form, and is not very distinct from the cords themselves. The third, fourth, and fifth ganglia are approaching nearer together, and are tending to form the two portions of the large thoracic mass which exists in the perfect insect, [Plate XIII. fig. 6.] and from which the nerves to the legs and wings are distributed. But the sixth ganglion still lies upon the division between the thorax and abdomen, and its nerves are still disposed in an irregular manner, in consequence of the change that has taken place in the direction of the muscles of the segment to which they are distributed. The other ganglia remain in the same segments of the abdomen as in the previous stages of development. The transverse series of nerves [fig. 1, 2. (*e, h, o, o*), fig. 6. (*o, p*)] have a little shifted their position, and instead of remaining, as in the larva, almost closely attached to the anterior part of the abdominal ganglia, they have moved forwards, and lie nearly equally distant between them; have become more uniform in size through their whole length; and have lost the ganglionic appearance they exhibited during the earlier stages of the pupa state. The cerebral ganglia continue very distinct from each other, while the optic nerves, which proceed from them laterally, are extending in every direction, and are nearly as large as the ganglia from which they are developed. The enlargement has taken place chiefly upon the anterior surface, outwards, forwards, and downwards; but these parts of the nervous system are still very far from being completed. The patch of gelatinous dark-coloured substance which is seen upon the base of the optic nerves, close to the cerebral ganglia, immediately after the Sphinx has entered its pupa state, although up to the present period it has not been increased or extended, has now assumed a distinctly organized appearance, its outlines being clearly defined. Its outer margin is smooth, and continuous with an exceedingly delicate transparent membrane covering the whole surface of the nerve. The interior margin is more distinct, and is corrugated and folded upon itself so as to resemble a partially closed sphincter. It is now removed a little further from the cerebral ganglia, preparatory to its subsequent expansion over the extremity of the visual organ, of which it seems destined to constitute the choroid. It exhibits exactly the same appearance during the development of *Papilio Urticæ*, LINN., [Plate XV. fig. 31. (*c*)] in which I have watched it even more attentively than in the Sphinx.

It is at this period of development that we are enabled to trace with the greatest precision the distribution of the vagus nerve [Plate XIII. fig. 3. (*E. e*)] to the œsophagus (*f, k*) and dorsal vessel (*h, h*), and its connexions with the anterior lateral ganglia

(*g, c.*); and the connexions of these with the cerebral ganglia (*b, A.*), the antennæ (*D. a*), the manducatory nerves (*d*), and the transverse or involuntary series (*c*). At a later period this becomes almost impracticable, owing to the completion of structures among which the nerves of connexion are distributed. Indeed, after this period it becomes more difficult to trace any of the nerves in the anterior part of the body, the whole insect being rapidly approaching to its perfect condition.

By the first week in June the processes which form the division between the thorax and abdomen, and the attachment for the great muscles of the body, are completed. The muscles themselves have acquired a consistency and strength which they have not before possessed; the exterior of the perfect insect is nearly completed beneath the pupa-case; the pink-coloured deposit is extended in the form of little scales over the upper and anterior part of each abdominal segment, and a similar deposit in the form of a black band, but with fewer traces of scales, exists also upon the posterior part of each segment; while the whole under surface of the body is covered with a thick, semi-opaque, greyish-coloured fluid, in which traces of minute scales are very evident. The antennæ, the legs, and the wings, folded in their envelopes beneath the thorax and first segments of the abdomen, are still exceedingly delicate and vascular, and are covered also with scales. The nervous system has now arrived at the last stage of development. During the period between this and the previous stage the optic nerve has been greatly enlarged and extended, and the dark-coloured patch has been expanded over its extremity, and seems now to constitute the choroid membrane. But the eye is not yet completed, although the optic nerve seems very nearly to have arrived at its maximum of development. The exterior portion of the organ, next the pupa-case, the cornea, is still of a transparent gelatinous substance, and the lenses appear to be the last parts of the eye which are completed. The cerebral ganglia are now extended transversely, and form, with the first subœsophageal ganglion, and the enlarged crura which connect them, one continuous mass around the œsophagus and anterior part of the dorsal vessel [Plate XIII. fig. 6. *A.*]. The second ganglion has entirely shifted its position, and receded towards the middle of the thorax, and has coalesced with the third, which has entirely disappeared, and seems to have joined in part with both the second and fourth, and the intervening cords. This aggregation of ganglia and cords [Plate XIII. and XIV. figg. 6. and 8, (2, 3, 4, 5.)] is situated in the middle of the thorax, and supplies all the muscles in that part of the body. The longitudinal cords are continued from the hinder part of the fifth ganglion, and just before leaving the thorax to enter the abdomen they give off the nerves which formerly belonged to the sixth ganglion [fig. 6. (6)], which is now entirely obliterated. The cords then descend into the abdomen, and immediately give off the nerves that belonged to the seventh ganglion, [fig. 6, 7.], which, with part of the cord that existed between the sixth and seventh ganglia, is also obliterated. The cords are then continued in a direct line along the abdomen, the eighth, ninth, tenth, and eleventh ganglia being situated as in the previous stages.

Such is the state of the nervous system at the period antecedent to the development of the perfect insect, which usually takes place about the middle or latter end of June. The time which the *Sphinx ligustri* remains in the pupa state is thus shown to be at least forty-two or forty-three weeks, as nearly as we are able to ascertain, since owing to the eggs not being all deposited in the same week or month, and consequently the larva not produced at exactly the same time, some broods are two, three, or even four weeks later than others.

A few days before the insect is ready to burst from the pupa-case, it becomes exceedingly restless and active, and writhes and turns in its cell repeatedly. That cell—the little hermitage it had constructed in the earth with much assiduity in the preceding autumn, by moistening the soil that was to form the inclosing walls with fluid from its silk-bags, and smoothing and moulding it into shape by rolling and turning its body while the material was yet in a moist condition, and afterwards lining the whole interior with a tissue of silky hangings—is no longer necessary to protect the feeble and delicate pupa from the intrusion of enemies. The insect is now vigorous, and its hard coriaceous covering being scarcely susceptible of injury, it makes a powerful effort to force the walls of its cell, and emerge from its subterranean abode. It gradually works its way upwards to the surface of the ground by repeated contortions of its abdominal segments, assisted by the pointed extension of the twelfth segment of the pupa-case, which serves as a lever against which the power of the insect is exerted. The depth in the ground at which the cell is situated is generally from six to eight inches, very rarely more, so that the insect has not far to travel. But it does not all at once arrive at the surface; its progress is slow and gradual until within a short time before it is ready to burst forth, which is generally in the early part of the day.

During the three days preceding its actual appearance, an alteration, which has for some time been taking place in the exterior of the pupa-case, becomes very evident. The coverings of the eyes, of the antennæ, the legs, and the wings are more convex and prominent, particularly of the latter, which extend on each side the thorax; and the union of the sutures of the approximated coverings of the limbs appear as if about to separate. A few hours previously to the liberation of the insect the coverings of the wings lose their solidity, and upon slight pressure are elastic and yielding, like dried membrane. This is also the case with other parts of the body, but in a much less degree; while the abdominal segments are elongated beyond their original extent. This occurs from the abdominal portion being the first part of the insect that is entirely freed from its attachment within the pupa-case. After this the thoracic portion of the pupa-case becomes fissured along its dorsal line, as well as transversely, behind the head and second segment, and the new-born insect gradually pressing itself through the opening, and carefully withdrawing its limbs from their respective coverings, comes forth with its wings ruffled and small, as if atrophied, but like its whole body completely covered with scales. The insect immediately seeks

a shady situation, where it may suspend itself perpendicularly at rest against a wall or the stem of a tree, and remain unmolested during their complete expansion. This occupies but a short period: in the Butterfly it seldom exceeds more than a few minutes; but in the Sphinx, whose wings are larger and stronger, it is not completed, and the wings fit for flight, in less than two or three hours.

2. *Of the perfect Insect.*—The nervous system of the Sphinx in its perfect condition offers many interesting points for consideration, although it differs but little in its general arrangement from the last stage of the pupa. Thus, there is no further alteration in the cerebral ganglia, nor in those which constitute the thoracic mass, from which nerves to the organs of locomotion are distributed; but the whole are covered in by a new structure, and do not lie, as in the larva, in the open cavity of the thorax. The cords and ganglia are now inclosed on each side between the muscles, from which they are separated by a semi-opaque membrane of a fibrous texture. This extends over their upper surface, and protects them from the œsophagus, which passes along above them. Before the last change in the pupa, in the beginning of June, we can readily trace the distribution of nerves and obliteration of ganglia, but after this period there is considerable difficulty. A very remarkable change, the obliteration of a ganglion in the thorax, occurs just before this period; but it is so rapidly effected, that I have never yet been able to observe it at the actual moment of its occurrence, and hence am unable to state, from positive observation, whether it be the second or third ganglion that disappears. A similar change occurs in *Papilio Urticæ*, LINN., and in this insect it takes place between the forty-eighth and fifty-eighth hour after entering the pupa state; but I have not been more successful in detecting it even in this instance. At first we might suppose it to be the second ganglion that disappears, as we have seen that a change is taking place in it. But this, I believe, is not the case, because the nerves to the two pairs of wings, which originally were each formed by two roots, the first pair [Plate XIII. fig. 1. (*f'*)] by a root from the cord between the second and third ganglion, and another from the third ganglion itself, and the second [fig. 1. (*i*)] pair by one root from the fourth ganglion, and one from the cord between the fourth and the third, become now united. Now were it the second ganglion that becomes obliterated, the origin of the nerves to the first pair of wings would necessarily be anterior to the whole thoracic mass. But instead of there being the third ganglion and cord between the origins of these nerves, as in the larva state, they are now united into two roots, and arise from those portions of the thoracic mass which pass on each side of the central attachment for the muscles [Plates XIII. and XIV. figg. 6. and 8. (*w*)] of the thorax. Each root passes diagonally outwards, the first in a direction backwards [fig. 8. (*a*)], the second in like manner forwards [fig. 8. (*b*)], until meeting each other they unite and form a small plexus [fig. 8. (*c*)], and then again dividing are distributed, the one [fig. 6. (*a*)] to the anterior, the other [fig. 6. (*d*)] to the posterior pair of wings. The reason for this curious union and complexity in the distribution of these nerves to the wings, is not at first very evident, but a little reflection

will show us that it is regulated by evident design, and is one of those beautiful provisions in the animal economy by which harmony in the functions of every part of the body is preserved. The wings, the organs of the most varied and rapid motion, endowed with an equal degree of sensibility and power, are required at every effort of the insect to act in the most perfect unison, and hence must be supplied with their energy from the same centre. That this is the reason for the union of these nerves, is, I think, apparent, from the fact that in the Bee, the Ichneumon, and other hymenopterous insects remarkable for their velocity and power of flight, the nerves to the wings originate almost precisely in the same manner as in the Sphinx and its affinities; while in others, as in the *Panorpa communis*, LINN., or Scorpion Fly, they originate by double-rooted pairs, just as in the larva of the Sphinx; and the insect is neither remarkable for its velocity nor equability of motion. And it may be further stated, that in winged coleopterous insects, in which the wing-covers are merely elevated, and are motionless during flight, the wings alone being actively employed, the nerves to the two organs are not always united, but often originate separately from the great nervous centres, and are continued to their distribution as separate trunks, like the nerves to the legs or the antennæ.

The cords in the abdomen of the Sphinx in its perfect state, like those of the thorax, are covered in by a curious structure, of the exact nature of which it is difficult to form a conclusion. It is spread over the whole like a broad riband [Plate XIV. fig. 9. (a)], from their commencement in the first, to their termination in the antepenultimate segment, and seems to bind down and protect the cords and ganglia in their course along the abdomen, whatever other office it may be thought to perform. The ganglia, and the nerves distributed from them, scarcely differ from those of the pupa, excepting only the two anterior pairs from the terminal ganglion. These, in the female Sphinx, are very much elongated, and are enfolded around the ovarial tubes and organs of generation, among which they are distributed. With a little care they can be easily separated from them. The terminal pair of nerves, as in other insects, is distributed conjointly to the rectum and organs of generation.

Besides the nerves and ganglia which constitute the symmetrical parts of the system, there are others, including those of the head and mouth, that require more particular notice. They are arranged in two classes: 1. *Nerves of the senses*; 2. *Nerves of involuntary functions*.

II. 1. *Nerves of the Senses.*

a. Nerves of the Antennæ.—These, in the Sphinx and other *Lepidoptera*, originate each by a single root from the anterior part of the cerebral ganglia, close to the base of the optic nerves. After entering the base of the antennæ they give off a considerable number of branches; but the real nature of the organs themselves is yet undetermined. It is evident that they are endowed with the sense of touch, and are used by many insects, Grasshoppers, Beetles, &c., as cerebral feelers. The structure of the antennæ

in the Sphinx, in which the under surface of each joint is encircled by a double ring of exceedingly delicate elastic cilia [Plate XIV. figg. 17, 18. (a)], seems more fitted for *feeling*, or perceiving the vibrations of the atmosphere, and thereby for performing a function analogous to that of hearing, as has been suggested by BONSDORF, CAMPARETTI, and other naturalists, than for any other with which we are acquainted. The sense of touch is evidently the primary endowment of the antennæ in articulated animals, as seen in the Myriapods; but this cannot be their use in many insects, *Libellulæ*, *Diptera*, &c., in which they are short and immoveable, nor in those *Coleoptera* in which they are terminated by lamellæ; while their structure in almost every class is totally incompatible with the function of smelling. But there is no class in which their structure could incapacitate them for feeling the pulsations of the atmosphere, and thereby performing a function analogous to that of hearing.

b. Nerves of Vision.—The compound eyes of insects are parts of great interest, but of difficult investigation. PROFESSOR MULLER, STRAUS-DURCKHEIM, and others have carefully examined them, but there is still a difference of opinion respecting their real structure. I have not yet sufficiently examined them to offer an opinion, my attention having been confined chiefly to the development of the optic nerves themselves, during the transformations of the insect. This can only be shown in those insects which have simple sessile eyes in their larva state, and numerous compound ones in their perfect, as in *Lepidoptera*, *Hymenoptera*, and some other genera. In the larva of the Sphinx the optic nerves are only two diminutive trunks, extending from the sides of the cerebral ganglia, and dividing each into eight filaments, given to the eight minute eyes on each side of the head. At the period of changing to the pupa state there is a deposit of dark pigment, very slightly organized, at the base of each nerve. As the changes of the insect advance, the optic nerves gradually enlarge at their base; and when this enlargement has gone on to a considerable extent, the dark pigment is carried forwards from the base of the nerves, and exhibits a corrugated appearance around its interior margin. When the changes have further advanced, the optic nerves are extended, of a pear-like form, from the sides of the cerebral ganglia, which they then equal in diameter. The enlargement of the nerves seems to be occasioned by the shortening of the cords which connect the cerebral with the subœsophageal ganglia, and the extension forwards of the nervous substance of the cords within the investing theca, the effect of which is not to enlarge the cerebral ganglia in a corresponding degree, but to develop the optic nerves, by the gradual extension and expansion of the nervous substance within them, in the form of successive series of purse-like layers of fibres [Plate XV. fig. 31. B.] one within the other. When the outer layer has arrived at its maximum of extension, it seems to become perforated at a point corresponding to the central part of the membrane, which is carried forward to become the choroid [fig. 31. (c.)]. The next layer advances, and then the next in succession from within outwards, so that the central portion of the nerve is the last part developed. The fibres of each series, from being bent like the segment of an arc,

gradually assume a more lineal direction, and diverging from the axis of the eye, the whole nerve, when completed, forms a series of flattened pear-shaped cones, one within the other, the apices of which constitute the base or origin of the nerve next the cerebral ganglia. The eye of the Sphinx, when perfect, being convex, the outer or first completed series of fibres is the shortest, while each succeeding series is longer and less earlier perfected in proportion to its distance from the circumference, so that the central fibres are the longest and last developed. Thus the same law which regulates the development of the osseous structure, as shown by DUTROCHET in the vertebræ of the frog, regulates that of the ganglia and nerves. The common covering of the optic nerve is formed of an extension of the theca which covers the cerebral and subœsophageal ganglia and nerves, and through which the ramifications of tracheal vessels penetrate in considerable abundance. In the optic nerve, in particular, they are very numerous; and I have never yet been able to detect their terminations, or to discover any other description of vessels in the nerves or ganglia, although there is scarcely a doubt that others do really exist.

