2

PRIZE THESIS.

INAUGURAL DISSERTATION

ON THE

PHYSIOLOGICAL INFERENCES

TO BE DEDUCED FROM THE

STRUCTURE OF THE NERVOUS SYSTEM IN THE INVERTEBRATED CLASSES OF ANIMALS.

SUBMITTED TO

The Medical Faculty of the University of Edinburgh,

IN CONFORMITY WITH THE RULES FOR GRADUATION,

BY AUTHORITY OF

THE VERY REV. PRINCIPAL BAIRD,

AND WITH THE SANCTION OF

THE SENATUS ACADEMICUS.

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TO

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M.R.C.S. F.L.S.

TO WHOSE KINDNESS THE AUTHOR IS INDEBTED FOR HIS

ENTRANCE INTO THE PROFESSION

OF WHICH IT IS HIS PRIVILEGE TO BE A MEMBER,

TO WHOSE JUDICIOUS GUIDANCE

HE OWES MUCH OF HIS SUBSEQUENT SUCCESS,

AND ON WHOSE TRIED FRIENDSHIP

HE RELIES WITH CONFIDENCE FOR THE FUTURE,

THIS THESIS IS DEDICATED

BY HIS

GRATEFUL AND ATTACHED PUPIL.

INTRODUCTORY REMARKS.

THE department of Physiology, which embraces the phenomena of the Nervous System, is universally confessed to be so difficult, that it needs all the light which can be brought to bear upon it from any quarter, for its perfect elucidation. Amongst the sources of information which lie open to the enquirer, Comparative Anatomy is certainly among the chief; and it is perhaps to be wondered at, that more use has not been made of the data which it supplies. It has been with the view of bringing together the results of the investigations of various recent labourers in this extensive field, in such a form as to admit of comparison and generalisation, that the present essay has been undertaken. One of the principal objects which the Author has kept in view, has been to ascertain how far Dr. M. Hall's doctrine, regarding the distinctness of the *excito-motor* from the *sensori-volitional* system of nerves, accords with the data furnished by Comparative Anatomy. It will be seen from the concluding summary, that the Author has thus been led to an affirmative opinion on this question; and he gladly avails himself of this opportunity of giving publicity to the result of his enquiries. That he formerly withheld his assent from this part of Dr. M. Hall's doctrines, was solely because he did not consider them substantiated by the evidence adduced by that gentleman in their support; and his opinion on this point remains unchanged.

In the following Essay is embodied the principal part of the Dissertation read by the Author before the Royal Medical Society, on the evening of March 15th. With regard to the anatomical details which occur in it, the Author can lay no claim to originality, (with the exception of the description of the structure of the ganglia in the Articulata, § 76); since they are selected from recent systematic works, and from the Memoirs on the subject, with which the extended spirit of enquiry that is now so prevalent has caused the transactions of various Societies, both British and Foreign, to abound. These Memoirs, however, usually concern but a single Class of Animals, and sometimes but a single Species; and the details given have reference, more to the particular functions of the beings described, than to the General Physiology of the Nervous System. In many instances, therefore, the Author has given a very different form to the descriptions, (still, he hopes, preserving their accuracy,) for the purpose of bringing them into comparison; and whatever merit this Essay may possess, must be looked for, therefore, in the comprehensiveness of the survey which has been taken, and the probability of the inferences drawn from the facts brought under consideration.

The following are the chief sources from which the Author has derived his information :—

General Treatises.

Grant's Outlines of Comparative Anatomy.

Leuret, sur l'Anatomie Comparée du Système Nerveux.

Rymer Jones's Outline of the Animal Kingdom.

Dugès, Traité de Physiologie Comparée.

Müller's Physiology, translated by Baly.

Memoirs on Special Departments.

Echinodermata. Sharpey in Cyclop. of Anat. and Phys.

Mollusca. Cuvier, Mémoires sur les Mollusques. Garner in Linnæan Transactions, vol. XVII.

Deshayes on Conchifera, in Cycl. of Anat.

Rymer Jones on Gasteropoda, in do.

Owen on Cephalopoda, in do.

Owen's Memoir on Nautilus Pompilius.

Articulata. Newport in Phil.Trans. 1832, 1834, 1836.

Burmeister on Entomology (translated by Shuckhard.)

Lacordaire, Introduction à l'Entomologie.

Milne-Edwards on Crustacea.	Cyclopaedia of Anatomy and Physiology.
Owen on Entozoa.	
Audouin on Arachnida.	
Milne-Edwards on Annelida.	

On the *Sympathetic* and *Stomato-gastric* System.

Müller in Nova Acta Curios. Nat. vol. XIV.

Brandt in Ann. des Sci. Nat. NS. Zool. tom. v.

CORRIGENDUM.

The second sentence of § 78 will be read better as follows,—" How is it that motions may be excited in the members of a single segment by irritating them, when, the cord being divided above and below, its two tracts have no structural communication ?"

ON THE

PHYSIOLOGICAL INFERENCES, &c.

I. ON THE SUPPOSED NERVOUS SYSTEM OF PLANTS.

1. FEW Physiologists who have given such attention to the subject as to be competent judges of the question, now maintain the existence of a Nervous System in Vegetables. No traces of such a structure can be detected by the anatomist, who is able to analyse the tissues of plants, in the higher orders at least, with much greater certainty than those of the lowest tribes of animals. Nor is there anything in the phenomena of life presented by them which need induce the philosophic physiologist to infer the presence of a structure which cannot be demonstrated to the senses. The belief that *vitality*, or the capability of exhibiting those actions which collectively form Life, is dependent upon a Nervous Structure, must be regarded as a remnant of the exploded system of the Vitalists, which was scarcely less

erroneous, as a general theory, than the hypotheses of the Chemical and Mechanical Philosophers, in opposition to which it was first erected. We observe a Seed, which consists but of an aggregation of vesicles, appropriating to itself, when placed in circumstances favourable to its growth, the nutrient materials supplied by the surrounding elements; and developing itself into the perfect Plant; and we watch this Plant performing all the changes involved in the functions of Nutrition, Secretion, and Reproduction, by the exercise of the properties which its tissues and organs respectively possess. To suppose that these changes are *governed* by a Nervous System, *because* a Nervous System is found *associated* with the organs which perform them in the Animal kingdom, is obviously an unphilosophical hypothesis. We have no right to assume causes whose presence we cannot discover; and we should be led rather to question the *essential* nature of their operation in the second case, from finding them absent in the first, than to argue, from their supposed operation in the second, that they must also be efficient in the first.

2. If we were to carry out this train of reasoning, we should be brought to admit that something like a "diffused Nervous System" exists in every particle of matter, inorganic as well as organic; since there is no doubt that many of the actions of the living economy are of a strictly physical nature, and that many, if not all, of the changes in its composition involve the operation of chemical laws; and if these result from "nervous agency" in one case, by parity of reasoning, they must also in every other. This would bring us back to the old doctrine of the "Life of the World," which has not wanted some recent advocates among those who prefer a philosophy of "cloudy vastness," to one of defined outline and complete detail.

3. The truth appears rather to be, that every particle of matter is endowed with properties of various kinds, of which some manifest themselves under the simple conditions which the ordinary changes in the inorganic world supply, and thus perform the actions termed *chemical* and *physical;* whilst others can only be called into play under conditions of a more complex nature, which are only supplied by a living organised system, where many particles being combined by a previously-existing life into one structure, exhibit actions of a peculiar character, dissimilar to any they have heretofore presented, which are denominated *vital.* There can be no doubt that, where a nervous system exists, the vital actions of the being are *influenced* by it; but it would require evidence of a different character from any that has yet been adduced to prove that they are dependent upon it; and the *onus probandi* certainly rests with those who maintain a doctrine so contrary to the analogy furnished by a large proportion of the animated world.

II. NERVOUS SYSTEM IN THE LOWEST ANIMALS.

4. It is obvious that just ideas on the foregoing subject should lie at the very foundation of our system of Nervous Physiology; and they will even influence our views of its anatomical character. For, in the extensive group of ACRITA, in which are associated the lowest of all the types of structure presented in the higher forms of the Animal Kingdom, the existence of a "diffused Nervous System" is commonly regarded by naturalists as the necessary alternative resulting from the want of any definite indications of its presence. Many well-informed physiologists even have fallen into this error for such we must regard it; and it may

be worth while to enquire into the basis upon which it rests.

5. Is a Nervous System essential to endow the tissues of these beings with *contractility?* We cannot so regard it, since we find that property possessed in a high degree by the tissues of many plants, to which these beings bear a much greater *general* resemblance than they do to the higher animals; and we have also reason to regard this property as independent of nervous agency, although generally called into exercise by it, even in the highest of the latter group. Nevertheless, a physiologist of some reputation has recently spoken of the tissue of the Acrita as consisting of an union of the nervous and muscular structures in a "diffused form," denominating it *tissu neuro-myaire.** That a nervous system is not required by them for the performance of the functions of nutrition and reproduction, otherwise than to supply, by its locomotive actions, the conditions of those functions, would appear from what has been already stated.

6. If these phenomena do not constitute any evidence for the existence of a nervous system in such beings, it may be reasonably inquired what ground we have for placing them in the Animal kingdom. All our reason for attributing to them *sensibility* is derived from the movements which they execute in respondence to external stimuli; but such movements are also executed by the Dionæa and sensitive plant. But some of their actions appear to show a certain degree of *voluntary* power, and therefore of consciousness; being independent, so far as can be ascertained, of the operation of external stimuli. Moreover, we often see an impression made upon one part (one of the tentacula of the Hydra, for example,) propagated to distant parts, and exciting respon-

* Dugès, Physiologie Comparée, tom. i. p. 72.

dent movements in them, more rapidly than we could imagine to occur without such a channel of communication as a nervous system *only* is known to afford. These phenomena, then, would lead us to suspect the existence of a nervous system in beings that exhibit them; *not*, however, in a diffused condition, but in the form of connected filaments. For what consentaneousness of action can be looked for in a being whose nervous matter is incorporated in the state of isolated globules with its tissues? How should an impression made on one part be propagated by these to a distance? And how can that consciousness and will, which are *one* in each individual, exist in so many unconnected particles? The essential character of a nervous system is its capability of conducting excitor and sensory impressions *to* a centre, and motor impulses *from* it; and this cannot be effected by any such structure as the one imagined to exist in these beings. As well might we say that a "diffused" circulating system exists, where every part of the tissues is in equal contact with the surrounding medium, and equally performs the functions of absorption, assimilation, and excretion.

7. If, then, we allow any sensibility, consciousness, and voluntary power to the beings of this group—to deny which would be in effect to exclude them from the animal kingdom—we must regard these faculties as associated with *nervous filaments* of such delicacy as to elude our means of research; and, when the general softness of their textures, and the laxity of structure which characterises the nervous filaments in the lowest animals in which they *can* be traced,* are kept in view, little difficulty need be felt in

* Thus, in the Conchiferous Mollusca, the sheaths of the nerves are so loose, and the filaments they inclose have so little tenacity, that they were mistaken by Poli for lymphatic vessels, and the ganglia for receptacula chyli. Having been injected by him with mercury, they were beautifully figured under this character in his splendid work, Testacea utriusque Siciliæ.

accounting for their apparent absence.* The case is very different from that of plants, in which the negative evidence afforded by anatomical research is far more to be relied on.

8. The only animal among the POLYPIFERA in which a nervous system has been stated to exist, is the common *Actinia*, or sea-anemone. A description of a series of ganglia and diverging filaments, connected with the muscular base, was given by Spix;† but it is now generally agreed by competent observers, who have searched for it in vain, that the account is erroneous, and that no nervous filaments can be detected in that situation. Very considerable muscular power is exercised, however, by the tentacula and muscular integument of the Sea Anemone; and *that* with a consentaneousness which strongly indicates the combining or *internuncial* power of a nervous system. From the analogy of the Radiated classes, to which this animal approaches, we should be rather led to search for nervous structure around the entrance to the digestive cavity; and Professor Jones‡ has recently described a delicate filament which he suspects to be of this character, running round the roots of the tentacula, and imbedded in a strong circular band of muscle, which surrounds the orifice of the stomach, and acts the part of a powerful sphincter in closing the aperture.

9. There has been much vagueness in the comparisons

* An interesting fact has lately been communicated to the author by his friend, Mr. Edward Forbes, in regard to this question. Having collected a number of specimens of *Cydippe* (Beroe) *pileus*,—an animal in which a nervous ring has been stated by some to exist, and by others to be absent,—he was led to remark that extremely slight variations in the transparency of the individuals, and in the light under which they were viewed, would occasion the presence or absence of the filaments to be decided on by the observer.

† Annales du Museum, Tom. xiii.

‡ Op. cit. p. 43.

frequently drawn between the springs of action in these creatures, and the agents which operate in higher animals. And this may be attributed to the tendency which is prevalent among many physiologists to grasp at a superficial resemblance, instead of seeking for a more fundamental analogy. Thus, some naturalists seem by their language to imply that the little *Hydra viridis*, or green polype, possesses as much sensibility, and is as completely under the guidance of volition, as man himself. But what is the character of this interesting little being? It is *a stomach*, the orifice of which is provided with tentacula, that contract when irritated by the touch of any adjacent body, and endeavour to draw it towards the entrance. To what action in the human body is this most allied? Evidently to that of the muscles of deglutition, over which we know that *will* has no power, and whose actions probably do not even involve sensation, being of a simple *reflex* character. These, like the tentacula of the Hydra, contract upon whatever is brought within their sphere, and convey it to the orifice of the stomach; the only difference is that, in man and the higher animals, another set of muscles is superadded to these, in order to prepare the aliment for the operations of the stomach, and to bring it *within reach* of the pharyngeal constriction. But, it may be urged, does not the inactivity of the tentacula, when the Hydra is gorged with food, prove that they are excited to action by the will of the animal? We think not; and for these reasons:—The cavity of the stomach is evidently continued into the arms; and it is evident that, when the former is distended, the tissues of the latter also will be gorged with fluid. It is easy to imagine that this condition may be unfavourable to the exercise of their contractility; just as the distension of the tissues of a plant, by any check offered to the function of exhalation, speedily suspends their absorbent action. But we have a still more satisfactory explanation in the fact, that the muscles of deglutition in man are not called into action nearly so readily and energetically when the stomach is distended, as when it is empty—a fact of which any one may convince himself by observing the relative facility of swallowing at the commencement and termination of a full meal. No one will assert that *this* variation is an effect of the will; indeed, it is often opposed to it, being one of those beautiful adaptations by which the welfare of the economy is provided for, but which the indulgence of the sensual appetites opposes. Most of the movements of this animal, and of others of the class, appear to be equally the result of external stimuli with that already described; and it is only in a few instances, principally those of absolute locomotion or change of place, that any evidence of voluntary action can be discerned. There is no doubt that many of these movements are influenced by light; but it may be questioned whether the animal is conscious of its presence *as light*, or whether it may not be acted on by this stimulus somewhat in the same manner as plants are known to be, which grow towards it.

III. NERVOUS SYSTEM IN THE RADIATA.

10. The general characteristic of the Radiated classes is the repetition of similar parts round a centre, which is the place of the mouth or entrance to the digestive cavity. In many of the species included in the group, however, this repetition is but obscurely traced; it is by these that the transition is effected to other classes. Wherever a nervous system has been traced, it has been found to partake of this

character, presenting the form of a ring surrounding the mouth, and sending off filaments to each of the segments of the body.

11. The peculiar softness of the tissues of the animals composing the class Acalephæ, renders the detection of a nervous system in them a matter of some difficulty and uncertainty.* No continuous filaments have as yet been certainly traced in the larger *Medusæ*, where the locomotive powers of the structure would lead us to suspect their existence. Ehrenberg, however, has recently described two nervous circles in their disks—one running along the margin of the mantle, and furnished with eight minute ganglia, from which filaments proceed to the eight red spots which he supposes to be eyes;—whilst the other is disposed around the entrance to the stomach, and furnished with four ganglia, from which filaments proceed to the four tentacula. In the little Beroe (*Cydippe pileus*), however, the nervous system can be seen without dissection, though not always with certainty (§ 7, *Note*); and it presents the form of a double ring around the mouth, with eight minute ganglionic enlargements, from which filaments diverge to the spaces between the longitudinal ciliated bands.†

12. In the Echinodermata, we shall find the same type of structure manifested with little variation. We may first enquire, however, into the character of the sensory and locomotive powers which the animals of this class possess. Their movements are of various kinds. Change of place is principally effected by the extension and contraction of the tubes which are protruded from the apertures in their covering.

* A *Medusa*, which, when taken out of the water, weighs fifty ounces, is reduced by drying to a few grains.

† *Grant*, in Trans. of Zool. Soc., vol. i.

These tubes possess a fibrous contractile structure, by which they are shortened when occasion requires; and their protrusion is effected by projection of fluid into them from cavities within the body. By means of suckers at their extremities, the animal fixes upon some firm surface those which it has advanced; and then, by contracting them, draws itself forwards. It may perhaps be doubted how far this *contraction* of the tubes is effected by any stimulus communicated from the nervous system, or whether it is not rather the effect of the elasticity of the tissue coming into play when the distending force is withdrawn; just as the claws of the feline tribe are retracted by their elastic ligament, when the protruding muscle ceases to act. We can hardly avoid the belief, however, that the internal reservoirs of fluid must be influenced by the nervous system, in order to produce that *consentaneousness* of action which is essential to the regular movements of the animal.

13. Besides these instruments of locomotion, the *Asterias* seems to possess the power of altering the form of its whole body, by bending its rays towards either surface, or approximating them laterally, by which it can adapt itself to the passages through which it is creeping, and even assist in drawing its prey towards the mouth. This seems effected by muscular fibres, running both longitudinally and transversely along the rays. The *Holothuria* has a muscular system of the same kind, but much more developed, by which the general cavity of the body may be dilated or contracted, and by its means change of place seems to be partly effected, as well as the regular inspiration and expiration of water, which is performed at definite intervals. The stem and branches of the ramifying respiratory apparatus itself are also provided with muscular structure, and contract when irritated; they are even able to carry on the respiratory move-

ments to a certain degree after the sac has been cut open.* The tegumentary covering of the *Holothuridæ* is particularly susceptible of irritation from external objects—the slightest touch often causing powerful contraction. We can scarcely regard either this or the respiratory movements as of a *voluntary* character; they would rather seem to be the result of a simple reflex action; and it is a curious evidence of their being but little subject to the control of the will, that the contraction is often so powerful as to rupture the membrane of the cloaca, and to force large portions of the intestine through the aperture. The density of the integument in the *Echinus* altogether prevents any such movements of contraction and expansion; and the respiratory currents in it, as in the *Asterias*, are produced by the vibration of the cilia which cover the membrane lining the shell and the other aerating surfaces. But in this animal there is another series of movements (besides that of the spines), no less remarkable—those of the dental apparatus—by which it is enabled to break down the firm calcareous shells of the crustacea on which it feeds, and other bodies of equal density.

14. The Echinodermata have not been usually regarded as possessing any other sense than that of touch, which seems to reside in their extensile feet, and especially in those modifications of them which are placed round the mouth, and serve especially as *tentacula*. Ehrenberg, however, is disposed to regard certain red spots, at the extremity of the rays, as rudimentary organs of vision; and he states that the nervous trunk is continued towards each, and swells into a sort of ganglion, where connected with it. The recent observations of Mr. E. Forbes seem to confirm this belief—that gentleman having pointed out a curious disposition of

* Cycl. of Anat., vol. ii., p. 41.

the spines round these spots, by which they can completely fold over and protect them; whilst he has also remarked that the animal seems by their means to take cognisance of objects of food at a little distance from them. It may be doubted, however, whether a distinct visual perception is produced through their instrumentality; or whether the impression thus excited is not rather of a more general character, analogous to that formed by the organ of smell. It may further be doubted whether the contraction of the tubular feet, in respondence to external irritation, necessarily involves *sensation*. Considering these organs as analogous in function and character with the fly-trap of the Dionæa, or the tentacula of the Hydra, on the one hand, and (so far as the prehension of food is concerned) with the muscles of deglutition in the higher animals, on the other, we should rather incline to a negative opinion.

15. The nervous system of the ECHINODERMATA appears to consist essentially of a filamentous ring surrounding the mouth, which presents ganglionic enlargements equal in number to that of the segments of the body; and from these diverge the filaments which connect this central apparatus with distant organs. In the *Asterias* this ring may be distinctly traced; and from each of its ganglia a large branch is transmitted to the corresponding ray, whilst two smaller ones pass downwards to be distributed to the stomach and other viscera included in the centre of the star. A similar ring is stated by Dr. Grant, (and more recently by M. Van Beneden,) to exist in the *Echinus*, which sends filaments to the dental apparatus, and others along the course of the vessels to the digestive cavity. According to Dr. Grant, also, a similar ring exists in the *Holothuria*, which sends nerves to the mouth and the surrounding tentacula; others to the stomach and alimentary viscera; and

others, again, to the muscular bands, which form part of the tegumentary apparatus. In the *Siponculus*, an animal which approaches the vermiform tribes in the aspect of its elongated body, though it still retains the essential characteristics of the Echinodermata, we observe two of the longitudinal filaments more developed than the rest; and these are situated on what may be termed the ventral surface of the animal, so as to indicate a transition to the double nervous cord of the Articulata.

16. In this nervous apparatus, then, it is evident that several distinct functions are combined. The nerves, which, from their distribution on the viscera, we should regard as analogous to the sympathetic of higher animals, are not isolated at their central termination from those which appear connected with the sensorial and locomotive functions. Nor are those which minister to the instinctive actions separable from those which convey the influence of the will. It is important to observe that, in the typical members of the group at least, every segment of the body is equal in its character and endowments, and that each has a ganglion appropriated to it. None of these ganglia are different from the rest, and neither, therefore, can be regarded as having any *presiding* character.

17. All the movements which take place in respondence to external* impressions may, therefore, be regarded with probability as originating in the ganglion of the segment upon which the impression is made, and as propagated to the rest by the connecting filaments which form the ring. These movements, it can scarcely be doubted, constitute by far the

* The term *external* is here employed in the usual metaphysical sense, to imply that which does not originate in the *mind*. The impression may arise from some state of the corporeal structure itself, such as that which occasions in man the sensation of hunger.

greater part of those which the animals exhibit; and the purely instinctive character of almost all the operations which they are known to perform, together with this remarkable equal subdivision of their centres, may well leave us in doubt how far they can be regarded as possessed of anything like our reasoning powers, or as actuated by the *voluntary* impulses which result from their exercise. It is remarkable, too, that all the ganglia should participate equally (as they appear to do) in the *special* sensation of sight.

18. We shall have some ground, then, for assuming in our future inquiries, that whenever a nervous cord *terminates* in a ganglion,* that ganglion may be regarded as the centre of the functions it performs; receiving the impressions made upon it, and exciting respondent motions, without any exercise of the will being necessarily concerned. We shall hereafter find, however, that this is seldom the case to its full extent; but that where a ganglion is situated upon a nervous cord, *part* only of its filaments usually enter the mass, whilst a portion of them pass over or alongside of it, towards some other ganglionic mass, which seems to have a presiding influence over the rest.