It is difficult to observe the radii of the optic nerve in the Sphinx, owing to the size and opacity of the part; but the sacculi of nervous matter are beautifully seen in the nerve of the eye of *Papilio Urticæ*, LINN., at about forty-eight hours after changing to the pupa state. It is necessary to remove the nerve with the cerebral ganglia from the head of the insect, and view it with a good lens by intense transmitted sun-light [Plate XV. fig. 31.].

c. Nerves of the Mouth and its parts.—These originate from the first subœsophageal ganglion, and from the crura which unite it with the cerebral ganglia. In the larva they supply the mandibles, palpi, and pharyngeal region; and in the perfect insect the two halves of the flexible and delicate proboscis, the structure and muscles of which, in order to show the arrangement of its nerves, I must briefly notice. This organ in the perfect *Lepidoptera* has recently been described by Mr. NEWMAN* in his Letters on the External Anatomy of Insects, and is shown to be analogous to the maxillæ, or lesser jaws. It is situated, in the larva, beneath the strong mandibles, which in the perfect state are obsolete, and exist only as very minute parts on each side its connexion with the head. It is an elongated, tapering, flexible organ, composed of two symmetrical halves, placed laterally together, convex on their external, and concave on their internal surface [Plate XIV. fig. 15. *a, b.*], and by their approximation forming a tube to the mouth, which is nearly of the same size through its whole length, excepting at the tip, where it is a little smaller. Each half is slightly ciliated externally, and along the whole anterior margin of its concave surface is furnished with a row of minute hooks, and near the tip, along its anterior and external surface, with a number of little elongated papillæ, which, probably, are organs of taste. In a state of rest, the proboscis is rolled up spirally between the labial palpi;

* Entomological Magazine, Part VI., January 1834.

and at its base, in some *Lepidoptera*, there are small maxillary palpi. It is connected above with the triangular arch or palate, the epipharynx*, which forms the roof of the mouth, and below with the hypopharynx, or analogue of the tongue, which forms the floor of the mouth, and conducts to the œsophagus. The mouth is only a dilated cavity between the proboscis and commencement of the œsophagus [fig. 15. c.]. Each half of the proboscis is furnished with two kinds of muscles, longitudinal and transverse, acting as flexors and extensors. The transverse muscles consist of many short semicircular fibres, which encircle the exterior of the proboscis [fig. 16. (c. c).] and are attached along the margin of the inner or grooved surface of the organ, which by their contraction they tend to elongate. These muscles are exceedingly small and numerous, and amount to at least one thousand in each half of the organ. They are assisted in their action as extensors by one of the longitudinal muscles (*b*), which arises within the anterior of the cranium, and is attached by a multitude of fibres, inserted at very acute angles along the anterior margin of the groove. This muscle, in conjunction with the circular ones, acts as a powerful elongator of the proboscis at the instant of taking food. The other two longitudinal muscles are flexors (*a, a*). One of these, the direct antagonist of the first, arises from the under surface of the head, and is inserted along the inferior margin of the groove, and assists in rolling up the organ. The other, a more powerful flexor than the last, is the largest of the three longitudinal muscles. It arises from the lateral and under surface of the head, and is attached to the inner surface of the exterior, or most convex part of the organ, by many long fibres inserted at very acute angles into a slight tendinous ridge, so as to compose one large penniform muscle [fig. 16. (*a*).]. Each half of the proboscis is also supplied with one large and one small tracheal vessel [Plate XV. fig. 19. (*f. h*)], derived from those of the head (*g*). These extend from one end of the organ to the other, giving off numerous branches, and gradually decrease in size, and distribute longer, and a greater number of branches the nearer they approach the end of the organ, so that, as in other parts of the body, they are lost in the surrounding structures. The nerves of the proboscis extend along the course of the tracheal vessels (*a, b, c, d, e*). In the larva we have seen that the nerves to the mandibles come from the anterior of the subœsophageal ganglion [Plate XV. fig. 34. (1. *f*).]; and the same is the case with the nerves of the proboscis in the perfect insect [Plate XIV. fig. 10. (*a. 1*).]. The nerves of this organ in the larva are of inferior size; in the perfect insect they are largely developed. They originate on each side the subœsophageal ganglion as single trunks, one to each half of the organ. Immediately the nerve has entered the hinge anterior to the mouth, it is divided into four branches. One of these (*b*) passes backwards, apparently to the palpus, and others forwards into the organ. The innermost branch (*c*) is small, and gives off very minute filaments. It passes in a direct line immediately beneath the grooved or mucous surface between it and the large trachea, and does

* NEWMAN.

not appear to give filaments to the muscles; while the main branch (*d*) of the nerve passes exterior to the tracheal vessels, and seems to be given chiefly to the flexor muscles, which lie along the exterior of the organ. The course of the fourth nerve (*c*) I have not distinctly traced; it appears to run along the smaller flexor. Now there are two pairs of nerves which exist in the larva, and come from the crura, near the base of the cerebral ganglia, just below the origin of the pneumogastric, which I have been unable to discover in the perfect insect. I suspect, therefore, that these nerves, during the development of the insect, have united with the mandibular and maxillary to form the large trunk to the proboscis. This appears probable, as I shall presently show that coalescence of nerves actually does take place, and that the nerves belonging to the subœsophageal ganglion are forced upwards during the development, so as to appear as if coming from the lower part of the crura [Plate XIII. fig. 7. (1)] on each side the pharynx. If this be correct, a question arises, What are their functions? The larger branch given to the muscles, chiefly the flexors, is clearly analogous to the great mandibular nerve of *Vertebrata*; and it is not unreasonable to suppose that the small branch which passes along the groove of the proboscis, where an exquisite sensibility of taste is required, may be analogous to the gustatory, and in the larva be one of those nerves which are distributed around the mouth and palate. This opinion is further supported by the nerves originating in the larva just below the pneumogastric, and above the subœsophageal, ganglion, which ganglion, in the perfect insect, gives the nerve to the proboscis. Now this is in perfect accordance with, and beautifully illustrates, the philosophic views of Sir CHARLES BELL, who has shown that every portion of an organized being is supplied with an additional set of nerves for every additional function it is required to perform. In the larva, the mandibles are hard and powerful, requiring, probably, little more than simple sensation and motion. But in the perfect insect, the proboscis is delicate and flexible, and, so far as we are enabled to judge, highly susceptible of impressions, one of which, doubtless, is taste.

II. 2. *Nerves of Involuntary Function.*

a. The Vagus, or Pneumogastric.—This nerve, the *recurrent* of LYONET, originates immediately above those nerves which seem to have united with the manducatory. It has been shown to arise by two roots, [Plate XIII. fig. 3. (*e*),] one from each crus. These, after passing forwards and uniting in a ganglion in the middle line above the palate, run backwards, as a single trunk, [*e*, *f*,] beneath the cerebral ganglia, the brain, between the dorsal vessel and œsophagus. Just at entering, and for a short distance within the thorax, it gives off filaments to the dorsal vessel [fig. 3. (*h*, *h*)], while the main trunk passes along the middle of the œsophagus, unto which it distributes filaments, until it arrives at the cardiac portion of the stomach, [fig. 3. (*i*),] where it gives a few filaments to the air-bag, or crop, and then divides into three branches, which run along the middle and sides of the stomach, and are again subdivided and distributed

around it. The ganglion at the union of the roots of this nerve distributes a few filaments from its anterior surface, forwards upon the palate, and apparently also to the extremity of the dorsal vessel, which, after passing along the œsophagus beneath the brain, here divides into several trunks. Two of these pass downwards, one on each side the œsophagus, to the proboscis, others outwards, and others upwards, to the eyes, antennæ, and front part of the head. Behind the brain, within the region of the head, the vagus is connected by a branch on each side with the anterior lateral ganglia (*g*), which are also connected with the superadded or transverse series (*c*). The constancy of its existence, and the situation and distribution of the vagus, in insects, are points of deep interest for consideration. I have never found it in any other situation than that which it occupies in the *Sphinx ligustri*. These are positive indications of the analogy it bears to the great pneumogastric nerve in *Vertebrata* *. It is clear that it ministers to a very important function, the involuntary motions of the stomach and alimentary canal, which are as distinct and as constant as in the *Vertebrata*. Yet we find an exceedingly large ganglion at its origin (*ε*); and the remains of this ganglion may be traced upwards through fishes, reptiles, and mammalia, to man himself, in whom we have it remaining only as a slight enlargement. What, then, is the office of this ganglion? Does it communicate sensation to the parts, or is the ganglion merely a great centre of nervous energy, ministering to the involuntary functions of the alimentary canal, the place of which in the higher animals is probably supplied by a more perfect development of the sympathetic system? The interest of this consideration is increased, from the circumstance, that even while the insect is in some of its earlier stages, before there is a complete approximation of the lateral cords and ganglia of the body, and even previous to the development of the organs of locomotion, as in the Bee, the ganglion of the vagus is nearly as perfect in form as when the insect has passed through all its changes. In the maggot or larva of the Wild Bee, (*Anthophora retusa*, KIRBY,) where the whole of the nervous system is exceedingly transparent, the ganglion is as complete as in the more organized and active caterpillars, and the same is the case in the larva of *Chrysomela tenebricosa*, LINN., and other species. In the latter insect it distributes several branches posteriorly to the sides of the œsophagus and pharynx, [Plate XIII. fig. 4. (*c, c*),] besides the nervous trunk (*d*), which passes backwards to the stomach, and which in its course becomes somewhat enlarged (*b*). In the perfect insect of the same species [fig. 5.], its form and situation are the same. In the same insect we have also remaining the nerves of taste (*e, e*). The general figure of the ganglion of the vagus is heart-shaped, or triangular, with the apex directed backwards; but in the ground beetle, *Carabus*, LINN., it is elongated oval, lying transversely above the palate. It is interesting to remark that the vagus always originates from the crura, immediately below the cerebral ganglia or brain; and even in *Crustacea* we find it still arising from the crura [Plate XVII. fig. 40. (*d, d*)]. Now from this uniformity of origin, its possessing a ganglion, and its distribution to an organ endowed

* Philosophical Transactions, 1832, p. 386.

with involuntary motion, there is reason to believe that it is a compound structure, and partakes both of the motor and sensitive principle, but of an involuntary nature, and not therefore belonging to the symmetrical system.

b. Anterior lateral Ganglia.—The size of these ganglia, relatively to that of the cerebral ganglia, is very considerable [Plate XIII. fig. 3. (a)]; and hence, doubtless, STRAUS-DURCKHEIM was induced to call them “accessories of the brain.” In the larva and pupa of the Sphinx, they are situated behind the brain, one on each side of the upper part of the œsophagus, anterior to a pair of large constrictor muscles [Plate XIV. fig. 14. (h)], which are attached to the lateral posterior part of the head. Their connexions are remarkable: they occupy an intermediate situation between all the different nerves in this part of the body. A large nerve on each side the head connects the ganglia with the brain, and a small branch which passes transversely connects this nerve with the pneumogastric. Another nerve passes direct from the ganglion, and connects it with the transverse or superadded series. Other small filaments pass outwards laterally from the ganglion to the surrounding structures; and, lastly, there is a nerve which runs forward from the ganglion beneath the optic lobes, and forms connexions with the nerves to the antennæ and proboscis. Here, then, we have a series of connexions which seem to indicate the real nature of the ganglia, and their analogy with the superior cervical ganglia of the sympathetic system in vertebrated animals. Indeed, it is in these highly organized *Invertebrata* that we might expect to find a distinct sympathetic system, seeing that as we ascend in the scale of creation, from the *Polypifera*, or half-vegetative beings, to the most perfect animals, in proportion to the number, variety and importance of the functions to be performed, the number, extent, and complexity of structures are increased, and are more dependent upon each other, and every part of the body is less and less capable of maintaining for itself a separate existence.

c. The Transverse, Superadded, or Respiratory Nerves.—These nerves have for a long time engaged the attention of naturalists, and have been delineated by LYONET, HEROLDT, and others; but their true function has never been established*. There is a point of interest attaching itself to these nerves greater than to any others in the whole system of the insect. Hitherto there has been no distinct analogy shown between the nervous system of the vertebrated and that of the invertebrated classes in the possession of two series of nerves, the one for motion and the other for sensation; and it has been imagined by some that these transverse nerves may perhaps be analogous to the motor, while the longitudinal cords and ganglia are analogous to the gangliated sensitive system. Others believe the transverse nerves of insects are analogous to the true visceral or sympathetic. Perhaps I may be excused, therefore, for entering somewhat at length upon their distribution and structure.

* I have called these nerves *transverse*, from the direction of their principal branches; *superadded*, from their being nerves given to muscles, in addition to nerves from the moto-sensitive or spinal cords; and *respiratory*, from their distribution being chiefly to muscles which appear to be most concerned in respiration.

In the larva and pupa of the Sphinx, we have seen that these transverse nerves divide and distribute their branches anterior to every ganglion. In the thoracic segments, some of their branches [Plate XIII. fig. 2. (*e, h*)] unite with nerves which are already formed by two roots (*f, i*), one from the cords and the other from a ganglion, and which are destined for the future wings. In the abdomen, after giving some very small filaments to the nerves from the gangliated cords, they are distributed to the muscles of the segments, in addition to the nerves derived from the gangliated cords, and which, there is reason to believe, are compound nerves, and communicate both sensation and motion. I am therefore inclined to regard the transverse as super-added nerves, analogous to the respiratory nerves of the higher animals. In my former paper upon the Sphinx in its larva state, these nerves were believed to be arranged in distinct series, originating separately from the posterior part of each ganglion. Subsequent examinations have convinced me that the whole form one continuous system [Plate XVI. fig. 35. (*c*)], and do not originate separately by single tracts from the ganglia, but, as suspected and suggested to me by Professor GRANT, pass over the ganglia (*h*), and are continued along the median line between the cords (*k*) until they divide (*c, c*), to be distributed to the tracheæ and muscles. They are formed of three series of fibres, two of which are closely approximated, so as to look like a single tract [Plate XVI. fig. 35. (*k*)]. This comes down between the cords until it arrives just before a ganglion (*h*), where it divides nearly at right angles, and unites with the third series, which runs transversely across the body of the insect. A filament from each division (*h, h*) passes over the outer margin of the upper surface of the ganglion; then, converging again to the middle line, meets with its fellow from the opposite side: and these two filaments unite, and form one tract, after each filament has received a few fibres (*i, i*) from the upper or motor surface of the cords. The fibres thus united pass along the groove formed between the cords until they arrive at the next ganglion, where they divide, and distribute again as before. Each transverse series, besides the filament which passes over the ganglion, gives also a filament to the great or moto-sensitive nerve (*g, f*), which comes from the gangliated cords, and is distributed to the different parts of the segment. The terminal pair of nerves of this series is always distributed to the rectum, near its termination, in addition to the last pair of compound nerves from the last great ganglion.