IV. NERVOUS SYSTEM OF THE MOLLUSCA.

19. Feeble as are the animal powers in a great proportion of the Molluscous tribes, they would seem to be almost

* It is necessary, however, to limit the nature of the structure to which the term *ganglion* is here applied. It is intended to include those of the *symmetrical* system of the Invertebrata, and the brain and spinal cord of Vertebrata, which, as will be hereafter shown (§ 45, and 76—8), correspond in the relation of the white and grey matter they contain. The *intervertebral* ganglia of the spinal nerves, and those of the *sympathetic* system, have a very different structure (§ 45), and probably also perform functions of an entirely distinct character.

extinct among the members of the class TUNICATA or *Acephala Nuda.* No beings possessed of a complex internal structure, a distinct stomach and alimentary tube, a pulsating heart, and ramifying vascular apparatus, with branchial appendages for aerating the blood, and highly-developed secretory and reproductive organs, can be imagined to spend the period of their existence in a mode more completely *vegetative* than these. The greater number of them pass their whole lives in one situation, attached by a pedunculate prolongation of their external tunic to submarine rocks ; many of the inferior species associate together like the Polypifera (the higher tribes of which they much resemble,) to form a compound structure, in which several animals are more or less closely united ; and those which are not attached to fixed points have little independent locomotive power, but are driven about at the mercy of the waves.

20. These animals are enveloped in a tough elastic tunic (the analogue of the *valves* of the Conchifera) ; and within this is found a muscular coat, consisting of fibres crossing each other in various directions, by which compression may be exercised on the contents of the cavity it surrounds. Two openings penetrate these sacs ; one, termed the *branchial*, admits water to the general cavity, partly for the purpose of aerating the blood, and partly to bring food to the digestive orifice ; the other, termed the *anal*, gives exit to the current which has passed over the respiratory surface, and also to the contents of the intestine and ovaria. These openings are bounded by distinct circular sphincters, with which radiating muscular filaments are intermixed, that extend in longitudinal bands over the surface of the sac.

21. By means of this apparatus, the animal is capable of diminishing the capacity of the branchial sac, and thus of

ejecting, with considerable force, a part of the water it contains; whilst the elasticity of the external tunic spontaneously restores its usual dimensions when the contracting power is inactive. No movements of this kind, however, are commonly employed, either for the respiratory process, or for the prehension of food. A continuous and equable current of fluid enters the branchial orifice, and is propelled by the anal, without any other visible physical agency than the movement of the cilia which cover the aerating surfaces. The mouth, or entrance to the stomach, is situated at the bottom of the branchial sac, and is unprovided with any special sensory apparatus; it seems to derive its supplies from the respiratory current alone, and not to depend upon any prehensile movements; but particles unfit to enter it are probably stopped at the branchial orifice, (§ 24.) Moreover, as each animal possesses within itself all the organs necessary for the propagation of its race, and as these appear contrived simply for the passive evolution of germs, no powers of active motion are called into exercise by the performance of this function.

22. So far as the regular vital operations are concerned, therefore, we see no indication of *voluntary* actions in these animals, or even of that kind of respondence to impressions, which would lead us to suspect the existence of a connected nervous system. But, in the simultaneous contraction of the whole muscular sac, which is occasionally witnessed, we can scarcely fail to acknowledge the operation of nervous agency. If one of these animals be touched, when its cavity is full of water, a jet of fluid is thrown out to some distance; and sometimes a number "are so closely impacted together on the rocks, that the impression given to one causes it suddenly to retract, which acts also on the one next to it, and

so on throughout several of them, and each in contracting throws out a quantity of water."*

23. We find, accordingly, on examining into the character of the nervous system, that it is most simple in its structure and distribution. We have here no repetition of parts as in the Radiata, and one ganglion serves as the centre of all the actions to which this system ministers. This ganglion lies between the two orifices, and sends filaments towards each, as well as others that ramify upon the muscular sac, to which they seem almost exclusively confined. In Fig. 2, are seen the position of the ganglion, and the distribution of its filaments in *Ascidia Mammillata*.† The nervous filaments which pass to the branchial orifice diverge to enclose it, and meet again beyond, so as to form a complete ring; and sometimes, according to Dr. Grant, a small ganglion is found at the point of their reunion. Some small ganglia have been described by Meckel and others, as occurring among the viscera; but their presence is, with much reason, doubted by Mr. Garner.‡ If such should be proved to exist, it is manifest that they are to be regarded as rudiments of a sympathetic system; which does not, however, manifest itself in so distinct a form in any of the lower Molluscous classes.

24. The only organs of special sensation that this animal can be regarded as possessing, are the tentacular filaments which fringe the interior of the branchial orifice. Although nothing is absolutely known of their function, it would not seem improbable that they are susceptible of impressions from substances entering with the respiratory current; which, being propagated to the ganglion, may excite the

* Grant's Lectures on Comp. Anat. xxxii.

† Cuvier, Mem. sur les Mollusques. ‡ Loc. cit.

closure of the sphincter, by means of the motor nerves, and thus prevent the admission of injurious bodies. Should this be the case, we can hardly regard the action as of more than a *sympathetic* character, since the closure of the sphincters in the higher animals is, in like manner, independent of the impulse of volition, although capable of being influenced by it. It would seem probable, too, that by the same sphincter is regulated the quantity of water which shall enter for the supply of the respiratory and digestive systems, in accordance with their requirements, communicated in like manner through the ganglion; and the ciliary movements would appear to be under the same control, (although not so in higher animals,) since, in those beings which make use of them for the acquirement of food, such as the common wheel-animalcule, they stop and recommence in such a manner as to prevent the observer from assigning any other cause to their variations.

25. We next pass on to the CONCHIFERA, or *Acephala Testacea*, a class which, though somewhat higher in the scale than that just described, has a very close affinity with it. Instead of an elastic external tunic, we find a calcareous structure enveloping the body, formed of two valves united by a ligament, and by one or two adductor muscles. In this case, as in the former one, the elasticity of the ligament maintains the natural expanded state of the cavity of the shell; whilst the contraction of the adductor muscle, which is evidently under the control of nervous influence, draws the edges of the valves in close apposition to each other when the animal is threatened with injury. The mantle which forms the cavity that contains the viscera, is less muscular than in the Tunicata; and the respiratory current is maintained through its branchial and anal orifices, just as in that class, without any other apparent means of propul-

sion than the vibration of cilia. Sometimes these orifices are prolonged into tubes or siphons; whilst, in a great proportion of the class, the cavity of the mantle is left entirely open, by the incomplete adhesion of its lobes along the margin of the shell.

26. A good deal of variety exists among the members of this class in regard to the development of the locomotive and sensorial powers. In some of the lowest, neither would seem to be much exalted above those possessed by the Tunicata. The *Oyster*, for example, attaches itself to rocks by calcareous exudation from the secreting surface of the mantle, and passes the term of its existence in a state of inactivity which is only interrupted by the occasional closure of its shell. It is entirely dependent upon the motion of the surrounding element for its supplies of food; and, as its digestive cavities are found to contain only small particles of vegetable matter, it does not require for the prehension of its aliment any complex apparatus in which active movement is essential. Here, too, each individual possesses the entire reproductive apparatus within itself; and even if, as has been recently maintained, the proximity of two individuals is requisite for the fertilisation of the ova, it is quite certain that no change of place is involved in the function.

27. A somewhat greater advance, however, is witnessed in the sensory apparatus. Late observers state that distinct, though slightly developed organs of vision may be detected at the margin of the mantle.* These, no doubt; may serve to indicate to the animal the approach of danger, and cause it to employ its only means of defence,—the closure of its shell,—an action evidently analogous with the contraction of the enveloping muscle of the Tunicata. This

* Garner, loc. cit.

accounts for the fact known to fishermen, that the shadow of a boat passing over a bed of oysters, causes the animals beneath to close their shells. An important change also here takes place in the position of the sensitive tentacula which guard the entrance to the alimentary canal. These are now developed from the true mouth, which still remains within the cavity of the mantle; and the orifices of this cavity are almost destitute of them, even when prolonged into siphons. Where the cavity is left open, it is obvious that there is nothing to prevent foreign substances from immediate contact with the mouth, although the margins of the mantle still appear possessed of greater sensibility than its other parts. The two pairs of long flexible tentacula or palps, with which the mouth is furnished, seem designed to guard its orifice, by causing its closure against substances unfit to enter it, rather than to convey nutritious particles to the entrance of the tube, which is sufficiently accomplished by the respiratory current.

28. In the nervous system of the Oyster, we find but a slight advance upon that of the Tunicata; and this has reference more to the increased importance of the sensory organs, than to the development of locomotive powers. The principal ganglion (B, Fig. 3) is situated by the adductor muscle, between the branchiæ, and hence may be called the *posterior* ganglion.* It obviously corresponds, both in situation and in its relation to the respiratory organs, with the single ganglion of the Ascidia; though part of the functions of the latter are here performed by a separate centre. It sends branches to the mantle (*a*), others to the branchiæ (*b*), small twigs to the adductor muscle (*c*), and two trunks (*d*, *d*,), which connect it with the *anterior*

* Garner, loc. cit.

ganglia (A, A). These ganglia are very small in the Oyster, and are situated considerably below the entrance to the œsophagus (s); they are united by a transverse filament (*e*), which passes under that tube, but they also send forwards a large branch(*f*), which arches over the mouth. The principal branches from these ganglia, besides the connecting trunks, are distributed upon the tentacula and the anterior portion of the mantle. These anterior ganglia being alone connected with the special sensory organs, will obviously have a superior influence on the movements of the animal; but as they are not immediately connected with the adductor muscle, it is obvious that whatever motor impulse may result from irritation of the tentacula, must be propagated along the cords which pass to the posterior ganglia. On the other hand, the posterior ganglion may be considered, from its size and connections, as the centre of the actions performed by the organs which it supplies, when these are stimulated by impressions made on or originating in themselves. Such would probably be the case with respect to the respiratory movements, to direct which would seem to be the special function of this ganglion. Besides the branches which have been mentioned as proceeding from it, there are some minute filaments sent by it to the viscera; and it would thus seem, like the ganglia of the Asterias, to unite the offices of both systems which are separate in the higher animals.

29. The whole course of the lives of these animals shows them to be so little elevated in the scale of psychical endowment, that we can scarcely regard the motions executed by them as often possessing a voluntary character; they may rather be compared with the involuntary or sympathetic actions of the higher classes;—the closure of the shell, for example, resembling in its *protective* tendency the contrac-

tion of the pupil under the stimulus of light, or the closure of the glottis against irritating matters. It may not, perhaps, be a departure from rigid analogy to suppose that, whilst the movements connected with their vital operations result, like those having a similar *immediate* connection in the higher animals, from changes in the nervous system, in which *mind*, in its restricted sense, cannot be said to participate, these animals may experience a sense of enjoyment or well-being, arising from the fulfilment of these operations, corresponding with that which man experiences during the digestion of a sufficient but not excessive meal, and relatively higher in degree, because not subordinated to others.

30. In the higher species of this class, we find a peculiar locomotive organ developed, which serves a variety of important purposes. This organ, which is termed the *foot*, has a firm muscular structure, and is capable of very energetic action. Sometimes it is employed in burrowing in sand or mud; and sometimes in executing sudden and rapid motions—true leaps—by which the animal is enabled to change its place with great celerity. These motions are frequently executed in such a manner as to imply consciousness of the most advantageous direction for them, and therefore the operation of a guiding *will*. A curious instance of this kind has been elsewhere mentioned by the Author;* and he has since learned that it is no uncommon thing to see animals of this kind making their way along the sea-shore in the most direct line towards the water, as if conscious of its proximity. The foot is largest and strongest in the most active species, which never form any local attachment; but, in others, its principal function seems to be to form the *byssus* which attaches them to rocks, and it is then reduced to a rudimentary condition.

* Principles of Gen. and Comp. Physiology, p. 99.

31. Wherever the *foot* exists in the Conchifera, we find an additional ganglion in close relation with it, being usually situated at its base, and following its changes of position, as well as corresponding with it in degree of development. As the nerves proceeding from it, with the exception of the trunks that connect it with the anterior ganglia, are almost entirely distributed on this organ, it may with propriety be called the *pedal* ganglion; or, from its position, the ***infe-rior***. Of this we shall see a good example in the ***Pecten*** (Fig. 4). Here the anterior and posterior ganglia have pretty nearly the same relation as in the Oyster, except that the latter have partially separated, so as to form a bilobed mass, which, in other instances *(Modiola)*, becomes completely double. The anterior ganglia, however, are much larger in proportion; and, besides transmitting the usual branches to the posterior ganglia, they are connected by two considerable trunks with the pedal ganglion (c).

32. In considering the relative functions of these ganglia, it is important to remark that, whilst the *pedal* or inferior ganglion, and the *posterior* single or double ganglion, are always connected with the *anterior* ganglia, they are never immediately connected with each other. This would seem to indicate that their functions are distinct, though partly dependent on the influence of the anterior ganglia. With regard to the *posterior*, it has already been stated to be principally connected with the *respiratory* apparatus; and all the reflex actions of the parts which it supplies are probably effected by its instrumentality alone. The influence of the *pedal* ganglion over the foot is probably of a similar character. The general movements of the organ may be directed by the cephalic ganglia; whilst the particular actions by which it fixes itself upon a given surface, and adapts

its disk to the inequalities which it encounters, may be produced simply by impressions reflected through this ganglion by its afferent and efferent nerves. Although such a view must be admitted to be hypothetical only, as regards this class of Animals, it will be hereafter seen to derive remarkable confirmation from the actions of the suckers of the Cephalopoda in relation to their ganglia (§ 60, 67), and from similar experiments on the independent functions of the pedal ganglia in Insects and other Articulata (§ 80.)

33. The cephalic ganglia, although still beneath the œsophagus, must be regarded as having a presiding influence over the others, being the residence of whatever sensibility to impressions of a *special* kind these animals may possess, and therefore, in all probability, the instruments of their psychical operations. Their immediate connection with both of the other divisions of the nervous system evidently favours this idea; and any actions which result from visual impressions, or from irritation of the tentacula, may, therefore, be regarded as originating in them. In this point of view, whilst the anterior ganglia may be compared with the upper part of the cerebro-spinal axis in vertebrata, the branchial ganglia would be analogous to the medulla oblongata,* which is the recipient of impressions and the originator of motions connected with the respiratory function; and the pedal ganglion would be regarded as corresponding with one of the ganglia in the double column of the Articulata, and therefore (as will hereafter appear, § 79) with *one segment* of the spinal cord in Vertebrata.

34. In some of the highest species of this class, as *Mactra*,

* It will presently be seen that the *distance* of the branchial from the cephalic ganglia in the cases hitherto mentioned is no obstacle to this analogy; the position of the former being entirely regulated by that of the gills.

which show more activity than the rest, the cephalic ganglia are actually anterior to the mouth, and nearly meet over it, as shown in Fig. 5.

35. In the next class of Mollusca, the GASTEROPODA, we recognise a type of the nervous system essentially the same with that just described, but modified to correspond with the conditions in which the animals are formed to exist, and especially with the changes in the situation and development of their locomotive and sensory organs. Although none of this class possess very active powers of locomotion, few are entirely fixed; all are more or less dependent upon the exercise of these powers for their supply of food; and the higher tribes employ them also in the perpetuation of the race, since the connection of two individuals is in them an essential part of this function. Among the testaceous species, locomotion is principally effected by the alternate expansions and contractions of the fleshy disk termed the foot; by which the animal is enabled to crawl slowly along solid substances, whether on land or in water, with a slow but equable progression. In some of the aquatic species, this disc is convertible into a kind of boat, by the buoyancy of which the animal can suspend itself in an inverted position at the surface of the water, and then employ its tentacula and mantle as instruments of progression. Some of the naked aquatic species are still more active, moving through the water by the undulation of their whole bodies, like the leech or the vermiform fishes; and some appear materially assisted by an expansion of the mantle on the anterior part of the body, which contains muscular fibres, and probably acts as a fin. Besides these motions, all the testaceous species have others by which the place of the body is changed in reference to the shell; special muscles (obviously analogous to the *adductors* of the conchifera) being provided, by which the

parts that are occasionally protruded can be immediately retracted within it.*

36. In every division of the animal kingdom, we find the development of special sensory organs to bear a close relation with that of the locomotive apparatus. In the present instance, we observe an evident example of this general fact. The organs of vision, which, when existing at all among the Conchifera, were very imperfect, are here almost constant and more highly developed; the tentacula are more sensitive, and sometimes increased in number to six or eight; and there is reason to suspect that some of them occasionally minister to the sense of smell. These senses, as well as the locomotive powers of the animal, have an obvious relation with the supply of the digestive system, which is not here, as in the inferior classes, dependent upon the miscellaneous aliments conveyed to the mouth by the movement of the surrounding fluid medium, but is more limited as to the character of the food to which it is adapted, and conse-

* A very remarkable instance of the rapidity with which these muscles sometimes act is witnessed in the case of the *Patella* (Limpet) and *Haliotis.* The former animal, as is well known, usually adheres to those levels of rocks which are occasionally exposed to the air, and again submerged by the tide. They are favourite articles of food to crows, which sometimes pick them dexterously off the rocks,—placing the point of the bill beneath the edge of the shell, which, when the animal is at rest, is usually a little removed from the rock (as in the Oyster from its fellow); but, if this be not done with sufficient quickness, the animal draws its shell closely down to the rock, and holds the bill of the crow so firmly that the bird is often drowned by the rise of the tide. In like manner, men have been occasionally sacrificed in the attempt to remove a large species of Haliotis which inhabits the Tropical and Southern Ocean. This animal (whose shell is much valued for its brilliancy, both on the exterior and interior surfaces) usually resides at a depth of a few feet under water. If the diver be sufficiently quick in his operations to tear the animal from the rock before it can put its retractor muscles in action, the task is not difficult; but if these are once made to contract, the shell is drawn to the rock so closely as to retain the fingers beneath it too firmly for extrication. The latter fact was communicated to the author by his friend Mr. S. Stutchbury, who has known instances of its occurrence.

quently requires the means of becoming acquainted with the proximity of what it can digest. This is well seen in the common snail, which, "although at rest within the shelly covering that forms its habitation, will with great quickness perceive the proximity of scented plants which are agreeable articles of food, and promptly issue from its concealment to devour them." It is not a little curious, however, that although the general surface appears highly susceptible of impressions which excite responsive movements adapted to fulfil some important office in the economy, it does not seem to be susceptible of *painful* impressions in any thing like the same degree. This, which cannot but be regarded as a beneficent provision for the happiness of animals so helpless and so exposed to injury, would appear from the observations of various experimenters, and especially from the testimony of M. Ferrusac, who says, "I have seen the terrestrial gasteropods allow their skin to be eaten by others, and, in spite of large wounds thus produced, show no pain." The fact has an important bearing on our general views of the operations of the nervous system; since it would seem to confirm an opinion founded upon other phenomena, that the *impressions* which produce *reflex* actions through the nervous system do not always involve the production of *sensation.*

57. We may easily recognise in the nervous system of this Class the same general type which it presented in the Conchifera, with an advance, however, in the higher species towards a more developed condition. The *anterior* (now become *cephalic*) ganglia are larger in proportion, and exhibit a tendency to gain a position anterior to the œsophagus, and to approximate towards each other, so as to meet and form a single ganglion on the median line. The *branchial* ganglia are constantly to be met with, but their posi-

tion is extremely various. This centre always, however, bears a close relation with the gills, both in situation and degree of development; and even where apparently conjoined, as it frequently is, with the pedal ganglion, it may be distinguished from it by the distribution of its nerves, as well as by its separate connection with the cephalic ganglia, which is always noticed in such cases (§ 38 and 42). Sometimes the functions of this ganglion are subdivided between two, of which one is still appropriated to the branchiæ, whilst the other is connected with the general surface of the mantle and respiratory passages, and hence may be called the *palleal* ganglion. The position of the pedal ganglion (which is here generally double) also varies, but in a less degree, since it is generally in the neighbourhood of the head. Where no distinct foot exists, but the locomotive movements are executed by the action of the whole mantle (as in most of the naked species, both terrestrial and aquatic), we still find a ganglion to which they appear equally due (§ 42).

38. As an illustration of one of those simpler forms of the nervous system presented in this class, which connect its more complex type, (to be hereafter noticed,) with that of the inferior groups of the Mollusca, we may adduce that of the *Patella*. At the base of the tentacula, and rather anterior, therefore, to the œsophagus, we find a pair of ganglia (A, A, Fig. 6), which evidently correspond with the anterior ganglia in the Conchifera, and which are connected by a commissural band passing over the œsophagus. These, however, not only send nerves to the tentacula, but are also connected with the eyes, which are situated at their base. Beneath the œsophagus, and connected by *two* trunks with *each* of the cephalic ganglia, we find a broad mass, which, upon examination, appears to consist of four lobes placed in a

line. The two inner ones (c, c,) send nerves to the foot, and are thus evidently analogous to the *pedal* ganglia of the Conchifera. These are connected with the cephalic ganglia by one of the trunks which we observe on each side. Externally to them are the *branchial* ganglia (B, B,) which also are connected with the cephalic ganglia by a separate trunk, as well as with each other by a filament that may be distinctly traced through the pedal ganglia.* Besides supplying the gills and mantle, these ganglia, like their analogues among the Conchifera, send branches to the shell muscles, and some small ones to the viscera. That they are specially *branchial* ganglia, however, is proved by this. Mr. Garner has remarked that, in *Fissurella*, (an animal generally resembling Patella, but differing from it in having the branchiæ removed to the back of the neck,) in which Cuvier noticed the deficiency of the two external lobes of the subœsophageal mass, the ganglia really exist, but are removed to a different position,—namely, the base of the branchiæ on the back.

39. Besides these nerves, we find in the Patella, as well as among the Gasteropoda in general, a separate system connected with a very important set of organs, the gustatory and mandicatory, which are but slightly shadowed out among the Conchifera. In these animals we find the œsophagus dilated at its commencement into a muscular cavity, with a curious rasp-like tongue, which serves to reduce the food; often supported upon cartilages, and sometimes furnished with horny maxillæ. The nerves which supply these do not proceed directly from the cephalic ganglia; but are a part of a distinct system, which sends its ramifications along the œsophagus and stomach, and which is occasionally connected with the first by inosculating filaments. This set of

* Garner, loc. cit.

ganglia and nerves, which is even more important from its relative development in some other classes, and into the analogies of which in the nervous apparatus of vertebrata we shall hereafter enquire, (§ 92, 3,) may be called from its distribution the *stomato-gastric* system. In the *Patella* we find a broad ganglionic band (D) lying beneath the œsophagus, and forming with its nerves another ring round it. This band is connected, in most Gastéropoda, with the cephalic ganglia; but in the Patella, it sends its connecting filaments to two small ganglia (E, E,) anterior to the cephalic, which supply the lips, and which seem intermediate between the two systems. In the Cephalopoda, we find these labial or tentacular ganglia attaining considerable development; but in the Gasteropods, in general, they do not appear to be separated from the cephalic.