I have found these nerves taking nearly the same origin and course in the abdomen of the large green Grasshopper (*Gryllus viridissimus*, LINN.). After the united filaments in this insect have passed along the median line, or groove, between the cords, [Plate XVI. fig. 39.] and arrived above a ganglion, they gradually diverge at an acute angle, and not abruptly as in the larva of the Sphinx. Each division gives a filament to a small nerve, which runs to the diagonal muscles of the segment (*c*), and which does not originate from the ganglion, but from the upper surface of the cord, or motor tract, which is passing over it, and is probably a motor nerve. The filaments then

converge, as in the Sphinx; and, in passing along the cords, gather a few filaments from the motor tract of each, and after uniting in the middle line pass backwards to the next ganglion, to be distributed as before. In this species it is curious that the superadded nerves do not seem to unite with the great moto-sensitive nerve, but only with the small nerve behind it, which is given to muscles that, acting diagonally, seem to be much concerned in the function of respiration. But there are facts which might at first incline us to believe that these transverse nerves constitute the visceral or true sympathetic system in insects. Thus, their union with most of the nerves of the body; their connexion with the anterior lateral ganglia; the manner in which they receive additional filaments from the cords; and the existence of a ganglion upon the terminal filament in the *Gryllus vividissimus*, LINN. [Plate XVI. fig. 39. (c, b),]; and, above all, the existence of clearly defined ganglia at each distribution in the *Carabi* [fig. 38. (c),], or ground Beetles, and in the Mole Cricket, *Gryllotalpa*, in which the ganglia are very distinct, and situated above the great ganglions of the cords. On the other hand, it is only in a few genera of insects that these ganglia exist; and it has not yet been proved that respiratory nerves must necessarily be without ganglia. Indeed, it is not improbable that we may hereafter find a much closer connexion between the respiratory and sympathetic systems in the higher animals than has hitherto been imagined. Now the existence of ganglia upon these nerves, although in but a few genera, seems very decidedly to prove that they are not analogous to the simple motor nerves of the body, while their distribution being almost entirely to muscle, and but sparingly to the viscera, seems as clearly to show that they are not analogous to the sympathetic or visceral nerves of *Vertebrata*.

To prove more directly that these nerves are not simply those of motion, but are for the involuntary function of respiration, we must examine the means by which respiration in insects is performed. Nine pairs of spiracles, or breathing orifices, are placed in the larva along the sides of the body. Eight of these are in regular succession. They all communicate with longitudinal tracheæ, from which several large ramifying branches pass off transversely, nearly opposite to each spiracle. The longitudinal tracheæ extend from one end of the body to the other, and communicate freely with the spiracles. A similar arrangement of the tracheæ and spiracles exists in the perfect insect, but with this difference,—in the anterior part of the abdominal region, those parts which in the larva are ramifying tracheal tubes, are now altered in structure, some of them being developed into pulmonary sacs or bags, while in the thorax the tracheæ themselves are larger than those in the abdomen, and the spiracles are larger, and of a different form. In the thorax, and first pair in the abdomen, they are either elongated, semioval, or straight. The remainder of the abdominal ones are oval. The spiracles are acted upon by two sets of muscles, the one diagonal, and the other oval. The latter act the part of sphincters, the former are connected with the muscles of the segment. REAUMUR, BONNET, and others have clearly proved that the anterior pairs of spiracles in the larva (those of the collar and thorax in the per-

fect state) are of the greatest importance to the insect ; since if these be closed, the insect soon becomes asphyxiated when placed under water ; but if the anterior spiracles be left exposed while the remaining ones are submerged, it will live, and remain active for a great length of time. Their importance is also shown in their form and size in the perfect insect. It is in the anterior, this very part of the body, that we find the greatest abundance and complexity of respiratory nerves, even in the larva, where there scarcely seems more occasion for a greater number of respiratory nerves than in the abdominal segments. It is around the spiracles in this part that the respiratory nerves divide, and pass to many muscles which are associated with those of the spiracles in the function of respiration in the perfect insect ; and these are muscles which are to act upon the future wings. Now the action of these very muscles, which elevate and expand the wings at the instant of flight, is an act of inspiration, during which the spiracles are opened, and the air, rushing into them, fills the air-bags and tracheæ over the whole body, just the same as in birds, as remarked by Professor GRANT, the muscles of the chest and wings are associated simultaneously in action with those of the glottis and tracheæ, and exactly the same as the arms and muscles of the chest in man, and the anterior extremities and muscles of the chest in quadrupeds, are influenced at the instant of making any sudden or great exertion.

It is also remarkable that these nerves in general appear to be developed in size in proportion to the quantity of respiration of the insect. Thus, in the larva of the Blood Beetle, *Chrysomela tenebricosa*, LINN., and in the *Carabi*, they are exceedingly small ; while in the Sphinx and other insects that are capable of powerful and long-continued flight, respire large quantities of atmospheric air, and have the organs of respiration exceedingly large, they have arrived at their maximum of development.

During the development of the Sphinx, the respiratory nerves undergo a curious change of situation, which certainly indicates that they are not simply nerves of motion, but are for an especial function. In the larva they are situated very close to the anterior part of the ganglia, but in the perfect insect they have moved forwards very nearly half way between the ganglia. Now it is well known that during development there is a tendency in nerves to approach and unite with each other, the lateral cords and ganglia are more closely approximated, and the ganglia in the anterior part of the body approach and coalesce into one mass. But instead of all the transverse nerves uniting with the nerves from the ganglia, which, had they been simple nerves of motion, we should expect they would have done, we find them in the abdomen, carried forwards in the segments, and distributed separately to the same muscles as those from the ganglia.

Another striking fact indicative of their separate function is their being distributed largely, even in the larva, to the double rooted nerves for the future wings, and but slightly, so far as can be discovered, to the primary organs of locomotion, the legs. The nerves to the legs come directly from the gangliated cords, and communicate

both the motor and sensitive influence; the legs themselves are but little concerned in the function of respiration, and consequently are but slightly supplied with nerves from the superadded series. But the nerves to the wings, being already formed of two roots, could hardly require an additional one, were it not for some especial purpose, and did not each root confer a distinct endowment.

In addition to all that has yet been stated respecting the superadded nerves, there is a curious fact relating to the terminal pair, which seems further to prove that they are not simply nerves of motion. These nerves in the Sphinx, and all other insects, and in *Crustacea*, [Plate XVII. fig. 40. (r)] are given, as before stated, to the rectum, in addition to the terminal pair from the last great ganglion of the cords, and end in the sphincter muscles. Now if these were simple motor nerves, we should expect that they would be approximated to the terminal pair, which come directly from the last great ganglion of the cords, instead of merely passing along parallel with them, and ending separately, although in the same structures, viz. the sphincter and levator muscles of the anus. But it may be said that this does not prove them to be other than simple motor nerves, or that the nerves from the ganglion communicate both sensation and motion. This objection is clearly answered, and the terminal nerves from the last great ganglion of the cords are shown to communicate motion as well as sensation, from their distribution in the male of the Wild Bee before noticed, *Anthophora retusa*, KIRBY. This insect, which I have taken with its partner in coitu, has the male organ of generation terminating in a forcipated claw, which passes out beneath the anus by the same orifice. With this claw the male firmly seizes and attaches himself to the vagina of the female during the period of coition, which lasts only for a few seconds. The organ must therefore be endowed both with sensation and motion. Now the terminal pair of nerves from the ganglion, after passing backwards for some distance, divide into two branches, one of which ascends, and is given to the rectum, and levator, and sphincter muscles of the anus, which also receive in addition the terminal pair of nerves from the superadded series, while the other branch is entirely distributed to the male organ, and appears to be the only large nerve which is given to that part; so that the last pair of nerves from the terminal ganglion are directly proved to communicate both sensation and motion, and therefore must be of compound structure; while the last pair of the transverse series are as clearly shown to be superadded nerves.

II. 3. *Structure of the Cords, Nerves, and Ganglia.*

a. It has been admirably proved by Sir CHARLES BELL, in his series of experiments upon the nervous system in vertebrated animals, detailed in the papers submitted by him to the Royal Society, that, as regards the physical condition of the being, different parts of the spinal column are endowed with different properties, and minister to different functions—volition, sensation, and involuntary motion. The same train of reasoning which led that distinguished philosopher to the discovery of these facts

in the higher animals, must long ago have taught us, That since the laws of nature are simple and uniform, the same principle exists through the whole series of animated beings;—that however altered in arrangement or appearance in different parts of the series, structures corresponding to those which are endowed with especial properties in Man, and his immediate affinities, exist in every organized creature having the powers of locomotion and sensation. Yet however certain this principle must have appeared to every reflecting mind, we have not until recently been able to distinguish in invertebrated animals the particular structures from one another, and to show their analogy with similar structures of the nervous system in the vertebrated. Some, therefore, have imagined that the gangliated cords of the *Invertebrata* are simple structures, communicating both sensation and motion. This, however, I shall endeavour to show is not the case.

It was during the early part of the summer of 1833 that I first had an opportunity of conversing with Sir CHARLES BELL respecting the nervous system of insects, when he suggested a closer examination of the cords than I had then made, to ascertain whether a double nervous column, one portion for sensation, and the other for motion, exists in the *Invertebrata*, as in the higher animals. He at the same time pointed out one of the *Crustacea*, the Lobster (*Astacus marinus*, LEACH), as perhaps the most eligible for the inquiry. At that time I had no hopes of succeeding in demonstrating the parts by dissection, although I believed they really did exist. In the month of August, after many dissections and examinations of the animal in its recent state, I began first to hope for success; and in the beginning of September completed a preparation of the nervous system of the Lobster, which I still possess, that appeared to show the two motor and sensitive columns, and I immediately communicated the circumstance to my friend Dr. MARSHALL HALL. Early in October a second preparation was completed, which showed these columns far more distinctly than the first. Fearing the possibility of mistake, I showed the preparation to Dr. HALL, a few weeks afterwards to Professor GRANT, and many others: it is now in the possession of Sir CHARLES BELL.

The nervous system of *Crustacea* has been examined by many anatomists, EDWARDS, CARUS, HOME, and others. In the Lobster it is formed upon the same general plan as that of insects. It consists of two longitudinal cords, corresponding to the two halves of the body, united at certain distances by ganglia [Plate XVII. fig. 40. (1 to 14.)]. These cords are double, each being composed of two tracts, lying one over the other [fig. 42. (*u, v*)], analogous to the motor and sensitive tracts in the spinal column of *Vertebrata*. These tracts, however, are not readily distinguished until after the cords have been kept for a short time in alcohol, when they become very evident even to the naked eye. The ganglia [figg. 40, 41, 42. (*u, v*)] are fourteen in number, one cerebral (A), and thirteen subœsophageal (c, d). Seven of these are thoracic (c), and the remainder are post-abdominal or caudal ganglia (d). They all belong entirely to the sensitive tract, which lies nearest to the under or exterior surface of the animal. The tracts are in

close apposition until they arrive at a ganglion. The motor then becomes more distinct, and passes over the ganglion without uniting with it, and immediately afterwards is again closely approximated to the sensitive. A distinct line between the two tracts extends along the whole lateral surface of each cord, and is more or less evident in different parts of its course. It will thus be seen that the ganglia are situated almost entirely along the under surface of the cords, and it is from these that the sensitive* portion of the double or symmetrical nerves (*o, o, o, o, o,*) of the body take their origin. The manner in which the nerves from the motor tract unite with those from the ganglia of the sensitive in the Lobster, to form these symmetrical nerves, is not at first very apparent. Upon close examination it seems to be by fibres coming off laterally from the motor tract, just above the anterior margin of each ganglion, passing backwards and outwards, and immediately uniting with those from the ganglion into distinct trunks. The ganglia in the thorax are rounder, larger, and closer together than the caudal or post-abdominal ones, and give nerves to the true organs of motion, the legs; to the claws, mandibles, and feelers; to the glandular structures, and the circulatory vessels in the branchiæ and thorax. The caudal ganglia are of a much smaller size, and are of an oval shape. Each of these gives off two pairs of nerves (*o, o*), which again divide into two branches, and pass outwards close to the under surface of the body, supplying the large trunks of circulatory vessels which pass along the same course with them, and the external layer of muscles. The posterior division of the second pair from each ganglion is larger than the others, in consequence of its again dividing into two branches as soon as it reaches the lateral margin of the body. The largest of these branches (*p, p*) descends to supply the muscles of the false feet, the other ascends to those of the lateral surface of the segments. This is analogous to the means by which the false feet are supplied in the larva of *Sphinx ligustri*, and other Lepidopterous insects, in all of which they are supplied from the ganglia in the abdominal region, which are analogous to the post-abdominal of the Lobster. The terminal ganglion [Plate XVII. fig. 40. (14.)] is the largest, and gives off four pairs of large nerves, and, as in insects, was originally formed of two ganglia. The two terminal nerves (*s*) from this ganglion, which has coalesced longitudinally, pass on each side the rectum, and divide each into two branches. The terminal branch supplies, and is entirely lost, in the rectum and sphincter ani, and the other supplies the muscles which elevate and expand the anus

* While engaged upon the anatomy of the Lobster I obtained a large living specimen, which, although apparently vigorous and healthy, appeared to suffer but very little pain when pricked or pinched, and was of a much lighter colour than usual, its whole covering being quite blue, instead of the usual blackish purple. Upon killing the animal and examining its spinal cords, the motor columns and nerves were of the usual size and appearance, but all the ganglia of the sensitive columns, particularly those in the post-abdominal region, were exceedingly small, and each inclosed only a very small nodule of grey matter. May we not infer from this fact, that the degree of sensation in the nerves belonging to the spinal column very much depends upon the size of the ganglia and the quantity of grey matter they contain?

in the expulsion of fæces, and the middle lamella of the tail, in which the anus is situated. The remaining pairs of nerves (*w*) are given to the other lamellæ of the tail.

All the nerves I have now described in the Lobster belong to what Sir CHARLES BELL calls the regular or symmetrical, and come directly from ganglia; but there are others [fig. 40. (*q, q, q*)], which come directly from the upper surface of the cords, unconnected with those from ganglia. In the caudal region there are two sets of these posterior to each ganglion. They arise from the tracts by single trunks, each dividing into five or six branches, that ramify in every direction, and are given entirely to the muscles. Although at first sight they appear to form ganglionic enlargements (*q, q*) before dividing into branches, there are no ganglia upon them. This appearance is occasioned by the approximated fibres which constitute the trunk being spread out, instead of rounded like a cord. The two last of these nerves (*r*) originate singly from the tracts, and are given to the under surface of the rectum. In the thoracic region they come from the tracts [Plate XVII. figg. 40. and 42. (*l, l*)] immediately above the posterior part of the ganglia, and are given to the muscles of the branchiæ.

The detection of a double spinal column in the Lobster has since led me to examine more closely the nervous system of the Scorpion, one of the *Arachnida* (*Scorpio europæus*, LINN.). Upon showing my dissection of the Lobster to Professor GRANT, he directed my attention to a structure observed in the Scorpion by Professor MÜLLER, of Bonn, which has been thought to be the motor tract. This structure I had not at that time observed. It consists of a straight narrow slip, or riband, extending along the median line, above the cords and ganglia, from the great thoracic mass, over which it is expanded, to the last caudal ganglion, and is nearly of uniform size through its whole length. It is connected by some exceedingly small fibres with the nerves, while passing over the ganglia, and is, I believe, analogous to the transverse or involuntary nerves of insects. The true motor tract appears to be closely adherent to the sensitive in the Scorpion, the same as in the Lobster, and is scarcely observable even where it passes over a ganglion. It is nearly equal in size to the sensitive, with which it is connected. The nerves given off unite with those from the ganglia, just the same as in the Lobster.

The double structure of the nervous cords is more distinctly seen in one of the *Myriapoda* (*Scolopendra morsitans*, LINN.) [Plate XVII. fig. 43.] than in the Scorpion. The two longitudinal cords are united by twenty-three ganglia, and are composed of two tracts [figg. 44. and 45. (*a, b*)], lying one over the other, as in the Lobster and Scorpion. The ganglia are entirely on the under surface of the cords [Plate XVII. fig. 47. (*a*)], and the existence of the motor tract is very evident after it has been for some time in alcohol. It is marked by a line [fig. 47. (*d*)] which passes laterally over the ganglia, and is continued along the lateral surface of the cords. The nerves from the motor tract come off as filaments, anterior to those from the ganglion, with which they immediately unite. Four pairs of nerves are given off from each ganglion, and a fifth pair passes off from the motor tract [fig. 46. (*e*)] immediately posterior

to each ganglion, and is given to the internal series of muscles. A narrow slip or riband [figg. 44. and 45. (c)], about one third the diameter of each cord, extends along the median line above the cords from one end of the body to the other, as in the Scorpion. This, like the tract in the Scorpion, has been thought to be the motor tract, but is, I think, analogous to the transverse or involuntary nerves of insects. In passing over each ganglion this tract is connected with the nerves by four pairs of very minute filaments. It is interesting to remark the existence of distinct ganglia, from which the antennal nerves originate, situated upon and forming portions of the cerebral ganglia [fig. 48. (d)], just the same as the ganglia upon the antennal feelers in the Lobster [fig. 40. (b, c, d)]; and also to compare the size of the antennal nerves in *Scolopendra* with the optic nerves in the same animal, which are now gaining much importance in the animal series, and begin to share the cerebral ganglia nearly equally with the cerebral prolongations of the cords—the antennæ. In the *Scolopendra* we have thus a clear proof that the anterior or cerebral portion of the nervous system is formed originally by the coalescence of at least two pairs of ganglia, the antennal and optic ganglia, just the same as the caudal ganglion is formed by the ganglia of the penultimate united with the ganglion of the terminal segment of the body. The motor root of the great mandibular nerve is very distinct from the sensitive [E].