40. A higher form of the nervous system is that found in the *Aplysia*, which has been minutely described and well figured by Cuvier.* In this animal, we find that the cephalic ganglia have become entirely supra-œsophageal, and have coalesced to form one mass (A, Fig. 7). Beneath this are two lateral ganglia (C, C,) which are connected with it and with each other so as to complete the œsophageal ring. These ganglia supply the foot and mantle, and are, therefore, to be considered as *pedal* or locomotive ganglia. We here find indicated, however, the separation which exists in other Gasteropoda and in the Cephalopoda, between the nervous centres supplying the foot and the mantle; for the commissure which unites them beneath the œsophagus is not a simple nervous cord, but consists of two filaments which diverge to embrace the aorta, — a relation which they hold when proceeding from separate ganglia; and the cords

* Mem. sur les Mollusques.

which connect them with the cephalic ganglion, consist of *three* nerves on each side, of which two apparently belong to these lateral ganglia, and the third to the posterior ganglion next to be described. This ganglion (B) is situated at some distance from the others, lying among the viscera at the posterior part of the body, among which it is partly distributed. Hence it was regarded by Cuvier as a sympathetic ganglion; but there is more justice in the view of Mr. Garner* that it is principally a *branchial* ganglion, a large part of its nerves being distributed to the respiratory organs. It is connected by long filaments with the lateral ganglia; and part of these cords seem to pass on to the cephalic mass, forming the third of the filaments which connect it with the lateral ganglia. Besides these nerves, we find a *pharyngeal* ganglion, partly divided into two lateral lobes, lying beneath the mouth, and sending filaments to its muscles, to the salivary glands, and to the œsophagus, as well as connecting branches which unite it with the cephalic mass.

41. These characters become more positive in the nervous system of *Bullæa*, where we find the cephalic ganglia again separate (A, A, Fig. 8), and lying at the side of the œsophagus, along with two other pairs of ganglia (C, C, and E, E,) the distribution of whose nerves to the foot and mantle determines them to be *pedal* and *palleal* ganglia respectively. The branchial ganglion (B) is situated posteriorly, as in Aplysia and as in the Conchifera; and its cord of communication with the cephalic ganglia passes through the palleal ganglion. Two small pharyngeal ganglia are here found in the usual situation.

42. From these complex forms, which show us the distinctness of parts that appear simple, we may advantageously pass on to one which exhibits a highly-developed nervous

* Loc. Cit.

system in nearly the most concentrated aspect that it presents in this class—that namely of the *Limax ater* (common slug). Here we find the cephalic ganglia (A, A, Fig. 9) united into one large bilobed mass, lying completely above the œsophagus. Another large mass, or subœsophgeal ganglion, forms the lower part of the ring, and is connected with the first by *two* trunks on each side. A little examination will show that this ganglion is composed, like the similar mass in the Patella, of two pairs having distinct functions. The branches from the outer portion (B) are principally distributed to the respiratory sac; and this will, therefore, be analogous to the outer or branchial portion of the ganglionic mass in the Patella, being, like it, connected immediately with the cephalic by a trunk of its own. The inner portion (C) does not send its branches to the *foot* in particular, but to the general muscular surface in which this organ is, as it were, lost, and of which the whole is concerned in the progressive movement of the body. Hence we may fairly regard this as a *locomotive* ganglion. Two small pharyngeal ganglia are found within the principal ring, connected as usual with the cephalic.

43. Without going into farther detail, then, it is evident that in this class the sensory apparatus, the foot or locomotive organ, the branchiæ or respiratory organs, and the mantle with whose actions both these are concerned, are the organs which seem to require nervous centres for the reception of impressions, and the excitation of respondent motions. These centres are modified, both as to situation and development, in accordance with the situation and development of the organs which they supply; and it is from their connections only that we can judge of their character. For example, it was seen in *Aplysia* that the *pedal* and *palleal* ganglia were united, while the respiratory ganglion was

separated. In *Ianthina*, on the other hand, the *pedal* ganglia are distinct, whilst the *branchial* and *palleal* are partly incorporated with the cephalic. And in *Paludina*, the *pedal* ganglion being still distinct, one other pair supplies the organs of sense and muscles of the mouth, as well as the mantle, branchiæ and viscera.

44. Nothing has yet been said of the ultimate structure, and of the arrangement of the elementary portions, of the nervous apparatus in the classes in which its form has been described; because it is only among the Gasteropoda that any minute investigations have been made whose character can be relied on. It has been stated by M. Blainville, and generally believed, that the nerves of the Mollusca are not composed of definite filaments, like those of higher animals, but that they consist of a semi-fluid *globuleuse* matter enveloped in a fibrous neurilema. More recently, however, it has been ascertained by Ehrenberg, and after him by M. Leuret,* that the nerves consist, in these as in other animals, of definite tubular fibres, in which the granular medulla is contained. These fibres are universally cylindrical, and present no well-marked variations in size. It is very difficult, if not impossible, to isolate them, however, owing to the extreme tenuity of their tubular portion; but the transparency of the neurilema enables them to be readily viewed *in situ*.

45. The structure of the ganglia presents several points of interest. They are always characterised by the presence of a central nodule of granular matter which does not seem to possess any definite arrangement. This, in the Tunicata, does not differ much in colour from the other portion of the nervous structure, being of a light brownish shade. In the

* Op. cit. p. 24.

Conchifera it is more of an orange colour; and in the Gasteropoda it is of a reddish brown. It cannot be doubted that this corresponds with the grey or cortical substance of the nervous centres in Vertebrata. The manner in which it is disposed in reference to the nervous fibres, at once distinguishes the ganglia of the Mollusca from those of the sympathetic nerve, or of the posterior roots of the spinal nerves, in Vertebrata. In the latter we observe the fibres *continuous through* the ganglia, and the grey matter interposed among them. In the former, the grey matter is confined to the centre, and is traversed by *no fibres ;* and the roots of the nerves which terminate in the ganglion are observed to penetrate to it, and then to diverge,—becoming, as it were, lost in its substance.* This is alike the case with what are believed to be, from their connections, both sensory and motor nerves. This structure obviously, therefore, resembles that of the *centres* of the cerebro-spinal system in Vertebrata; the connection of the roots of the nerves with the grey matter of the spinal cord, as well as that of the fibrous with the cortical portion of the brain, being exactly the same as that just described. These ganglia, then, may be regarded as holding precisely the same relation to the nerves which issue from them, as do the corresponding parts of the centres in Vertebrata. What these corresponding parts are will be the next subject of enquiry.

46. The *cephalic* ganglia must be regarded as analogous —not to any single portion of the Encephalon in Vertebrata —but in some degree to the whole. We find nerves of special sensation proceeding from them, certainly to eyes, perhaps also to olfactive organs; as well as others of common sensation, supplying the tentacula and mouth. Hence we

* Leuret, loc. cit.

must admit, that they perform the functions of the optic ganglia of Vertebrata,* and perhaps also of the olfactory lobes; as well as of the portion of the medulla oblongata in which the sensory portion of the fifth pair terminates. Moreover, they certainly give origin also to motor nerves; and must thus perform the functions of the portion of the medulla oblongata from which the corresponding nerves arise in Vertebrata, as well as, perhaps, of the cerebellum. And, if we regard these animals as possessed of the perceptive, reasoning, and volitional faculties, in however low a degree, we must attribute to their cephalic ganglia some portion of the attributes of the cerebral hemispheres in the highest classes. This combination of functions will not appear so extraordinary, when it is recollected that *all* the central operations of the nervous system are performed in the Tunicata by *one* ganglion, and in the Radiata by a series, of which each is but a repetition of the rest; and it is quite conformable to the general principle of the gradual *specialisation* of function which may be observed in ascending the scale of organisation.

47. Of the *branchial* ganglion little more need be said than what has been already stated of the probable control which it exercises over the respiratory function. It will obviously be analogous to the portion of the medulla oblongata which is the centre of these actions in Vertebrata; and although generally at some distance from the cephalic ganglia, the two centres are always immediately connected by an uniting trunk.

48. The *pedal* ganglion can scarcely be regarded in any other light than as analogous to the spinal cord, or rather to

* A slight protuberance on the cephalic ganglia, analogous to the optic ganglia in the Cephalopoda, may indeed be occasionally seen at the point whence the optic nerves are given off.

a single segment of it. The organ of locomotion is here single, and confined to one part of the body. Its nerves may be compared, therefore, with those supplying one of the extremities of Vertebrata; and the ganglion, to the corresponding portion of the spinal cord, which generally exhibits a perceptible increase in the amount of grey matter where they enter it. It is well known that such a portion may be completely isolated without destroying the functions to which the spinal cord ministers; and we can scarcely doubt that these functions are identical in both cases. Such an isolation, however, in Vertebrata, destroys the continuity of the nervous fibres with the brain, to which they seem principally connected by the white portion of the spinal cord, whose fibres may be traced into a part of their roots; and we find that, in the Mollusca, the influence of the cephalic ganglia over the pedal nerves is always provided for by a communicating trunk proceeding from these centres towards the ganglion,—not passing through it, however, but subdividing into branches which enter into the composition of the trunks proceeding from it; so that *a portion* of the pedal nerves terminates in the pedal ganglion, whilst another portion is derived by a continuous trunk from the cephalic. This fact is a very important one in relation to the character of the divisions of the double nervous column in the Articulata, and of the spinal cord in Vertebrata.

49. It is an interesting fact, stated by M. Leuret as the result of his inquiries on the subject, that, although the cephalic ganglia are generally absolutely smaller than other nervous centres, they are always larger in proportion to the nerves which proceed from them. This is worth notice in relation to the investigations of Soemmering upon the proportion which the mass of the brain in Vertebrata bears to the diameter of the nerves proceeding from it.

50. It is obvious that the portion of the Nervous System of Mollusca, into the analogies of which we have thus inquired, cannot be in the least compared *as a whole* with the *sympathetic* system of Vertebrata, which it was formerly imagined to resemble. The distribution of some of its nerves to the viscera, however, may indicate that it partly performs the functions of that system, with which it is structurally intermixed even in Vertebrata, as the late inquiries of Müller have shown.* But the stomato-gastric system may, perhaps, with more probability be considered as executing its offices. Into the peculiar character of that system, we shall be more competent to inquire, when we have traced it through other classes of Invertebrata.

51. The nervous system of the PTEROPODA does not seem, from the few cases in which it has been examined, to differ much from that of the Gasteropoda. In the *Clio* it is described by Cuvier as consisting of three pairs of ganglia on each side, the anterior or cephalic meeting above the œsophagus, and the others being connected by filaments passing beneath it.

52. The class of CEPHALOPODA is a most interesting one in many respects, exhibiting to us the modification of the Molluscous type (which is perhaps most characteristically presented in the Gasteropoda) produced by their proximity to the vertebrated division of the animal kingdom. In no organs is this modification more evident than in the nervous system; for, whilst in the lowest members of the group we find it approximating closely to the form it presents in the higher Gasteropods, its whole character and relations in the most elevated species are so like those which exist in the lowest Fishes, that the analogies between their several parts

Physiology, Book III. Chap. ii.

may be traced with little hesitation. Before passing to the consideration of these, however, it will be desirable to advert to the conformation of the sensory and locomotive apparatus in the principal groups of this class.

53. Among the lower testaceous Cephalopods, of which the *Nautilus Pompilius* may be selected as a type, the sensory organs are but little elevated above those of the higher Gasteropoda. The eyes are still imperfect; no organs of hearing can be detected; and, if there seems ground for attributing to them the possession of an organ of smell, this may with nearly equal reason be regarded as existing in some of the class below. The most remarkable difference in their sensory organs consists in the number of the tentacula which are developed from the head, and which amount to little short of a hundred. Of these some appear more expressly modified for locomotion and prehension; and others, resembling in character and situation the antennæ of Crustacea and Insects, may probably be regarded as instruments of sensation. The head of this animal is also furnished with a flattened disk, which has been termed the *hood*, but which evidently resembles the *foot* of Gasteropods, and seems to be its principal organ of progression on a solid surface. The muscular system is, therefore, principally disposed at the anterior part of the animal. There are two large shell muscles, however, attaching the fleshy mass posteriorly to its testaceous envelope; and the mantle is furnished with a considerable amount of muscular substance which seems destined to dilate and contract its cavity. By this provision it would seem that currents of water are made to flow over the respiratory surfaces, on which, according to the testimony of several observers,* no cilia can be detected.

* Sharpey, Owen, and Garner.

54. In the higher order, which principally consists of the *Sepia Loligo* and other naked Cephalopods, both the sensory and locomotive powers attain a considerably-increased development. The eyes are larger and more perfectly organised; and distinct organs of hearing are found to exist. Instead of a number of feeble tentacula which can scarcely assist in locomotion, we find eight or ten powerful arms, adapted both for this function, and for prehension. For locomotion we find them in many species particularly modified by the membrane that connects their bases, and acts as a powerful circular fin, by means of which the animal swims through the water with great rapidity. On the other hand, the suckers with which they are enabled to take such firm hold of any object to which they are applied, admirably adapt them as prehensory organs. In other species, again, these tentacula are but slightly developed in comparison; and locomotion is effected by means of the vibrations of the long slender body, whose acting surface is assisted by the prolongation of the mantle into fin-like processes which are elevated upon cartilaginous supports. We shall now enquire into the characters which the nervous system presents in these two orders.

55. In the *Nautilus* (Fig. 10.) we observe the cephalic ganglia united on the median line, and lying across the œsophagus like a cord; its two extremities are swollen into ganglionic enlargements, which are evidently analogous to the optic ganglia of Vertebrata. This mass communicates with two collars which form the sub-œsophageal portion of the ring. From the transverse cord are given off not merely the optic nerves, but also filaments to the mouth and tongue, (which are apparently of a sensory character,) as well as branches that connect it with separate labial ganglia presently to be

noticed, which, as in the Patella, lie at a considerable distance anteriorly. The anterior sub-œsophageal collar seems to correspond, in part, with the pharyngeal band in the same Gasteropod,—here increased in size and importance on account of the increased development of the buccal apparatus, with its powerful mandibles, firm, fleshy tongue, salivary glands, and contractile pharynx, and brought into close approximation with the cephalic ganglion. The greater number of the tentacula receive filaments proceeding directly from the anterior part of the collar; but the internal ones are supplied from a ganglionic mass which lies at their base, and which, though principally connected with the pharyngeal band, also communicates with the cephalic ganglion. Besides supplying the internal labial processes, this ganglion sends twigs to what have been supposed by Mr. Owen to be *olfactory* laminæ, and, if these are so, would have to be regarded as in part an *olfactive* ganglion. Its correspondence with what has been denominated the *labial* ganglion in the Patella, seems pretty evident; and perhaps the latter is also to be regarded as connected with the sense of smell.

56. From the posterior collar,—which evidently corresponds with the sub-œsophageal ganglion of the Limax and other Gasteropoda, in which are united the pedal palleal, and branchial ganglia,—filaments are distributed to the shell-muscles, and four others arise from it which pass backwards along the course of the vena cava: of these the two internal form a plexus upon the vein; whilst the two external, which are trunks of considerable size, swell into ganglia, from which ramifications are distributed to the digestive and reproductive organs. This distribution resembles that found in many of the higher Gasteropods inhabiting

spiral shells; and the system of nerves may be termed *branchio-visceral.* The *external respiratory* nerves, however, that supply the muscular edges of the mantle, and the muscles of the funnel, by the movements of which the respiratory currents are produced, arise from the anterior sub-œsophageal mass, which has been spoken of as partly corresponding with the pharyngeal ganglion or medulla oblongata. There is nothing surprising in this change of situation, since we have already had to notice how constantly the position of the nervous centres is governed by that of the organs they supply; and, in this conjunction of the centres of the stomato-gastric and respiratory systems, and their approximation towards the cephalic ganglion, we recognise an evident approach towards the type of the Vertebrata.

57. The supra-œsophageal or cephalic mass of the Sepia, (Figs. 11, 12,) evidently possesses a much higher character than that of the Nautilus. In the latter there existed, on the median line, only a sort of commissure, narrower than the rest of the band; whilst in the former we observe a distinct cordiform mass, from the lower and lateral parts of which the commissural bands proceed, that unite it with the optic ganglia, and with the sub-œsophageal mass. Although the latter is here single, it has a double connection with the cephalic ganglion; an anterior and posterior band uniting them on each side. Anterior to this, as in the Nautilus, is a *labial* ganglion which is connected both with it and with the cephalic ganglion, and which supplies with branches the superior part of the mouth, especially the lips. Two branches proceed from it anteriorly, which encircle the œsophagus, and meet in a pharyngeal ganglion, of a double or bilobed form, on its under

side at the base of the tongue.* We have here, therefore, the same separation of parts as in the Patella, the *stomato-gastric* system being again insulated from the cephalic; the only difference is one of situation, the labial ganglion being in that instance anterior to the pharyngeal, whilst it is here posterior. Several filaments proceed from the pharyngeal ganglion, along the œsophagus, and descend to the stomach, where they reunite into a ganglion, from which branches diverge to supply the digestive system, and particularly the muscular parietes of the gizzard.†

58. From the anterior part of the sub-œsophageal mass arise the nerves which proceed to the tentacula; and these are evidently destined principally to the purposes of locomotion. This fact, therefore, indicates that the functions of this part are more restricted than those of the anterior collar of the Nautilus, which sent off nerves to the sensory as well as to the motor tentacula, and also to the mouth, pharynx, and their muscles, which are here supplied from separate ganglia. This anterior portion also gives off, as in the Nautilus, the nerves which supply the siphonic apparatus and which thus regulate the expiratory current of water.

59. From the posterior division of the sub-œsophageal mass, which is partially separated from the anterior by the aorta, are given off, first and nearest the median line, the branchio-visceral trunks, of which part form a plexus upon the vena cava, as in the Nautilus, whilst the larger portion is distributed upon the viscera and branchiæ; the visceral di-

* Brandt, loc. cit.

† Mr. Owen appears to be in error in asserting that these anterior ganglia correspond with the labial ganglia of the Nautilus; since their filaments are almost entirely disposed on the lower part of the mouth, and on the œsophagus, salivary glands, &c. See Garner, loc. cit.

vision assisting the pharyngeal to form the gastric ganglion, and the branchial having an elongated ganglion at its points of separation. Behind and externally to these arise two large cords which have no distinct analogues in the Nautilus, since they are destined to supply the posterior part of the mantle, which is here a very important muscular organ, but there was covered by the shell. Before their distribution, however, they form a large stellated ganglion, from which the nerves radiate; but where the mantle is prolonged into fin-like processes, the branches which supply these *do not* pass through the ganglia. The anterior part of the mantle is supplied by a distinct set of small nerves, corresponding with those which alone exist in the Nautilus. The active motions of the posterior part of the mantle are here the great agents in producing the rapid respiratory currents, required for the complete aeration of the blood of animals whose movements are so energetic. Amongst these respiratory nerves arise, as in Vertebrata, the small filaments which supply the acoustic organs. The anterior part of the mantle is supplied by a distinct set of small nerves, corresponding with those which alone exist in the Nautilus.

60. Some interesting peculiarities in the distribution of the nerves supplying the arms are worth notice in this place. Just before the divergence of these members, the nervous trunks give off a filament on each side, which meet corresponding filaments from the neighbouring trunks, and thus form a continuous circle uniting the nerves of all the arms.* It can scarcely be doubted that the purpose of this structure is to produce that *consentaneousness* of action among them, so necessary for active locomotion, especially where their

* Cuvier, Mem. sur la Poulpe, p. 36.

movements are the only means of progression enjoyed by the animal, as in the Poulp. Along each trunk is a series of ganglionic enlargements, which correspond to the suckers on the surface of the arm, and send radiating nerves to them. According to Dr. Sharpey,* each trunk consists of a pair of cords, of which *one* only presents ganglionic enlargements, whilst the other passes over these, without contributing to their formation. Another interesting circumstance is pointed out by Mr. Owen.† "In the Cephalopods, whose shells are rudimentary and internal, and whose bodies are enveloped in a naked, and as we must suppose sensible mantle, the nerves which supply that part radiate from a ganglion, which, as in the posterior roots of the spinal nerves in the Vertebrata, is interposed on the chord which brings them in communication with the central mass. In *Nautilus* on the contrary, whose body is encased in an insensible calcareous covering, the analogous nerves are wholly expended on the largely developed muscles which attach the shell to the body; and these nerves, like the motor filaments of the spinal nerves, pass into the muscles directly from the brain, without the interposition of any such ganglion." If this ingenious view be correct, we should here perceive the first indication of the intervertebral ganglia of higher animals. But there is, we think with Mr. Garner, as much reason for regarding it as a *palleal* ganglion, analogous to those met with in Gasteropoda, and the centre of the respiratory movements of the mantle (§ 64); whilst the trunk that passes over it, and is continuous with the œsophageal collar, would influence its movements as an organ of general locomotion.

61. In both these orders of Cephalopods, the nervous

* Müller's Physiology, i. 676.

† Memoir on the Nautilus, p. 57.

centres are protected by cartilaginous supports which obviously foreshadow the *neuro-skeleton* of Vertebrata. In the Nautilus, the œsophageal collar rests upon a firm cartilage, which does not, however, enclose it, but gives attachment to the powerful muscles of its neighbourhood. In most of the superior order, the cephalic ganglion, with the sub-œsophageal mass, are enclosed in a cartilaginous envelope, the cavity of which, however, they do not entirely fill; the intervening space, like that within the cranium of Fishes, being occupied by a gelatinous fluid disposed in cells formed by the arachnoid membrane. The expanded wings of this cartilage support and protect the eye-ball; and in its substance the organ of hearing is imbedded. The nuchal cartilage, which is placed behind it, not only gives attachment to the muscles of the mantle, but protects the great lateral nerves; and this, with the long cartilaginous plates which support the fin-like processes, where they exist, is evidently the rudiment of the osseous column, which protects the spinal cord in Vertebrata, but which, in the lowest of that division, is reduced to the form of a simple cartilaginous tube, as in the Cyclostome Fishes.

62. The central portion of the cephalic mass in the *Sepia* may perhaps be regarded as more analogous to the cerebral hemispheres of Vertebrata than any thing we have as yet seen in the Mollusca, since the optic ganglia are here distinctly developed in a separate form. Should the labial ganglia participate in the function of smell, their connection with the cephalic mass would evidently resemble that of the pedunculated olfactory lobes in many Fishes. As this central mass contains grey matter, it is obviously something else than a mere commissure between the optic lobes, as some have represented it; but as it also gives off the lingual and

maxillary nerves, we must regard it as participating in the functions of the medulla oblongata.

63. However strange it may appear to assert that the sub-œsophageal mass is a kind of concentrated spinal cord, a little consideration will show that this is really the light in which it should be viewed. In tracing the arrangement of the nervous centres in the Mollusca, we have found the principle of *connections* our only safe guide; and its application here becomes of some importance. From the anterior portion of the mass are given off, as already mentioned, the nerves which supply the feet or rather tentacula; and it is therefore to be regarded as a *locomotive* ganglion, or rather as formed by the union of many such. It is only the situation of the locomotive organs around the head that occasions the giving off of these nerves from one spot, and *that* the *anterior* portion of the collar. Knowing, as we do, the varieties of position which this ganglion is capable of assuming, we cannot doubt that, if the feet had been all at the opposite extremity of the body, the ganglionic masses would have been removed to that situation; or that, if they had been disposed along the body, as in Articulata, we should have had either a series of such ganglia, as in that group, or one prolonged ganglionic mass, like that presented by the spinal cord of Vertebrata. That in either of these groups a concentration may take place equivalent to that which we here witness, need scarcely be pointed out; in the *Crab*, for example, we have all the locomotive ganglia united into a single centre, and this only occupies the thorax, because the legs are connected with that division of the body; whilst, in the *Lophius piscatorius*, and other fishes whose locomotive organs are principally disposed in the anterior part of the body, we find the *true spinal cord* or ganglionic

mass soon terminating on a *cauda equina* consisting of nerves alone, like the bundle which passes backwards from the œsophageal collar of the Sepia.