Although a double nervous column was thus proved to exist in *Crustacea*, *Arachnida*, and *Myriapoda*, it was not until lately that I have been able to identify and to distinguish the motor and sensitive columns from each other in insects. Their actual existence, therefore, could only be inferred from the discovery of them in other *Articulata*. It has been shown in another part of this paper, that the transverse series of nerves in insects cannot be analogous to the true motor nerves, from their having ganglia upon them in several genera. It was in the *Carabus*, LINN., the very insect in which the ganglia of the transverse nerves are most distinct [fig. 38. (c)], that I first identified the double structure of the cords in insects, and clearly distinguished the motor from the sensitive column (a, b). The motor roots are given off, and unite with the sensitive from the ganglia to form the symmetrical nerves, exactly the same as in the Lobster. The motor, sensitive, and transverse or involuntary nerves are all very distinct in the Green Grasshopper, *Gryllus viridissimus*, LINN. [Plate XVI. fig. 39. (a, b, c)]. Indeed they are so distinct under the microscope as to have been readily seen by a friend who was with me when examining the specimen. But it is in Lepidopterous insects, *Papilio*, *Phalæna*, and *Sphinx*, that the detection of the three kinds of nerves, motor, sensitive, and transverse or involuntary, has given me most satisfaction; because it is in these genera that the transverse nerves, from their large size and from the apparent absence of any other motor column, have been believed to be analogous to the motor nerves of vertebrated animals.

In the larva of the *Sphinx ligustri*, soon after it has entered its last skin, the three kinds of nerves are more distinct than at a subsequent period. The two sensitive columns, or gangliated portions of the cords, lie close to the under surface of the

body, and consist each of a column of fibres, which at certain distances inclose a nodule of granulated, opake, grey matter, which constitutes a chief part of the ganglion. A few fibres of the sensitive column pass on that side of the nodule which lies to the median line of the body of the insect; while the larger portion of the column passes on the outer side of the nodule, from which the nerves are given off, and the two portions of the column uniting again behind the nodule thus constitute a ganglion. As the development of the nervous system proceeds, the ganglion thus formed in the sensitive column of one cord is closely applied to, and firmly united in, the median line, with a corresponding ganglion in the sensitive column of the other; and the two thus combined form a double ganglion of the spinal or symmetrical system. The motor column [Plate XVI. fig. 35. (b)], consisting entirely of a series of longitudinal fibres, giving off nerves at certain distances, lies upon, and is closely approximated to the sensitive (a), which it very nearly equals in diameter, and is only clearly distinguished from it while passing over the ganglia, and by a line which runs along the sides of each cord. The motor nerves are given off from the column at the anterior margin of each ganglion (h), along which they pass diagonally outwards, until they reach the nerve from the ganglion (f'), with which they immediately unite. In the caudal ganglion of the Sphinx [fig. 36.], which at this period consists of two double ganglia, the motor column (b), after being thus distributed to the first, passes on to the next, and terminates in each half of the column dividing upon the middle of the ganglion into two portions (b b), that unite with the terminal nerves which are given to the rectum and generative organs. In the thoracic part of the insect, the double-rooted nerves to the wings are formed, first by the anterior root, which is derived entirely from the motor column, and next by the posterior, which is formed by one part from the motor and one from a ganglion of the sensitive column. In addition to these, the nerves of the wing receive several large nerves from the transverse or respiratory series, the anatomy of which has been described in a former part of this Paper*.

In the *Papilio urticae*, LINN. [fig. 37.], and *P. Iö*, LINN., the ganglia are exceedingly large compared with the size of the cords. When examined with a very strong light, the motor column may be seen from the under surface of the cords through the ganglia quite distinct from the sensitive, and it continues so along the sides of the cords into the nerves of the wings. This is an interesting fact, on account of the wings being supplied with nerves in *Papilio*, LINN., directly from the cords, and not as in *Sphinx* from the cords and ganglia. The motor nerves pass around the exterior of the ganglia, and the column itself passes over them, exactly the same as in other *Articulata*.

We have thus a series of facts which distinctly show the existence of a nervous system analogous to that of vertebrated animals through all the higher *Articulata*; and it cannot be doubted that the same structure exists throughout all the articu-

lated classes. The motor tract, as we should naturally expect would be the case, is equal in size to the sensitive, the power of motion being evidently the primary endowment of organized beings, and existing where sensation can hardly be expected to be found, and where there is only the simplest form of the nervous tissue, entirely without ganglia.

If the nerves and cords be examined immediately after removal from the body of an insect, they exhibit a fibrous appearance; but if macerated a few hours in water, they then look as if formed of series of globules, or rather of disintegrated, irregular parts, as remarked by Dr. HODGKIN in the nerves of the higher animals. It is very certain that the large fibres exchange or interweave a few filaments with each other, to constitute the two tracts of the cord; and this is also the structure of the nerves in general. It is by approximation of several fibres that the large nervous trunks are formed during the development of the Sphinx; the transverse nerves unite first with those from the motor root which comes from the cord, and next with those from the ganglion. This union begins, first by a shortening of the nervous columns in a longitudinal direction; and this is followed by the transverse nerves, and motor root to the wing, becoming greatly thickened, and gradually approximated from the distal extremity inwards to the middle line of the body. This approximation continues until these are united in like manner with the nerve from the ganglion, so that the development of the nerves to the wings takes place from the periphery to the centre, exactly the same as in the lateral development of the cords, as observed by M. AUDOUIN and Dr. MILNE EDWARDS in the smaller *Crustacea*. The nerves to the wings are thus formed of three series of fibres, which are traceable as distinct tracts along a great part of the whole nerve; although closely approximated nerves do not coalesce, but only interchange filaments. The nerves of other *Articulata* exhibit the same appearance as those of insects. The fibrous texture is best seen, and is very distinct, in some of the *Crustacea*. In the Sphinx, and other insects, after coagulation in alcohol, the nerves are contracted in diameter.

b. The terminations of nerves are very difficult to distinguish. They appear to end in, and unite with, the tissues unto which they are distributed. In the Wild Bee I have traced some of the extremities of nerves from the last ganglion, apparently into the very substance of the exterior, or hard covering of the segments of the abdomen. In the larva of the Blood Beetle, *Chrysomela tenebricosa*, LINN., I have traced some of the filaments from nerves of the third ganglion into the cellular texture of the vesicles, or bags, which inclose masses of adipose matter; but I could not discover that any of the filaments entered the fatty masses. They appeared to terminate in the texture of the vesicles. I have found them distributed likewise over the tracheal vessels, and once succeeded in tracing some filaments from a large nerve on the internal side of the posterior thighs of *Gryllus viridissimus*, LINN., to the chief tracheal vessel along which it runs. The filaments were expanded over the vessel until they appeared lost in its texture. The same is the case with some filaments from the transverse or respiratory system in the *Sphinx* and in *Cossus ligniperda*, STEPH. The

respiratory nerve divides and passes on each side the ramifying tracheal vessels as they come from the longitudinal one; the posterior division forms a very minute plexus at their base, and both distribute some filaments upon the ramifying branches, which appear to be lost in their substance. While the respiratory nerves pass on both sides of these tracheæ, a large branch from the gangliated cords, the symmetrical system, passes only on the posterior, and gives off a few filaments to the surrounding muscles in its way round the side of the body to the dorsal muscles.

c. The ganglia, when just removed from the recently killed insect, are of a more opaque colour than the nerves. When placed in alcohol they do not contract in size, but become still more opaque, and appear, therefore, in their chemical composition, more analogous to coagulated albumen, while the nerves, which remain nearly transparent, seem more analogous to fibrin. There is as much uncertainty respecting the ultimate structure of ganglia as of nerves. When macerated in water for a few hours they readily decompose; the cerebral ganglia much sooner than the others. From this circumstance some have supposed that cerebral ganglia contained ventricles, but I have been unable to discover any, although I have searched for them very closely. From the appearance of the ganglia in *Papilio Iö*, LINN., before noticed, it seems probable that a few fibres pass through the ganglia, both longitudinally and transversely, to the body of the insect, and that ganglia are in reality composed of a nodule of grey matter intermingled with, and inclosed among the fibres of the sensitive column. This is further supported by the entire disappearance of ganglia, as in the sixth and seventh, during the transformations of the insect, while the nerves which come from these ganglia remain, and then come from the cords. Whatever be the ultimate structure of ganglia, there seems to be some modification of their chemical composition different from that of nerve. As the optic nerves, which are developed during the pupa state, are formed of fibres, there certainly appears reason to suppose that the structure of the cerebral, and consequently of other ganglia, is to a certain extent fibrous, whatever be the peculiar arrangement or interchanging of the fibres.

All the cords and ganglia, but particularly the latter, are profusely supplied with exceedingly minute tracheal vessels, which penetrate the nerves and most internal part of the ganglion. The minuteness of these extremities is such that I have failed to detect them even with a powerful triplet. I have in general used a triplet, or WOLLASTON'S doublet, in examining these minute structures.

Having traced the nerves of the Sphinx through all their changes, and examined their distribution and structure as compared with other *Articulata*, it now remains to show the manner in which the changes which take place in them are induced and effected.

III. *Development of the Nervous Columns.*

a. During the time I was most engaged in watching the development of the Sphinx, in the spring of 1832, considerable difficulties presented themselves, and many

things were not sufficiently explained, owing partly to want of specimens, and partly to the uncertainty of the period at which the changes take place in different individuals. I determined, therefore, to repeat my observations upon another Lepidopterous insect, of a different genus, and for this purpose chose the commonest of our British species, the Nettle Butterfly, *Papilio urticae*, LINN. HEROLDT has accurately noticed the changes in *Papilio brassicae*, LINN.

I selected for my observations a large number of the larva of the Nettle Butterfly, and fed them in breeding cages until they suspended themselves preparatory to changing to the pupa state. The moment of throwing off the old skin was carefully watched, and the precise time of its occurrence noted. By these means an adequate number of specimens was collected, and the time the insects had remained in the pupa state accurately known, and the specimens were then dissected at stated periods. The manner in which the insect prepares to undergo its change, and the mode of its occurrence, are known to every naturalist; I shall therefore confine myself to the changes of the nervous system, in illustration of what takes place in the *Sphinx ligustri*. The nervous system of *P. urticae*, LINN., very closely resembles that of the Sphinx, and has the same number of ganglia.

Two hours after the insect has suspended itself to undergo its transformation, a considerable change in the arrangement of the nervous system takes place. The cerebral ganglia are distinct from each other, but are not yet enlarged. When viewed from above, each presents a pear-shaped appearance, the anterior part of the lateral surface being elongated forwards and gives origin to the antennal and optic nerves. At the base of the optic nerves, even at this early period, there is the same appearance of dark pigment as in the *Sphinx ligustri*, from which it is clear that this is deposited in the earliest stages of transformation, both in the Butterfly and Moth. The subœsophageal ganglion is nearly twice its original size, and the crura which connect it to the cerebral ganglia are considerably shorter, as well as the cords that connect the second, third, fourth, and fifth ganglia. The two last are separated only by a short interval, and are slightly enlarged. The fifth, sixth, and seventh ganglia are closer together, the cords between them disposed irregularly, and the longitudinal position of the ganglia altered. The ganglia from the seventh to the eleventh remain as in the active larva.

By unremittingly watching a number of larva through all their preparatory states for changing, we can easily judge, within a very short period, when the transformation will take place. Just before throwing off the old skin there is much activity throughout the whole insect, and if it be dissected about *half an hour* [Plate XV. fig. 21.] before this occurs, the nerves for the future wings, and the cerebral, and second, third, fourth, and fifth ganglia are all slightly enlarged, and the first ganglion very considerably. The cords which connect them diverge from each other, while those between the fifth, sixth, and seventh ganglia are more folded than in any other part of the body.

Immediately after the insect has assumed the pupa state [Plate XV. fig. 22.], all the ganglia are brought closer together, and the cords are disposed more irregularly than at any other period, in consequence of the shortening which has taken place in every segment of the body, by which the cords have been rendered too long to lie in a direct line. Those cords which connect the first five ganglia are somewhat increased in size. It is at this period there is the greatest activity, and sometimes irregularity in the progress of the changes. The fourth and fifth ganglia, and their intervening cords (which are those parts in which the first great changes commence), are often nearer together and have more coalesced at this period in some specimens, than in others at five or six hours later. This coincides with what occurs in the *Sphinx ligustri*, in which the precise period when the coalescence of ganglia takes place cannot positively be stated, since it varies a little in different specimens, and depends probably upon the temperature of the atmosphere, and upon the vigour of the insect at the time of changing,

One hour after transformation [Plate XV. fig. 23.], the cerebral ganglia have become more closely united, the nerves to the antennæ more distinct, and the rudiments of the optic nerves more developed at their base. The fourth and fifth ganglia are still approaching each other, and the cords are larger in diameter at their connexion with the fifth, the anterior part of which has become less distinct, and seems about to coalesce with them. The distance between the remaining ganglia is still decreasing, and the investing membranes, or exterior surface of the cords, exhibit a corrugated appearance, as if in the act of becoming shortened. In the *Sphinx ligustri*, besides the longitudinal cords and ganglia, and nerves given directly from them, we have seen there are others lying upon them,—the transverse or superadded nerves. There are like series in *Papilio urticae*, L., the distributions of which are nearly similar. The first series begins immediately behind the first subœsophageal ganglion (*b*), where the nerves run directly outwards, along the course of the trachea, which are distributed over the first ganglion, and come directly from the first spiracle. Some of the branches unite with nerves from the second ganglion (*d*), while the main branch of this segment runs in the course of the muscles at the back part of the head. Behind the second ganglion, branches unite with the large nerve which comes from the cord between the second and third ganglion to supply the first pair of wings (*f*), and which is apparently single, and does not originate, as in the *Sphinx*, one root from the cord and the other from a ganglion. Behind the third ganglion, the nerve from the cord to the second pair of wings (*i*) receives a branch from the third series (*h*), while the greater number of the nerves pass outwards to the muscles. A series of these transverse nerves exists, as in the *Sphinx*, just anterior to each of the remaining ganglia (*o, o, o*), unto the nerves of which they give a few filaments, while their main branches are distributed separately among the tracheæ and muscles, excepting only those of the fourth, fifth, and sixth series, which become approximated to the nerves from the corresponding ganglia, and in the development of the *Butterfly* at this period, afford

us an instance of the commencement of an interesting fact before alluded to, the formation of nervous trunks by the approximation and union of many fibres. The series anterior to the fifth ganglion [5. (o)] is now greatly diverging, and the ganglion and nerves are passing forwards and becoming united with it.

Seven hours after changing [Plate XVI. fig. 24.] there is still an enlargement of the cerebral ganglia, optic nerves, five first ganglia, and their intervening cords. The fourth and fifth have advanced closer together, and the very short cords which connect them are so much increased in diameter as to resemble a separate ganglion (*x*): the distance between the fifth and sixth is diminished, and all the remaining ganglia are slightly enlarged. The cords between them, just anterior to each ganglion, are also slightly enlarged, and are less irregularly disposed than in the previous stages. The transverse nerves are beginning to assume their temporary ganglionic appearance (*o, o, o*), and the terminal nerves from the last ganglion are enlarging for the supply of the developing organs of generation.