64. The *posterior* portion of the sub-œsophageal mass is evidently most analogous to the medulla oblongata, giving origin as it does to the auditory and respiratory nerves, as well as to those of general sense and motion. That it should be here placed *behind* the mass which we regard as analogous to the spinal cord, will not be wondered at when the relative situations of the parts supplied by these respective centres is taken into consideration. It is unnecessary, however, to draw a definite line of division between them, since they really constitute but *one* organ: and we find this part supplying, in some of the species, locomotive nerves even more important than those of the feet—those, namely of the fin. It is an important fact, that the ganglion upon the palleal nerves formerly mentioned is constant in all the naked species; whilst the trunk that passes over the ganglion is only found in such as possess the fin-like processes of the mantle, and is distributed entirely upon those parts. We should hence be led to believe that this ganglion is connected with the respiratory functions of the mantle, which are constant in *all* of this order, and is *not* analogous to the intervertebral ganglion upon the sensory nerves, as Mr. Owen supposes. Perhaps the question might be settled by a reference to its anatomical structure—which of the two arrangements formerly mentioned (§ 45,) its white and grey portions present.

65. It can scarcely be doubted that the *branchio-visceral* nerves sent off from the posterior part of the collar, with their venous plexus, are partly of a *sympathetic* character, since we know how closely this last system of nerves is united with the sensori-motor in the classes beneath, not

having yet acquired any distinct centre of its own. Such a one would here seem to exist, however, in the visceral or cœliac ganglion, to the formation of which these nerves contribute, (§ 59), and which sends branches to the alimentary canal, generative organs, ink-bag, &c. The branchial portion of this system, however, does not enter this ganglion, but forms a small one of its own, before its distribution to the gills. This, therefore, may be regarded as principally analogous to the respiratory portion of the par vagum ; and its function will evidently be to convey to the general centre those impressions from the branchiæ, the stimulus of which is necessary to keep up the respiratory movements. Such an union of the sympathetic and par vagum appears to exist, through an interlacement of their filaments, to a greater extent than has hitherto been supposed, even in Man and the Mammalia—but it is far greater in Fishes ; and it appears from the recent experiments of Dr. J. Reid, that the sympathetic is partly concerned (perhaps through the filaments of the par vagum which it contains) in conveying these impressions. The consideration of the *stomato-gastric* system we shall again defer for a time. (§ 92, 3.)

66. We shall next enquire what inferences of a general character can be deduced from the facts which have been brought together in regard to the structure and distribution of the nervous system in the Mollusca and Radiata. In the *first* place, we have found no case in which nervous fibres exist without connection with a ganglionic mass, characterized by the presence of grey matter, or of something equivalent to it. We know that, in the higher animals, the separation of a nervous trunk from its centre renders it incapable of serving as the medium of reflex actions of any kind, whether sensation and volition be concerned in them or not ; and we may fairly infer that the same principle ex-

tends to the lower, in which the same distinction of parts is manifest. There would seem, then, much reason to believe that ganglia are situated wherever impressions made upon the afferent nerves are destined to excite motions; and, farther, that the change by which this is effected takes place between the white and the grey matter. Thus, we have the nerves of the foot partly terminating in one ganglion, those of the respiratory apparatus in another;—and so on.

67. It may be remarked, in the *second* place, that, wherever the presence of special sensory organs confined to one part of the body gives to that part a predominance over the rest, (the entrance to the alimentary canal being always in their neighbourhood), we find the ganglia with which they are connected possessing a special relation with all the rest, which these do not possess with each other. It is obvious that, where visual organs are developed, the impressions made upon these will determine the movements of the animal, more than those of any other kind; and it would seem to be chiefly owing to the information which they communicate, that the cephalic ganglion has such an evident presiding influence over the rest, even when smaller than any one of them. This is, however, more the case in animals whose movements are rapid, and in which, therefore, the perception of *distant* objects is more important, as in the Articulated classes. Except in the Cephalopoda, the subservience of the nervous system to the nutritive functions of the Mollusca is so great, that it might almost be regarded as an appendage to the digestive organs, destined for the selection and prehension of aliment. But in the more active members of that class, it derives a more elevated character from the development of the organs of special sensation and of locomotion. It has been seen that fila-

ments from the cephalic ganglia enter into the composition of all or nearly all of the nerves of Mollusca; the trunks which connect them with other ganglia not terminating in those ganglia, but intermingling with the nerves which proceed from them. In the structure which Dr Sharpey has detected in the arms of the Cuttle-fish, we find a very interesting example of this general fact, (§ 60); and it is by no means difficult to assign its use in accordance with the views here laid down. The suckers seem capable of contracting and fixing themselves, either in obedience to the will of the animal, communicated to them along the non-ganglionic cords from the central mass, or in respondence to a stimulus excited by contact, and acting through the afferent and efferent nerves of their ganglia alone. But it may be said that, in all these cases, the ganglia in the course of the trunks are equivalent to the intervertebral ganglia in vertebrated animals, and merely distinguish the sensory from the motor portion of the trunk. Such an idea is, however, completely refuted when we apply it to the nervous system of the lower Mollusca, where we find the cephalic ganglion gradually diminishing in size, until the posterior or *branchial* is obviously the *principal* centre of the actions of the animal, and cannot, therefore, be of the nature of an intervertebral ganglion. Going still lower—to the Tunicata—we find this respiratory ganglion the only one remaining. The gangliated cord of the Sepia, therefore, evidently repeats, on a small scale, the same characters as have been shewn to exist in the larger centres of other Mollusca. And this is demonstrable by experiment, as well as by structural analogy; for when the arm of a Cuttle-fish is severed from its body, and the nervous cord, as a whole, has no termination in a ganglionic centre, any sucker may be stimulated to contract,—the effect being obviously produced through the nerves of its own ganglion. It is well known, that the intervertebral ganglion bestows no independent action on the spinal nerve, which is powerless when separated from its true ganglionic centre; and we cannot, therefore, but regard it as next to certain, that the ganglia in question are so many independent centres of reflex action, whose operations are controlled, directed, and combined by the cephalic ganglia, through the medium of the fibrous band that passes over them, and mixes its branches with theirs.

68. We may observe, *thirdly*, that in passing downwards to the Tunicata, we find the nervous system losing one part after another, until the respiratory ganglion is all that remains. This must be regarded, however, as combining in some degree the functions of the rest (so far, at least, as the general structure of the Animal allows these functions to be performed); but the control over the movements of the respiratory sac is evidently its principal office. The mere act of respiration, or the aeration of the blood, can scarcely be regarded as dependent upon any influence derived from the nerves, for the reasons stated at the commencement of this Essay, and also because it may be effected out of the body; but the working of the mechanism by which the conditions of the change are brought into play would seem an important part of the functions of the nervous system wherever such exists. Now, it has been shown by experiment that in the Vertebrata the whole of the nervous centres may be removed, except that segment of the cerebro-spinal axis which connects the principal respiratory nerves—in fact, the *respiratory ganglion*,—and yet the animal may continue to exist for some time. It is curious to see how such experiments are, as Cuvier expressed it, "ready performed for us by Nature," in this class of Animals.

69. We may trace, in the *fourth* place, a close relation between the predominance of the cephalic ganglion, and the evidence of the operations of sensation and volition, as manifested in the movements of the animal. So long as food is within its reach, we can scarcely regard its prehension as of any higher character than that of the infant when it applies its lips to the nipple of the mother; and this action, we know, is not dependent on the presence of a brain, and is therefore, we think, not the result of sensation or volition, although in the perfect condition accompanied by the former. But when the animal has to exercise its organs of special sensation, and to put its general locomotive apparatus into activity for the purpose of seeking its aliment, its operations must be regarded as of a higher order; yet the greater part of these may still, perhaps, be considered *instinctive*, that is to say, not involving any reasoning powers, or any notion of *purpose* on the part of the animal itself. We may take a well known case in illustration,—the ejection of the contents of the ink-bag, which takes place when the Cuttle-fish is pursued. This has been regarded by some as of a *voluntary* character, and as indicating a *design* on the part of the animal to conceal itself from its pursuers. But such a supposition involves an amount of reasoning power on the part of the animal which we can scarcely attribute to it; and if the action were not performed as well the *first* time as it might be on a subsequent occasion, it would obviously be of little use. Is it not rather an involuntary or *emotional* action, analogous to the expulsion of the contents of the rectum and bladder under the influence of fear, which many of the human species know by experience to result from an impulse uncontrollable by the will? This view of its character is strengthened by the fact that the secretion of *ink* is really analogous to that of *urine*.

We shall now inquire how far these inferences are applicable to the nervous system of the Articulata.

V. NERVOUS SYSTEM IN THE ARTICULATA.

70. The animals composing this group all present, in a more or less evident degree, a division into segments, which have an obvious tendency to resemble one another, as in the Radiata. In the higher classes, however, this segmentation is obscured by the modifications which cause the different segments to assume dissimilar forms, and perform distinct functions. In those species, however, which may be regarded as typical of the group,—as among the Myriapoda,—there is an almost perfect equality in all the segments. In such the nervous system is merely a repetition of similar parts, disposed, not in a circle as in the Radiata, but in a continuous line. The most anterior, however, has an evident predominating influence, for the reason formerly specified (§ 67) ; and this influence will be found to diminish with the loss, and to increase with the development, of the faculties of special sensation which have their seat there. The locomotive powers are just as predominant in the Articulated series as are the nutritive functions among the Mollusca. Accordingly, we find the development of the nervous system to bear a special reference to them; and the sensori-motor divisions of it can be more distinctly separated from the portion which ministers to the organic functions.

71. A very brief sketch of the gradual development of this system in the lower Articulata will be here sufficient ; since it is in the higher groups that its peculiarities can be best studied. In the *Strongylus*, one of the Entozoa,

(Fig. 13) we find a single cord running from one extremity of the body to the other, but separating into two portions to embrace the orifices of the alimentary canal, where some slight ganglionic enlargements appear; from this are given off slender filaments at short intervals, which encompass the body, whose whole surface seems equally sensitive. A similar cord has been stated by Cloquet to exist in the *Ascaris lumbricoides*, divisible, however, into two filaments along its whole length; but this observer also describes another similar cord as running on the dorsal surface, and as communicating with the first by a sort of œsophageal collar. This statement has been recently controverted by Leuret,* who maintains that the dorsal cords are evidently vascular; and certainly their situation is not such as we could easily explain, regarding them as nervous, except upon the supposition that they are analogous to the stomato-gastric system which will be hereafter described in the higher Articulata. In the *Linguatula*, a single stellated ganglion is described by Mr. Owen as situated beneath the œsophagus, from which nerves diverge to supply the muscular apparatus of the mouth, and the prehensile hooklets; whilst two large cords pass backwards along the edges of the abdomen to near the posterior extremity, where they gradually become expanded and blended with the muscular tissue (Fig. 14).

72. A somewhat similar arrangement has been traced in the Rotifera, whose nervous system, notwithstanding their minuteness, is very distinct. In Fig. 15 is represented that of the *Hydatina*, which consists of a circle of ganglia surrounding the entrance to the alimentary canal, and giving off filaments to the powerful muscles of the jaws, and to the ciliary apparatus of the wheels, and also a nervous

* Op. Cit. p. 55.

cord that proceeds backwards to the posterior extremity of the body. In the species now described, this cord is single and destitute of ganglia; but in others it is evidently double, and one or two pairs of ganglia exist upon it. Here, then, we see a concentration of the ganglia at the anterior part of the body, in opposition to the general type of the group to which this class belongs, but in accordance with the disposition of the locomotive apparatus.