At *twelve hours* [Plate XV. fig. 25.] the fifth ganglion, by its coalescence with the cords that united it to the fourth, has assumed a triangular appearance, the broadest part being posteriorly. The transverse series, anterior to the fifth ganglion, which at seven hours was beginning to be united to the nerves from this ganglion, is now so completely joined to them as almost to have disappeared, there being only a triangular elevation upon the anterior part of the ganglion to indicate its previous existence [5. (o)], thus affording us a further proof of the adhesion of contiguous parts, and of the manner in which nervous trunks are formed.

At *eighteen hours* [Plate XV. fig. 26.] all the parts have become more concentrated; the ganglia, cords, and nerves, particularly those to the wings, are more enlarged; and the transverse nerves, although continuing separate, give filaments to the nerves from the ganglia, and themselves exhibit at their division more the appearance of ganglia; while the fourth and fifth ganglia and cords have now so completely coalesced as to appear like an irregular elongated mass. The cords in the abdomen lie more in a direct line, but just anterior to each ganglion are still a little enlarged.

At *twenty-four hours* [Plate XV. fig. 27.] the fourth and fifth ganglia have advanced still closer together; the fifth is slightly larger than the fourth. The cords just before the sixth ganglion are dilated, and the transverse nerves of the thorax are enlarged, keeping pace with, or rather preceding, the development of the respiratory organs.

At *thirty-six hours* [Plate XV. fig. 28.] the optic nerves have attained a size almost equal to that of the cerebral ganglia, and after this period become very little larger; and the first subœsophageal ganglion has coalesced with the cerebral ganglia, and forms with them a complete ring around the œsophagus. The fifth ganglion has now decreased in size, and is smaller than the fourth, while in some specimens the nerves which were given from it now come from the cords immediately behind it, and thereby seem to indicate that part of the nervous substance of the ganglion has been transmitted forwards. The sixth ganglion, which at twenty-four hours is decreased in size,

has disappeared; and the nerves which came from that also come now from the cords, very near to those of the fifth ganglion, and thus further show that the substance of the ganglion has been transmitted forwards. The seventh ganglion is decreased in size.

At *forty-eight hours* [Plate XVI. fig. 29.] the whole of the cords have regained the longitudinal direction, so that there must have been either consolidation, absorption, or elongation forwards of the nervous substance, for the purposes of development. The seventh ganglion has now entirely disappeared.

At *fifty-eight hours* [Plate XVI. fig. 30.] a further change is effected. The second and third ganglia approach and coalesce, and the double ganglion thus formed is only separated from the larger thoracic mass, composed of the fourth and fifth ganglia, and part of the sixth, by very short but much enlarged cords. The transverse plexus are united with the nerves to the wings, and the whole mass of ganglia and nerves have been carried forwards, and lie more in the middle of the thorax. The optic and antennal nerves have nearly attained their full development, and the plexus of nerves and ganglia in the thorax, which in the larva exhibit an intricate arrangement, are now united, and form only a few large trunks, which can hardly be recognised as the same structures. The arrangement of the whole nervous system is nearly the same as exists in the perfect insect. Yet all this has taken place at a comparatively early period of the pupa, three days not having elapsed since the insect underwent its metamorphosis. It is interesting to observe that while the nervous system has been thus rapidly progressing, the alimentary canal, generative system, and other organs are still very far from completion, and, as compared with the nervous system, have made but little progress. It therefore seems as if necessary that the nervous system should be first completed.

These observations upon the Butterfly were made in June 1832, when the length of time that the insect remained in the pupa state was generally thirteen days and a few hours. They were carefully repeated in the following August, when the temperature of the season was considerably higher, and then the insect seldom continued more than nine, and often not more than eight days in pupa; thus clearly proving the decided influence which increased temperature exerts over development in accelerating the latter stages, since I could not discover that the earlier period, during which the changes in the nervous system were taking place, was very much accelerated by it.

These observations coincide with those upon the Sphinx. But it is interesting to remark the difference in the length of time which the changes occupy in the two insects, relatively to the length of time which they pass in the pupa state. The Butterfly, during the summer, is scarcely fourteen days, and often not more than eight in the pupa, and very nearly completes its changes in the nerves in three days. The Sphinx, on the other hand, passes nearly nine months in the pupa state, during more than eight of which its nervous system is undergoing change. But it may still be

remarked that the greatest rapidity and extent of change in the Sphinx occurs during a short period immediately subsequent to its becoming a pupa. This is in perfect accordance with the changes in the Butterfly.

b. The means by which the development of the two insects take place are similar. They depend chiefly upon a shortening of the longitudinal and diagonal muscles of the body, when the parts of the future insect which have been forming in the larva have arrived at the greatest development they are capable of in that condition, and, as in the foetus of vertebrated animals, at the completion of the full term of utero-gestation, induce a necessity for change. When this is to take place in the Sphinx, the larva ceases to eat, becomes restless and active, and after forming a cell in the earth lies at rest with its body coiled up, and soon loses the power of locomotion. During this time a contraction of all the longitudinal and diagonal muscles of the body is taking place, particularly of the fourth, fifth, and sixth segments; and the minute vessels which connect the old skin of the larva to the new one of the pupa beneath it are ruptured, and a fluid is effused which greatly assists in separating the old from the new covering. The body of the insect is considerably shortened. This contraction occasions a permanent shortening of the longitudinal muscles, which then gain new attachments, by which portions of each segment of the body, now soft and delicate, are drawn one beneath the other, forming broad duplicatures of the external teguments. This contraction and shifting of the muscles is carried to such an extent in the fourth, fifth, and sixth segments, as to form a large duplicature around the whole body, and to constitute the future division between the thorax and abdomen. The fifth segment is almost lost in the fourth, and the sixth, the first of the abdomen, is greatly diminished. The third segment is not at all decreased along its dorsal surface. It constitutes the greater portion of the thorax.

By these changes in the tegumentary and muscular structure of the body the ganglia of the cords are brought nearer together, and confined in their respective places in the segments by the nerves running transversely from them. The cords, from being too long to lie in a direct line, are folded irregularly between the ganglia. The greatest folding and irregularity of the cords is between the fourth, fifth, and sixth ganglia, where, from the almost entire obliteration of two segments, it might justly be expected. A disposition is induced in the first five ganglia to become aggregated into one mass, by their impingement upon each other, occasioned by the approximation and union of segments to form the thorax, which is assuming a fixed condition, and becoming the centre of development. It is in this manner that the nervous structure appears to be elongated forwards for the enlargement of particular parts. The cords in the abdomen recover their original direction, but are not much increased in diameter, and the sixth and seventh ganglia entirely disappear, while the ganglia and nerves in the thorax are enlarged, and aggregated into two masses; the crura of the cerebral ganglia are much shortened, and the optic nerves are at the same time proportionably developed. From these facts we may conclude,

that it is by an elongation forwards and outwards in every direction,—by the approximation of nervous trunks already formed,—and by the interweaving, exchange, and recombination of filaments into new trunks, that the development of the nervous system in insects is completed.

Description of the PLATES.

PLATE XIII.

Fig. 1. Nervous system of *Sphinx ligustri*, as seen in the pupa state in the month of April, exhibiting the relative situation of the nerves and ganglia, and the manner in which they are distributed to, and pass under the longitudinal muscles.

A. A portion of the exterior of the dorsal surface of the pupa case, reflected to show the muscles and nerves. Magnified $2\frac{1}{2}$ diameter.

Fig. 2. The cerebral and thoracic ganglia and nerves, magnified ten diameters. The letters of figg. 1. and 2. correspond with each other.

A. Cerebral ganglia.

B. Optic nerves developing.

C. Nerves which connect the anterior lateral ganglia with the antennal nerves.

D. The nerves to the antennæ.

E. The vagus or pneumogastric ganglion and nerve.

a. Anterior lateral ganglia.

b. First series of respiratory nerves.

c. Pair of small nerves from the cord.

2 . Second ganglion of the cords.

d. Nerve to first pair of legs.

e. Second respiratory nerves.

f 3. Double-rooted nerve to first pair of wings.

g. To second pair of legs.

h. Third respiratory nerves.

i. To second pair of wings.

k. To third pair of legs.

l. Nerves of fifth ganglion, which sends branches to the dorsal muscles of eighth segment.

m. Nerves from the sixth ganglion.

n. Symmetrical nerves, which, after passing under the longitudinal abdominal muscles, pass up to the dorsal.

o, o, o, o, o. Respiratory nerves of the abdomen.

Fig. 3.

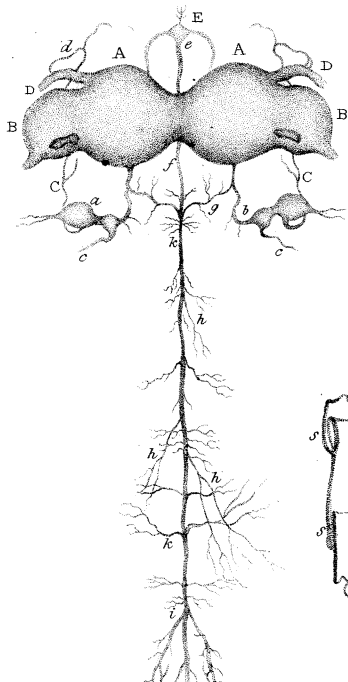


Fig. 1.

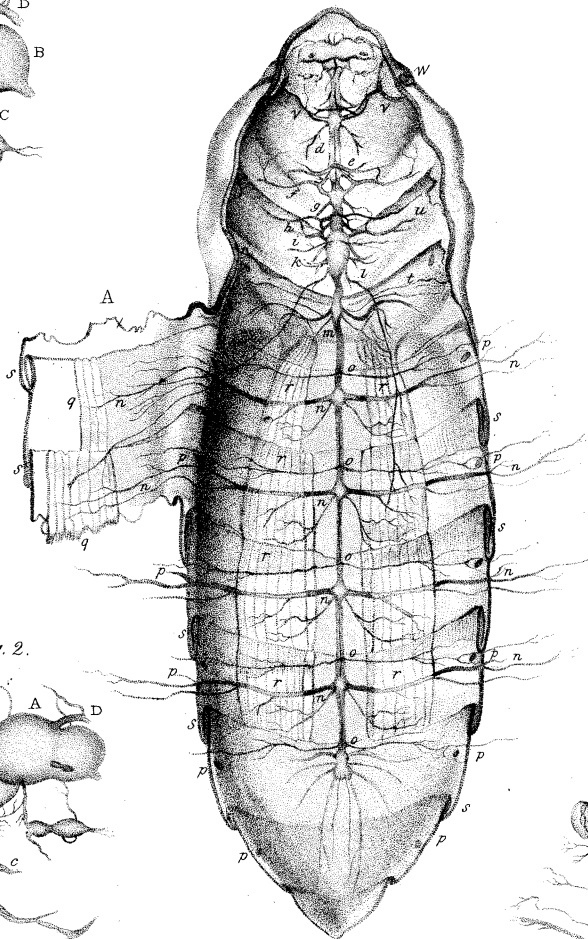


Fig. 4.

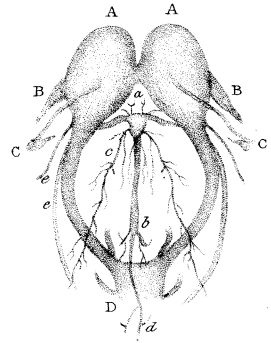


Fig. 2.

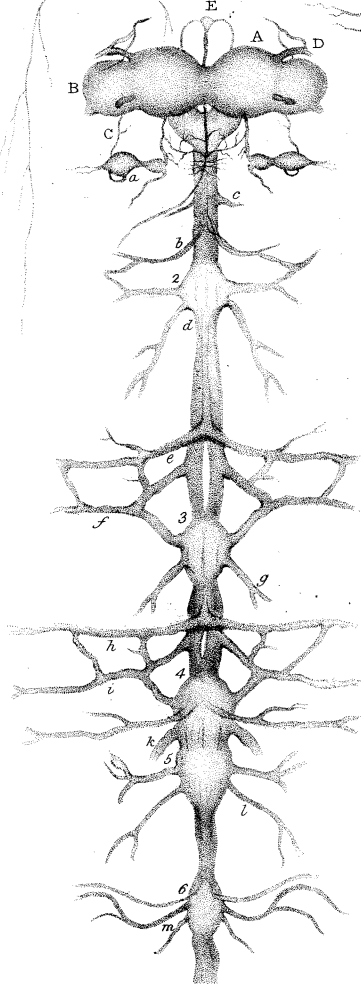


Fig. 5.

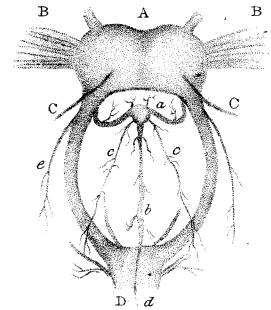


Fig. 6.

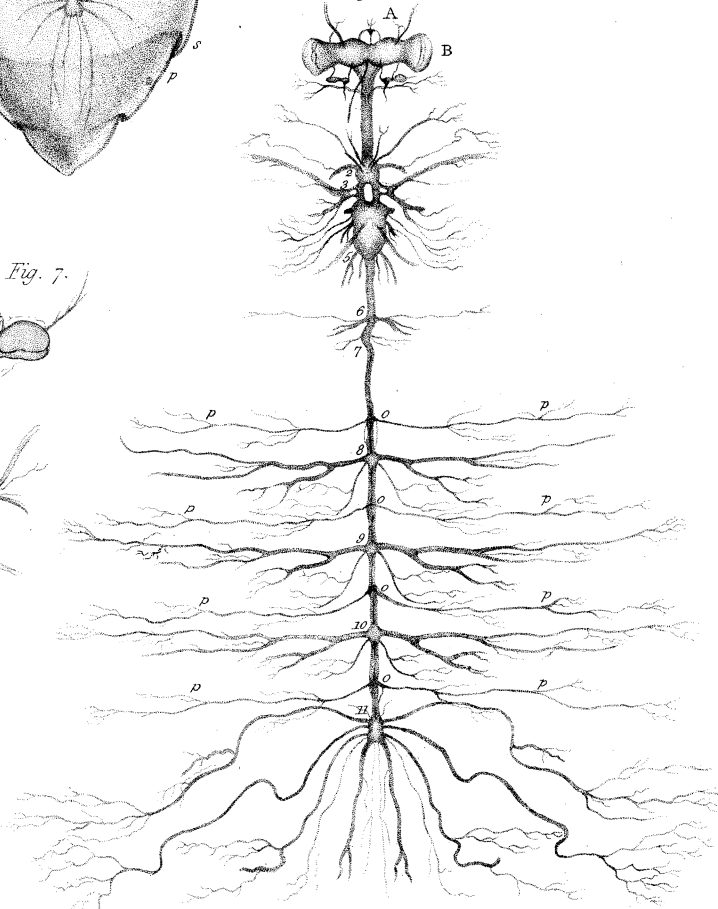
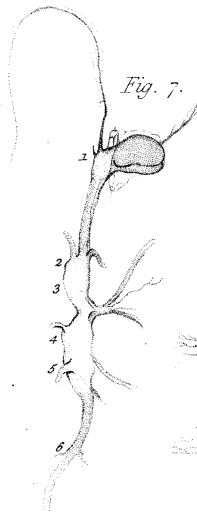


Fig. 7.



- p, p, p, p, p.* Extremities of the respiratory nerves, which, after passing over the longitudinal abdominal muscles, divide and pass on each side of the spiracles
- q.* Dorsal longitudinal muscles.
 - r.* Abdominal longitudinal muscles.
 - s.* Duplicatures of the segments.
 - t.* Division between thorax and abdomen.
 - u.* Between third and fourth segments.
 - v.* Between the first and second segments.
 - w.* Anterior spiracles.

Fig. 3. The supra-oesophageal ganglia and nerves : magnified fifteen diameters.

- A. Cerebral ganglia.
- B. Optic nerves developing.
- c. Nerves of connexion.
- D. Nerves of the antennæ.
- E. The vagus nerve.
- a.* Anterior lateral ganglia.
- b.* Nerves which connect them with the cerebral ganglia.
- c.* With the first respiratory or transverse nerves.
- d.* With the antennæ.
- g.* With the vagus or pneumogastric.
- e.* The ganglion and nerve of the vagus.
- f.* Its trunk after passing beneath the cerebral ganglia.
- h, h, h.* Branches given to the aortal portion of the dorsal vessel, or heart, which runs immediately above the vagus.
- i.* Division of the vagus at the cardiac extremity of the stomach.
- k, k.* Branches given to the oesophagus, along which the vagus runs.

Figg. 4 and 5. Nerves and ganglia of the head in the larva and perfect state of the common Blood Beetle, *Chrysomela tenebricosa*, LINN. Fig. 4. Larva.

Fig. 5. Perfect insect.

- A. Cerebral ganglia in the larva, scarcely at all united, and exactly as seen in the early stages of the larva in the Bee and Sphinx.
- A. Cerebral ganglia.
- B. Optic nerves.
- c. Anterior lateral ganglia.
- D. First suboesophageal ganglion.
- a.* The two nerves or origins of the vagus, forming between them the ganglion.
- b.* A ganglionic enlargement on the trunk of the nerve.
- c.* Nerves given to the sides of pharynx and oesophagus.
- d.* A division of the vagus at the commencement of the stomach, as in the larva of the Sphinx.
- e, e.* The pharyngeal and nerves of *taste*.

Fig. 6. Nervous system of the perfect insect *Sphinx ligustri*.

A. Cerebral ganglia.

B. Optic nerves. The figures refer to the number of the ganglia.

o, o, o. Respiratory nerves.

p, p, p. Their division at the spiracles.

Fig. 7. Lateral view of the cerebral and thoracic part of the nervous system in the perfect state of the Sphinx, magnified two and a half diameters.

PLATE XIV.

Fig. 8. The thoracic ganglia and nerves of Sphinx in the imago state. Figures as before.

a. Nerve to the first pair of wings.

b. The double-rooted origins of this nerve.

c. A plexus or ganglion formed at the union of the two roots.

d. The nerves to second pair of wings.

e. Some separate filaments which are given to the muscles.

f. Nerves to the second pair of legs.

g, h. Tracheal vessels.

Fig. 9. The anterior portion of the abdominal nerves and columns, covered by the investing structure (a), seen only in the perfect state of the insects.

b. Respiratory nerves.

c. The moto-sensitive or symmetrical nerves.

Fig. 10. The cerebral ganglia and nerves of the proboscis, magnified fifteen diameters.

a. The great nerve to the proboscis.

b. Its entrance into the organ.

c. The external branch.

d. The main branch given to the muscles.

e. The internal, or branch which runs along the grooved or internal side of the organ.

B. Optic nerve.

D. Antennal nerve.

Fig. 11, 12, 13. Exhibit vertical sections of the larva, pupa, and imago states of *Sphinx ligustri*, LINN.; showing the relative situation of the circulatory, alimentary, and nervous systems in the three stages, and also the duplicatures of the external integument as occasioned by the contractions and re-attachments of the muscles at the period of changing from the larva to the perfect state. The silk-vessels and part of the organs of generation, &c. are omitted. The figures refer respectively to the number of the segments. Magnified two and a half diameters.

a, b. The dorsal vessel with its appendages.

The alimentary canal.

c. The oesophagus.

Fig. 15.

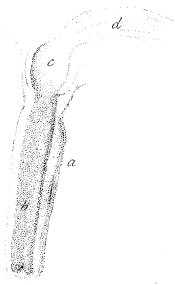


Fig. 17.



Fig. 18.



Fig. 16.

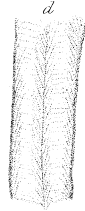


Fig. 16.

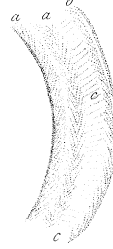


Fig. 14.

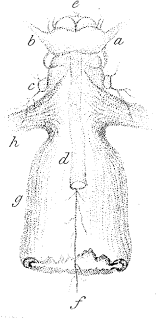


Fig. 10.

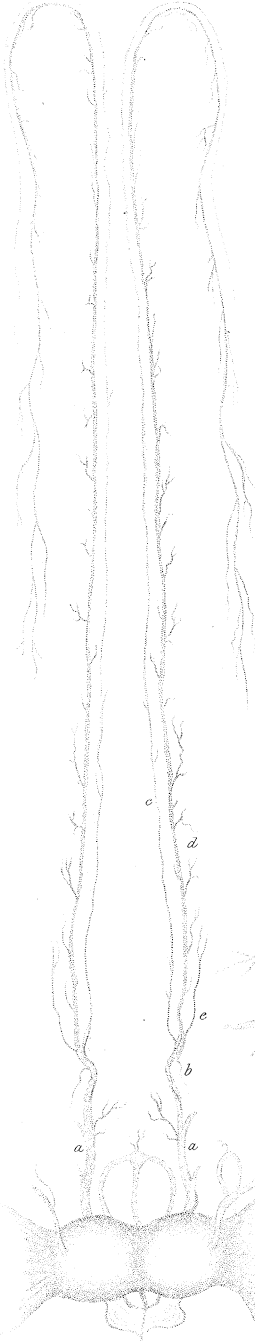


Fig. 8.

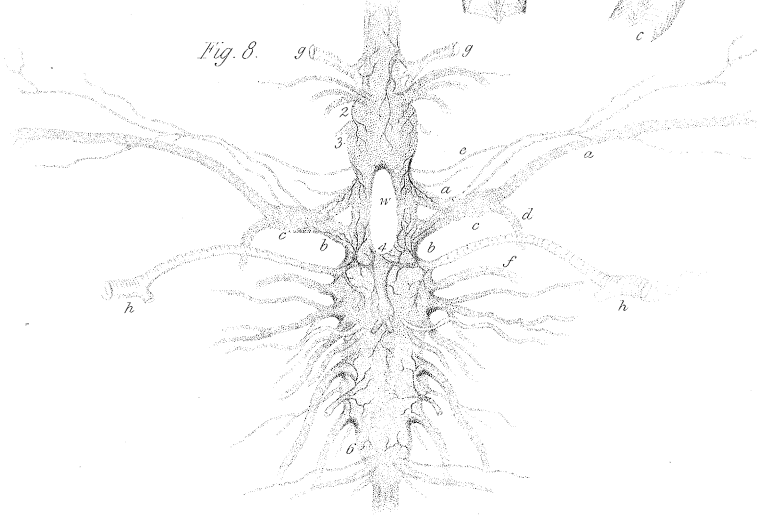


Fig. 11.

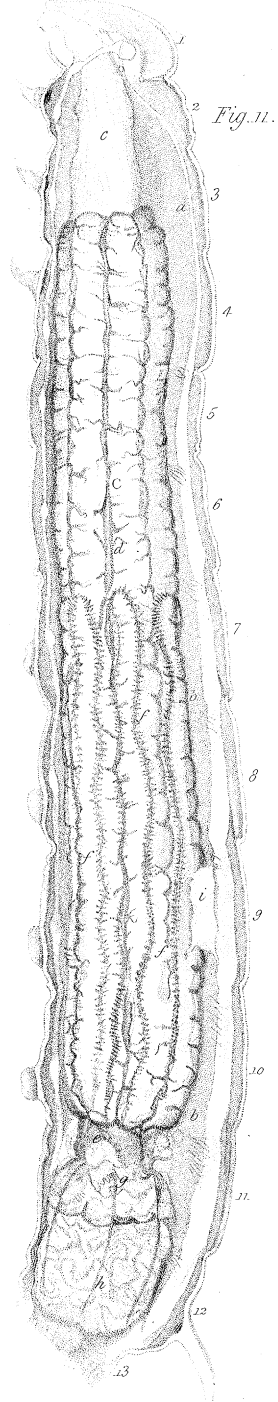


Fig. 13.

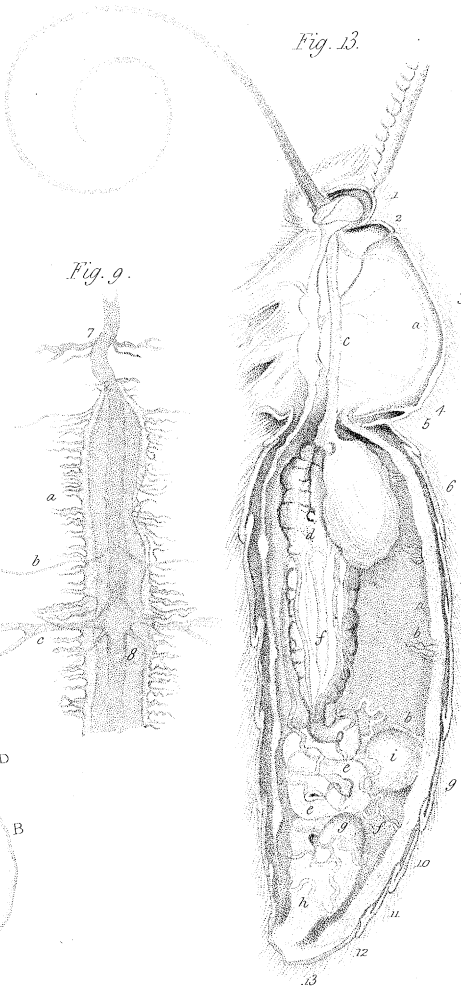


Fig. 12.

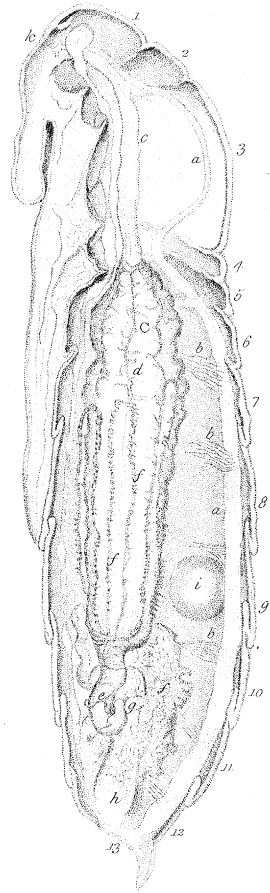


Fig. 9.

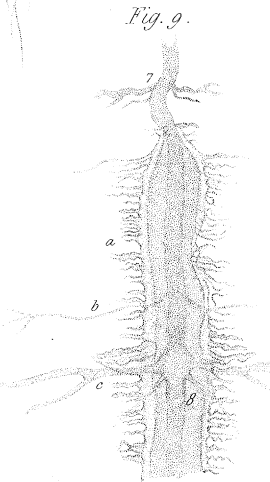
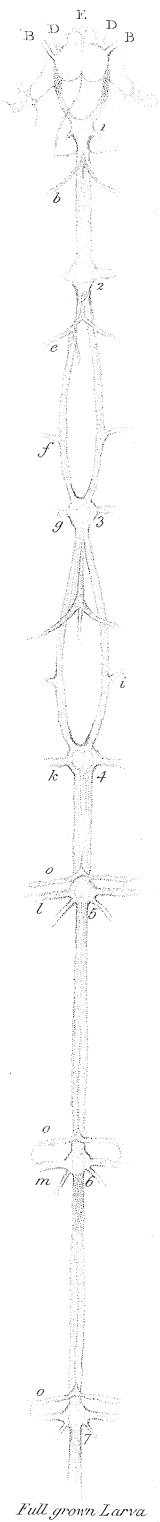
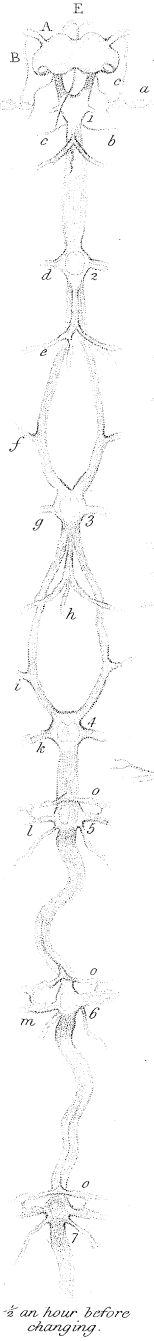


Fig. 20.



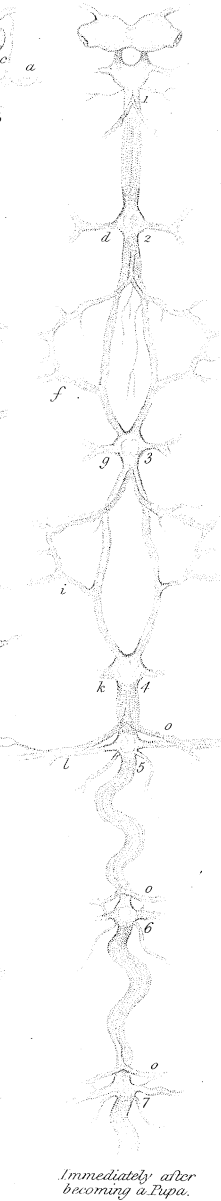
Full-grown Larva

Fig. 21.



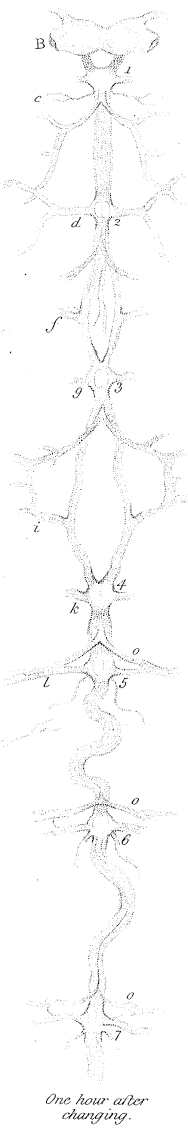
½ an hour before changing.

Fig. 22.



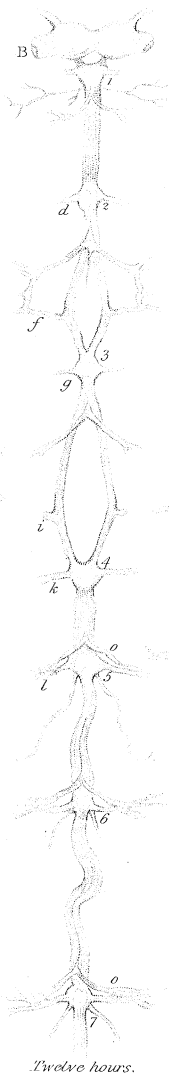
Immediately after becoming a Pupæ.

Fig. 23.



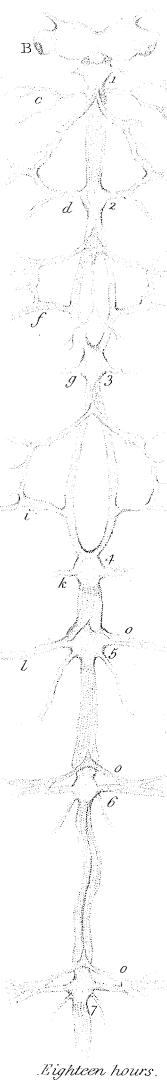
One hour after changing.

Fig. 25.



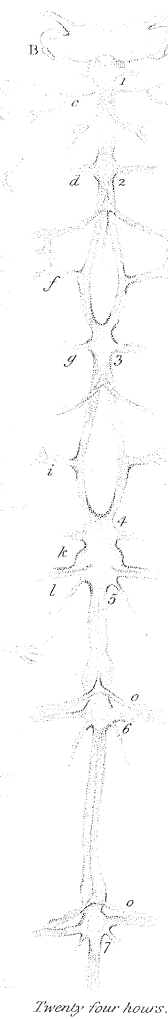
Twelve hours.

Fig. 26.



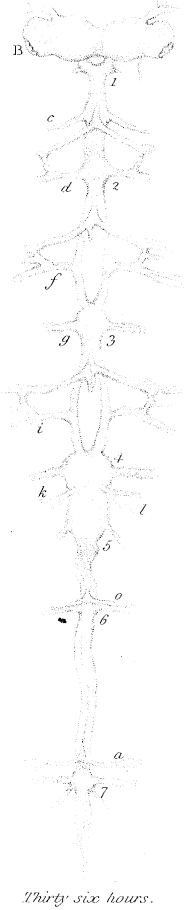
Eighteen hours.

Fig. 27.



Twenty four hours.

Fig. 28.



Thirty six hours.

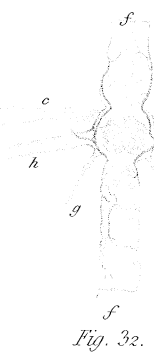


Fig. 32.

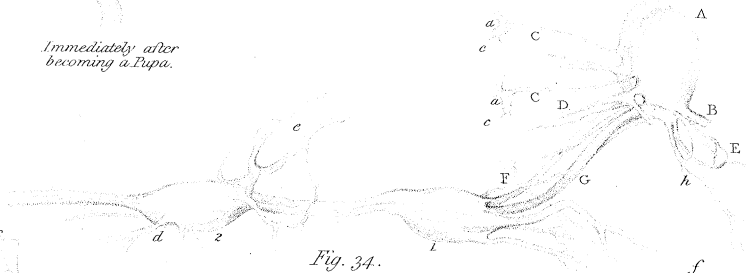


Fig. 34.

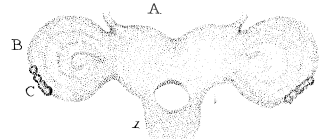


Fig. 31.

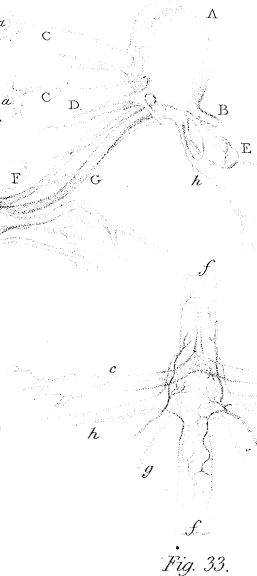


Fig. 33.

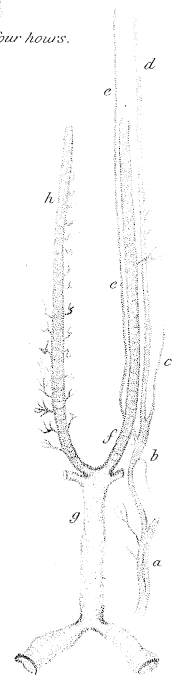
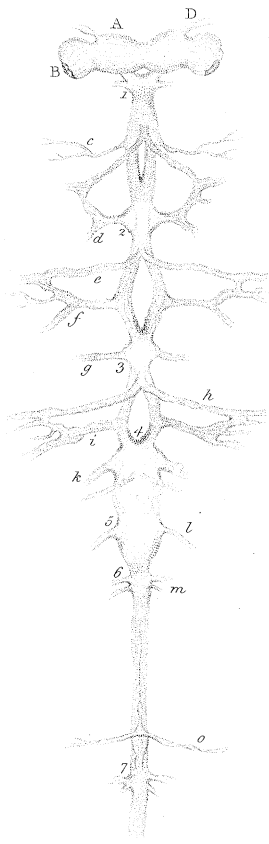


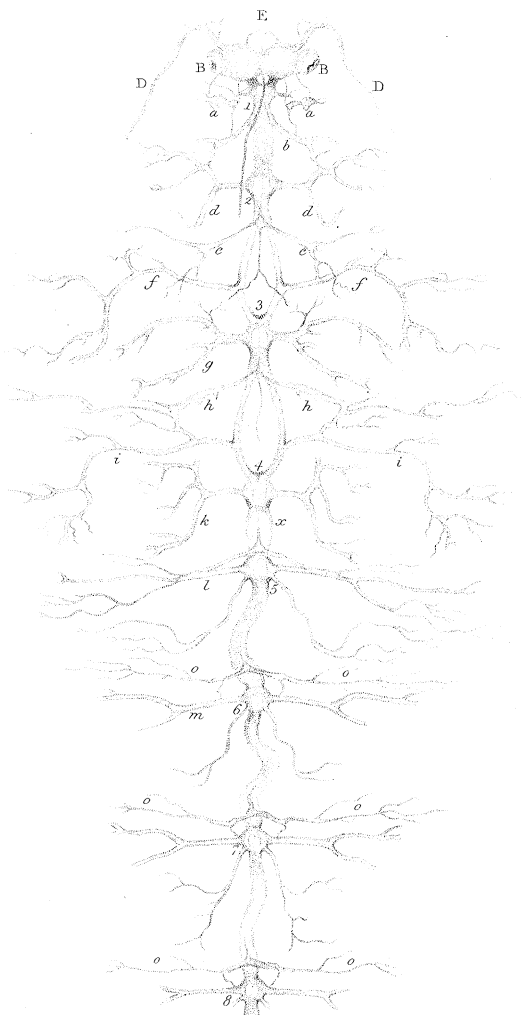
Fig. 19.

Fig. 29.



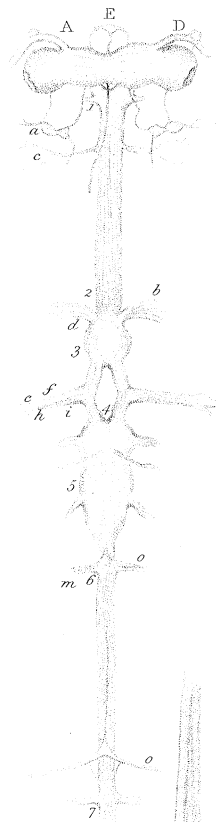
Forty eight hours.

Fig. 21.



Seven hours

Fig. 30.



Fifty eight hours

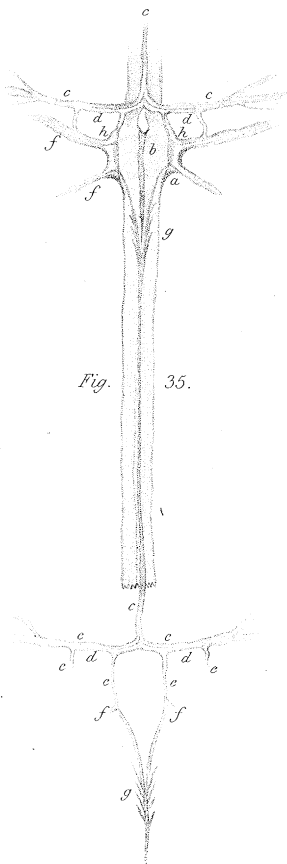


Fig. 35.

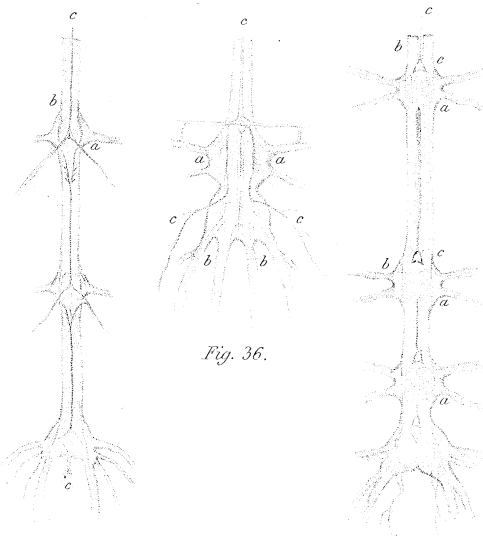


Fig. 36.

Fig. 39.

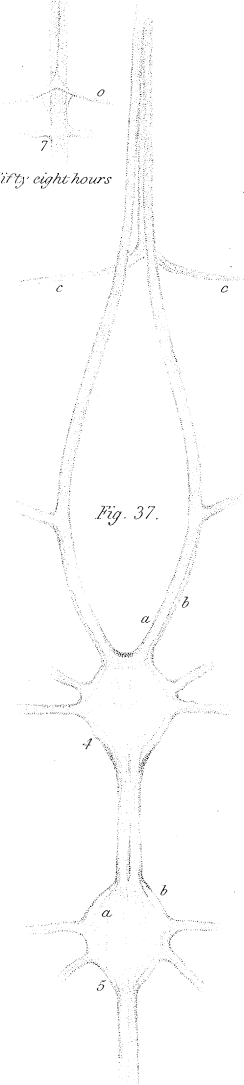


Fig. 37.

Fig. 38.

- d.* The stomach.
- e.* The small intestines.
- f.* The biliary vessels.
- g.* The cæcum.
- h.* The colon and rectum.
- i.* The testis.

Fig. 14. Œsophageal portion of the alimentary canal in larva of *Sphinx*, exhibiting the constrictor (*h*) muscles of the pharynx (*d*), aortal portion of the dorsal vessel (*a, b*), cerebral ganglia, and optic nerves developed from them (*c*); anterior lateral ganglia (*e, f*) and ganglion and nerve of the vagus in situ, seen from above.

Fig. 15. Internal view of part of the proboscis of the perfect insect.

- a.* The transverse muscles.
- b.* The groove.
- c.* The œsophagus.

Fig. 16. Longitudinal and transverse muscles of the proboscis of *Sphinx*.

- a.* Flexors.
- b.* Longitudinal extensors.
- c.* Transverse extensors.

Fig. 17. Lateral view of four joints of the antennæ *Sphinx Elpenor*, LINN.

Fig. 18. View of the articulating surface of the antenna.

PLATES XV. and XVI.

Fig. 19. Tracheæ of the proboscis, showing their relative situation with that of the nerves. Letters *a* to *e* as in fig. 10.

- f, h.* The tracheæ.
- g.* Their united origin.

Fig. 20. to 30. Plates XV. and XVI. Exhibit the gradual change and development of the nervous system of *Papilio urticae*, magnified 12 diameters. The figures and letters refer as in figg. 1. and 2. of *Sphinx ligustri*.

Fig. 31. Posterior view of the cerebral and œsophageal ganglia of *Papilio urticae*, L., as seen during the change at forty-eight hours after change to the pupa state.

- b.* The optic nerves, developing and showing the sacculi of fibres and development of the choroid membrane (*c*).

Fig. 32. One of the abdominal ganglia of *P. urticae*, viewed from below by means of transmitted light, and showing the two inclosed approximated nodules of grey matter, and also the transverse nerves, as seen at twenty-four hours after change to the pupa state, magnified 30 diameters; the transverse nerves (*c*), the spinal cords (*f*), the compound symmetrical nerves (*h*), the small diagonal nerves (*g*).

Fig. 33. Abdominal ganglion at forty-eight hours after changing, seen from its upper surface by transmitted light. References the same as fig. 32.

Fig. 34. A lateral view of the supra-oesophageal or cerebral ganglia and nerves, and of the first and second suboesophageal of the larva of *Sphinx ligustri*. The letters and figures from A to F as in fig. 1.

g. The lateral cords which connect the cerebral with the suboesophageal ganglia, and pass on each side the oesophagus. (h) The nerve which is given to the side of the mouth, and is perhaps the nerve of *taste*.

d. Nerves to the first pair of legs.

e. Some of the transverse nerves which pass round on each side of the cardiac part of the stomach.

Fig. 35. One of the abdominal ganglia of the Sphinx, with the portion of cords and transverse nerves (c), showing the motor columns of the cords (b) passing over the double ganglion of the sensitive (a), and the manner in which the double tract of the transverse or respiratory nerves (c) divides at right angles before a ganglion (d), and sends on it filaments (e) which, after uniting with the transverse portion of the nerve (d), and with the motor-sensitive nerves (f), converge and join again in the median line above the cords, having first derived a few filaments from the motor column (g).

Fig. 36. The double terminal ganglion of the larva of the Sphinx, showing the transverse nerves (c), and division and termination of the motor column (b, b).

Fig. 37. View of the under surface of the posterior thoracic nerves and ganglia in *Papilio Iö*, LINN., showing the transverse (c), motor (b) and sensitive tracts (a).

Fig. 38. The same in the abdominal parts of cords in *Carabus monilis*, L., in which the ganglia of the transverse nerves are very distinct (c).

Fig. 39. The same in *Gryllus viridissimus*, LINN., but without ganglia on the transverse nerves.

PLATE XVII.

Fig. 40. The nervous system of the Lobster, (*Astacus marinus*, LEACH,) natural size.

1 to 14. Ganglia.

A. Cerebral ganglia.

B. Passage for the oesophagus between the crura.

C. The suboesophageal thoracic ganglia.

D. The post abdominal or caudal ganglia and nerves.

E, E. The origins of the vagus.

a. Optic nerves.

b. Nerves from a distinct ganglion to the large antennæ.

c. Nerves from another ganglion, anterior to the last, to the small antennæ.

These four ganglia to the four antennæ are situated anteriorly, and a

Fig. 42

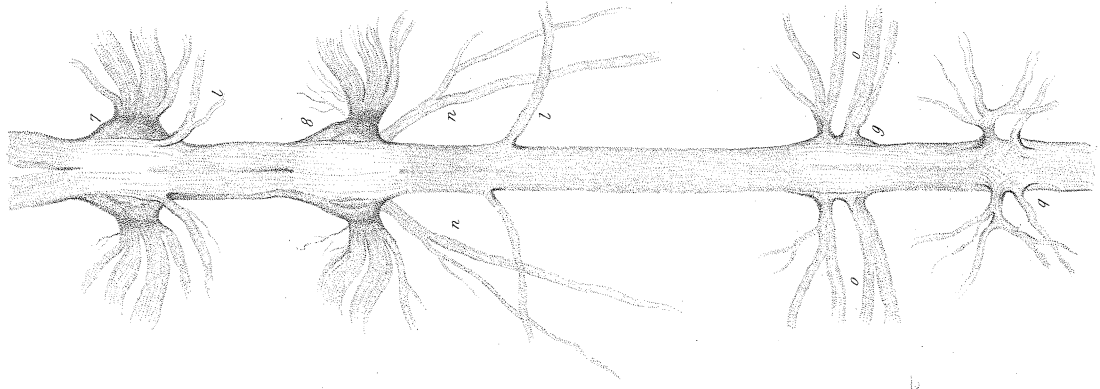


Fig. 44



Fig. 40

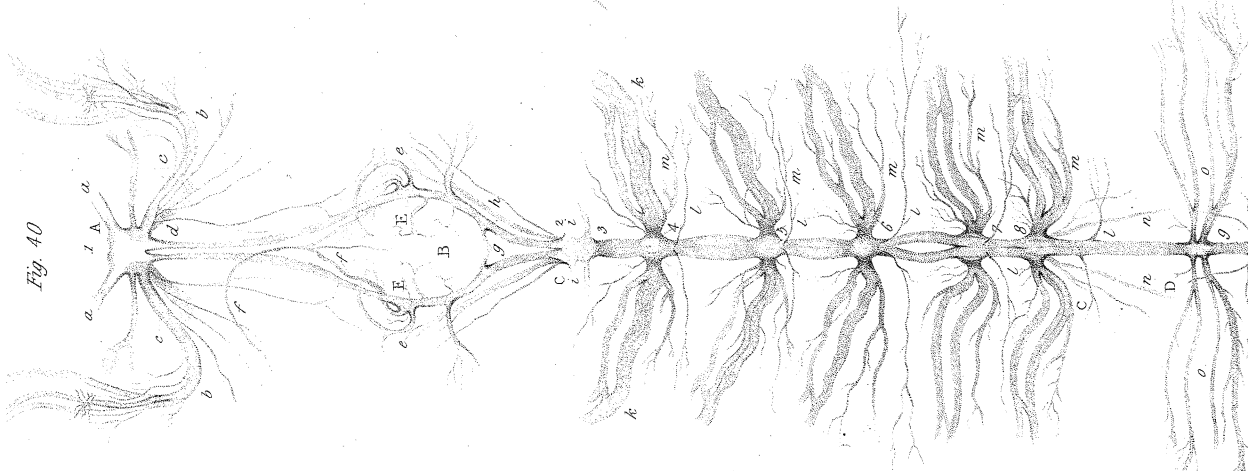


Fig. 41

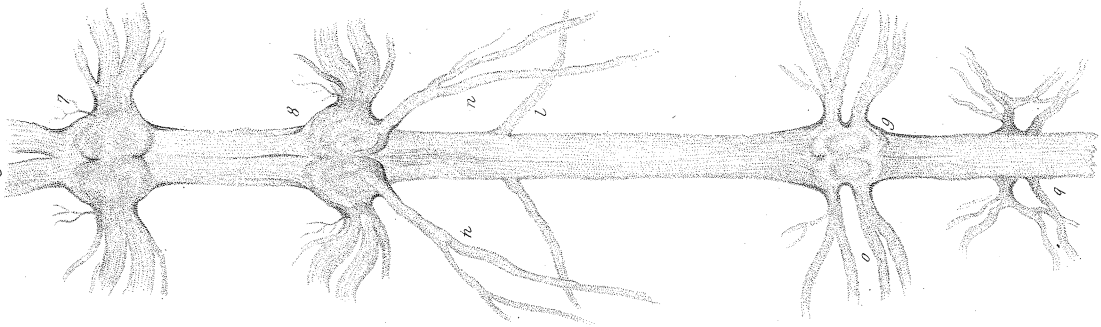


Fig. 43





Fig. 43

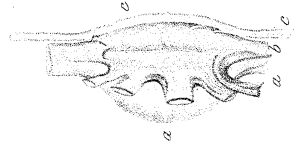
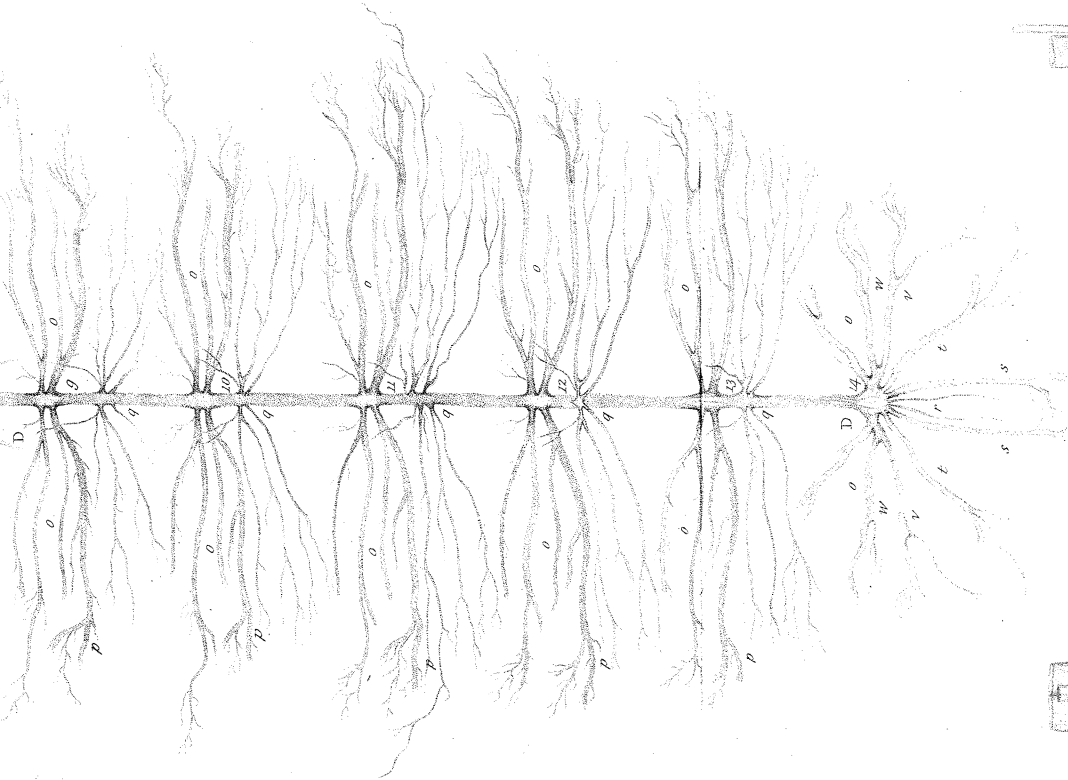


Fig. 47

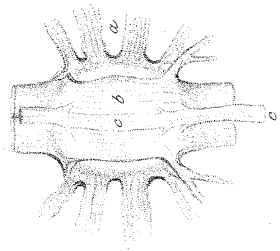
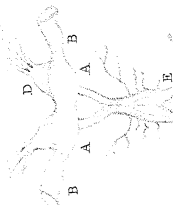


Fig. 49

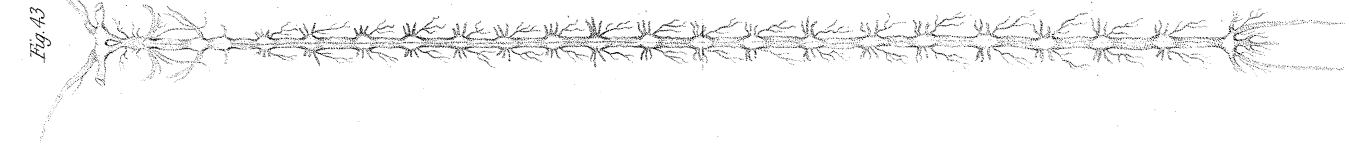


Fig. 44



Fig. 47

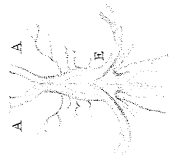


Fig. 48



Fig. 46



- little lateral to the cords, and are connected with the sensitive column (*d*).
- e, e.* Origins of the vagus and of a nerve, as in insects, distributed to the sides of the mouth.
- f.* The continuation of the vagus along the dorsal surface of the stomach, and in connexion with the anterior distribution of the anterior aortal vessel, as in insects.
- g.* The glosso-pharyngeal nerve.
- h.* Mandibular nerves.
- i, i.* Nerves to the inferior lip and palpi.
- k.* To the large claws.
- l, l, l, l.* Nerves derived from the upper surface of the cords to the branchiæ.
- m.* To the circulatory vessels.
- n.* From the ganglia.
- o.* Moto-sensitive or symmetrical nerves from the ganglia.
- p.* Their division to the post-abdominal feet.
- q.* Nerves from the upper surface of the cords.
- r.* The terminal pair to the rectum.
- s.* Terminal nerves from the cords and ganglia.
- t, v, w.* To the lamellæ of the tail.
- Fig. 41. The under surface of the 7th, 8th, and 9th thoracic ganglia, exhibiting the compound structure of the ganglia, which are situated entirely on the under surface.
- Fig. 42. The same portion of the nervous system viewed from the upper surface, and exhibiting the two halves of the motor column passing over the ganglia.
- Fig. 43. The nervous system of *Scolopendra morsitans*, LINN., of natural size.
- Fig. 44. A portion of the same magnified, and showing the involuntary or respiratory tract (*c*) passing in the median line above the motor column (*b*), which is seen distinct from the ganglia of the sensitive (*a*).
- Fig. 45. A lateral view of the same.
- Fig. 46. The motor surface of a ganglion (*a*), and motor (*b*) and involuntary tracts (*c*).
- Fig. 47. A lateral view of the same, showing the ganglia on the under surface, and the line (*d*) which separates the motor from the sensitive columns; the involuntary tract passing above them (*c*).
- Fig. 48. The cerebral and first subœsophageal ganglia of *Scolopendra*.
- A. Cerebral ganglia.
- B. Optic nerves.
- D. Antennal nerves with large ganglia at their base.
- E. The subœsophageal ganglion giving origin to the great mandibular nerves, and exhibiting their double origin.

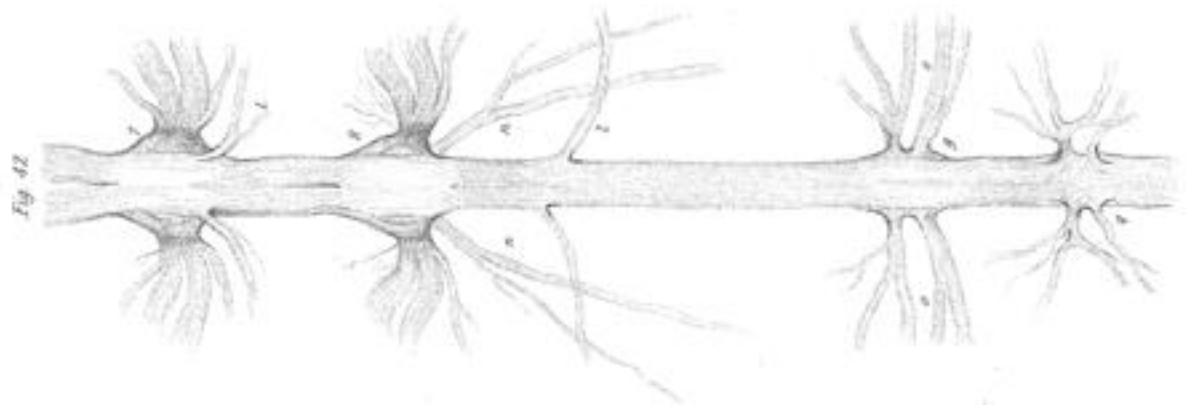


Fig. 42

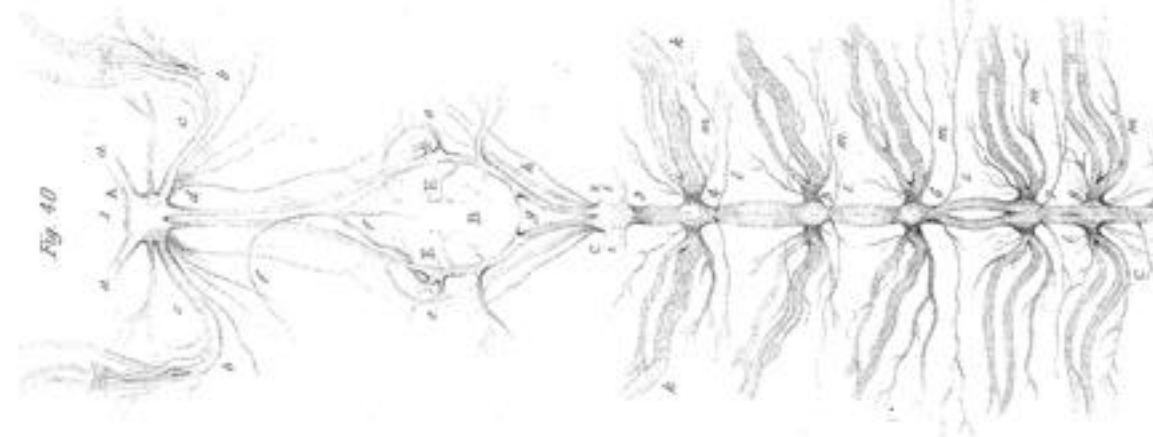


Fig. 40

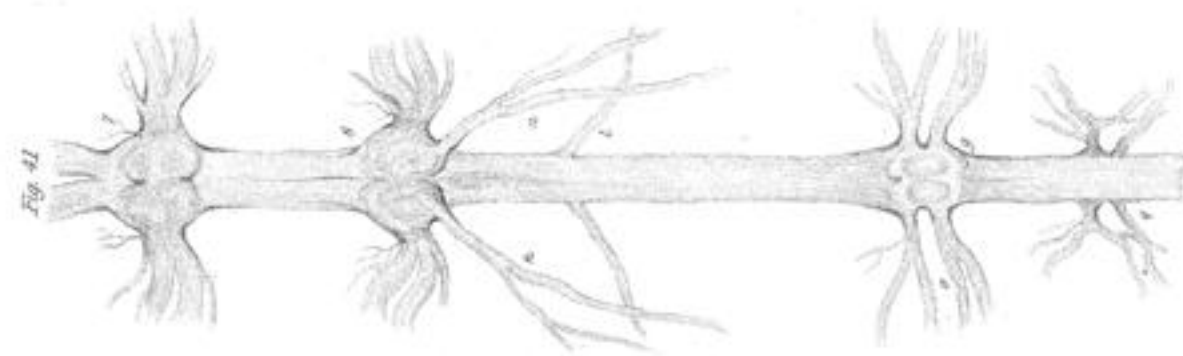


Fig. 41

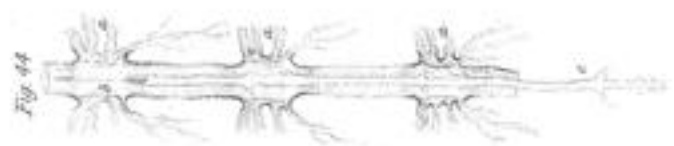


Fig. 44



Fig. 45

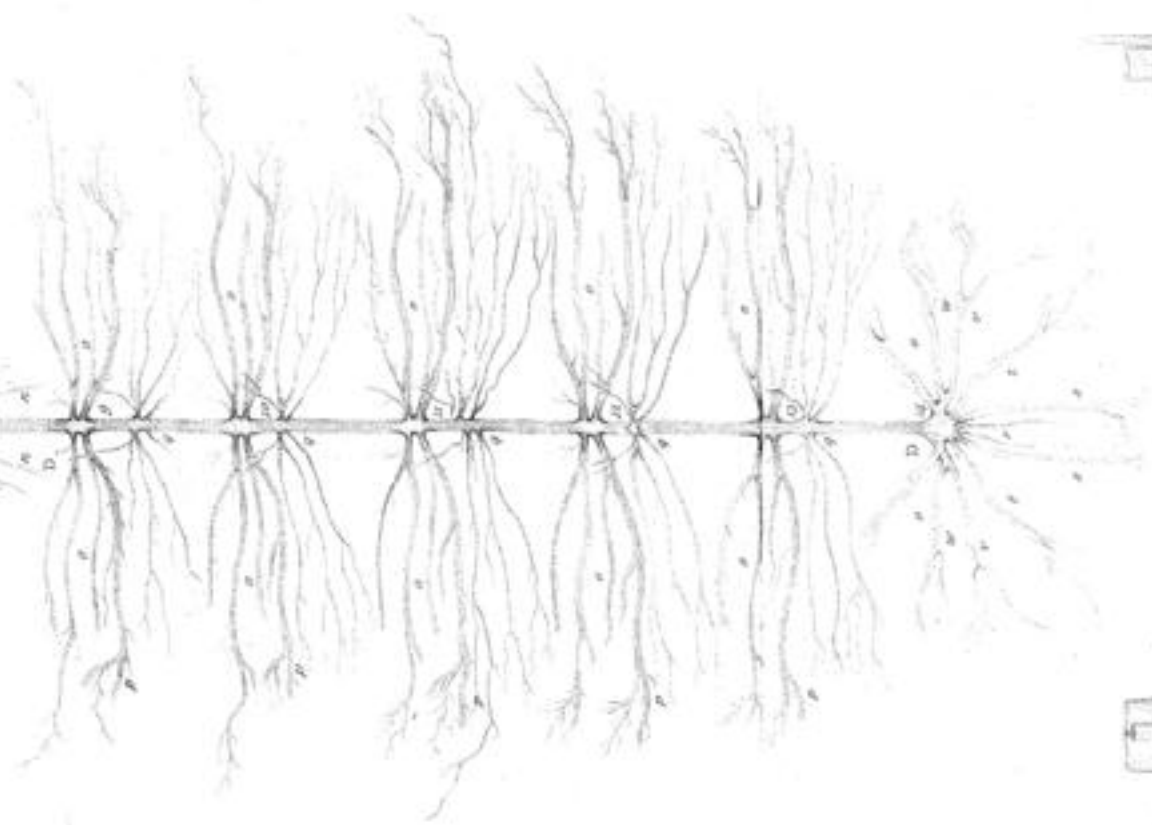


Fig. 43



Fig. 47

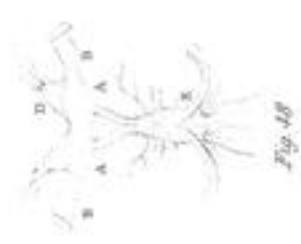


Fig. 48

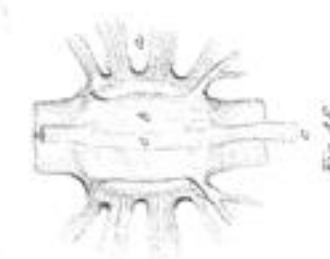


Fig. 46