73. In the CIRRHOPODA we find another variety in the disposition of the nervous system, the same essential type, however, being retained; and it was the discovery of the double ganglionic cord in these animals that first led to the suspicion that they should be classed with the Articulata, and not with the Mollusca, to which their general conformation and habits apparently liken them. In Fig. 16 is shown the nervous system of the *Anatifa;* which is seen to consist of a slender nervous collar surrounding the œsophagus, and sending filaments to the neighbouring parts, but scarcely forming ganglia above it,—this creature being, in its fixed adult state, destitute of the eyes and antennæ which it possessed when in its early condition of a free-moving Crustaceous animal; from this nervous ring a double column proceeds along the body, on which ganglia are found at the points that give origin to the nerves of the members.

74. In the lower ANNELIDA, such as the *Earthworm*, the conformation of the nervous system is but little different from that just described in the Strongylus. A nervous cord traverses the whole length of the body, forming a ring at its anterior extremity, through which the œsophagus passes. At the anterior portion of this, we find two small ganglia, from which nerves proceed to the mouth and sensitive lips; but there are as yet no eyes. Nervous trunks are given off at intervals along the ventral cord; and, according to the

recent statements of M. Leuret,* these are given off alternately in double and single pairs; a slight ganglionic enlargement of the cord being apparent where the double pairs are given off, but not at the intermediate points. This fact is interesting, as showing, even in this low grade, the outline of a peculiar structure which will be described in the nervous system of Insects. The nervous system of the *Leech* bears a general resemblance to that of the Earthworm; but we here find the rudiments of a separate *stomato-gastric* system also.† A minute ganglion exists at the base of each of the three teeth which form the mouth; these ganglia are connected together and to the cephalic by slender filaments; and they seem also to be in connection with other filaments which may be traced on the alimentary canal. In the higher Annelida, such as the *Aphrodita*, the same general type is witnessed in a higher grade of development. Eyes and antennæ exist, although imperfect in their character, and the cephalic ganglia meet above the œsophagus. The ganglia of the ventral cord are much more distinct, but nearly equal along their whole length (Fig. 17).

75. We next arrive at the Myriapoda, which present the type of the nervous system of the Articulata in a sufficiently developed form to serve as a basis for our enquiries. The cephalic ganglia receive the nerves of the eyes and antennæ, and are united on the median line; but they are still of small size, in accordance with the low development of the sensory organs. The ganglia of the longitudinal cord are well marked, and nearly equal from one end of the body to the other; each sends off nerves to its respective segment; and the branches proceeding from the different ganglia have little communication with each other. Between the ganglia

* Op. cit. p. 58.

† Brandt, loc. cit.

we find intermediate nerves given off, as in the Earthworm. (Fig. 18.) Besides these, we find a separate system of visceral or stomato-gastric nerves, of complex distribution. (Fig. 19). A small ganglion is placed on the median line in front of the cephalic mass, with which it is connected; and from this filaments proceed to the mouth and pass down the œsophagus to the stomach. There is another set of ganglia and filaments placed laterally; the ganglia, which are sometimes two on each side, are situated behind the cephalic mass, and communicate with the anterior ganglion by filaments passing beneath it; they also communicate with each other, with the nerves passing off from the ventral cord, and with the *recurrent* trunk (as it has been termed) proceeding downwards from the anterior ganglion; and the plexus to which they give origin is distributed upon the digestive organs.

76. We shall here stop to enquire into the ultimate structure and arrangement of some of the divisions of this nervous apparatus. The nerves themselves are composed of cylindrical tubes, like those which exist in the Mollusca, but more firm. The cephalic ganglia have exactly the same structure as that formerly described (§ 45); that is to say, they contain a nucleus of grey matter, in which the roots of the nerves seem to lose themselves. When we examine one of the ganglia on the ventral cord, and the nerves which seem to originate from it, we find that each nerve has three series of roots, one of which terminates, as in the other cases, in the grey matter of the ganglion; another interlaces with those of the opposite side; whilst the third is *continuous* with the fibrous portion of the cord, which may be traced uninterruptedly to the cephalic ganglia. When the structure of the cord itself is analysed, it is seen that the fibrous tract or column is throughout distinct from that which contains

the ganglionic enlargements; and that it does not contribute towards the formation of these, but passes over them (as was first observed by Mr. Newport) like the analogous trunk in the arms of the Cuttle-fish. This is not to be confounded with the third and narrower tract, which is still more distinct, and possesses ganglia of its own; of this, which seems connected with the respiratory function, but which is considered the motor tract by Dr. Grant, the structure and character will be described in Insects, where it is more fully developed.

77. After what has been said of the offices which the ganglia seem to perform in the Mollusca, and of the relation which they bear to the cephalic mass, we should have little difficulty in applying the same views to this portion of the apparatus in the Articulata, had not another explanation of a very plausible character, but founded on what we deem loose and flimsy analogies, been generally received by physiologists. When we examine the actions of this cord, we at once perceive that those of all its ganglia are similar to one another, being related only to the movements of their respective segments, and of the members which belong to them. In fact, they are *so many repetitions of the pedal or locomotive ganglion of the Mollusca.* It is easily proved that the movements of each pair of feet may be produced by that ganglion alone with which it is connected; since a single segment, isolated from the rest, will continue to perform these movements for some time under favourable circumstances. Thus, if an earthworm be cut in two whilst crawling, each portion will continue to advance, though the anterior only will permanently preserve its vitality; and, if a Centipede or Millipede be divided into several portions under the same circumstances, each will execute movements of progression for some time. But it is evident that these

must be placed, in the living animal, under some general control, by which the consentaneousness of action that is essential to regular locomotion may be produced. This is easily proved by experiment. If in a *Mantis*, for example, the nervous cord be divided between the first and second thoracic ganglia, so as to isolate the ganglionic centres of the posterior legs, the limbs will continue to move energetically, but not with a combined object, and no progression will be the result. We can scarcely suppose this general control to be exercised otherwise than by the fibrous tract which connects each of the nervous trunks immediately with the cephalic ganglia, as in the Mollusca; and this must, therefore, conduct to these centres the impressions which produce sensations in them, and convey downwards from them the locomotive impulse; whilst the ganglion of each segment, with the filaments proceeding from its grey matter, will form the circle necessary for the simple reflex actions of the members.

78. But, it may be asked, what advantage has this view of the character of the ventral cord over that which is current amongst physiologists? To which question a reply may be best given by asking another. Upon what evidence is that view supported? The doctrine that the ganglionic portion of the cord is *sensory*, and the fibrous or non-ganglionic *motor*, is principally based on the assumption that the ganglia are analogous to those found on the posterior roots of the spinal nerves, into which the motor fibrils do not enter. The comparison of the structure of the two, however, completely disproves this assumption. The fibres which enter the intervertebral ganglia *pass through* them to their true centre—the spinal cord; where they are partly lost in the grey matter, and partly continuous with the white. On the other hand, part of the filaments which enter *these* ganglia *terminate* in their grey substance; whilst others become

continuous with the fibrous column,—just as in the spinal cord of Vertebrata. It is evident, then, that their true analogy is with the segments of that cord; the fibrous tract resembling its white columns, whilst the ganglionic nodules may be compared with its grey centre, which often presents similar enlargements, and which is to be regarded as a continuous chain of ganglia. Such, perhaps, we find shadowed forth in the lowest of the Vermiform tribes, where the segments are so numerous that no distinct ganglia are formed, but the single longitudinal cord seems to possess the same character throughout. Moreover, the true analogues of the intervertebral ganglia are discoverable in some Crustacea, which present minute enlargements upon the nervous trunks at a little distance from the cord.* The argument drawn from the proximity of the so called motor column to the viscera, and its consequent analogy with the anterior columns of the spinal cord, is obviously not alone sufficient to support the doctrine in question; especially since the respiratory column still intervenes, proving that the *arrangement* of the centres is altogether different.

78. The results of experimental enquiry seem to us conclusive against the doctrine of the sensory and motor functions of the ganglionic and fibrous columns of the ventral cord of the Articulata. How is it that motions may be excited in the members of a single segment by irritating them, if there is no communication between these two portions of the cord? As they may be separately traced, in many instances at least, up to the brain or cephalic mass, *that* would seem the only point through which reflex actions could be produced,—which we know is very far from being the case. As no experimental proof of the correctness of

* Leuret, op. cit. p. 76.

this doctrine has yet been adduced, and as its chief support is an analogy which has been shown to be fallacious, it can scarcely maintain its ground against any other which is more consonant with structural analogy and with physiological phenomena.

79. Such, it may be urged, is the opinion formerly adduced—that the ganglionic portion of the cord ministers to those reflex actions which are independent of the will, and perhaps also of sensation; whilst the fibrous column is a continuation, as it were, of a portion of each nervous trunk to the cephalic ganglia. The independence of the segments, as far as their reflex actions are concerned, and their common subordination to one presiding centre of the will, are fully explained on this supposition. It is also quite conformable to the analogy both of the Mollusca and of Vertebrata. We have seen that, in the former, where the ganglia are more isolated from one another and from the presiding centre, each ganglion appears to be the centre of the simply reflex actions occurring in the organ with which it is connected; but that a part of the nervous fibres which seem to enter it really pass on to communicate with the central mass, where alone, it may be surmised, *sensations* can be felt, and *voluntary* impulses excited. And, on the other hand, in the Vertebrata we find the ganglionic or mixed portion of the spinal cord, and the simply fibrous tracts, performing functions respectively analogous; for, when any segment is isolated from the rest, reflex actions may be excited through it, in the production of which the white columns can scarcely participate, being structurally distinct from each other and from the ganglionic portion of the cord, and continuous only with the fibrous portion of the brain; whilst pathology supplies us with instances of the converse occurrence, namely, the destruction of the ganglionic portion

by disease, without the functions of the parts below being impaired—*their* ganglionic portion being segmentally independent, and their communication with the brain being maintained by a continuity of white or fibrous structure.* Other pathological cases demonstrate that, when reflex actions are excited through a segment of the spinal cord unconnected with the brain, sensations are not involved in their performance; and we might, therefore, infer from analogy that the ganglia of the cord in Articulata are not the seat of *sensibility*, any more than the spinal cord of Vertebrata. On this point, however, we cannot arrive at any certainty; and perhaps there is some reason, on the contrary, to believe that, in these classes, sensibility is more extensively diffused through the nervous centres than in the higher, since we find the endowments of all the ganglia becoming more and more similar as we descend the scale, until in the Star-fish they seem identical, and each appears the seat of some amount of sensibility to visual impressions.

80. The number and variety of the reflex actions which take place in Articulata after decapitation, is very remarkable; and they seem to have a consentaneousness proportioned to the closeness of the relation between the nervous centres in different species. Thus, in the *Scolopendra*, we find the ganglia of each segment distinct, but connected by

* Mr. Mayo long ago suggested the analogy between the fibrous portion of the spinal cord, and the trunks uniting the ganglia of the Articulata (Physiology, 2d Edit.) But this analogy is not altogether correct; for these trunks partly connect the ganglia themselves (like those between the isolated centres of *Bullæa* § 41), and are partly independent of them. More recently, Dr. M. Hall has suggested that the ganglionic portion of the cord ministers to the reflex actions of the respective segments, whilst the white tract conveys the motor influence of the cephalic ganglia. We can scarcely suppose that it has this function, however, without also conveying sensory impressions *to* those ganglia, as there is no reason to believe that this is done peculiarly by the ganglionic column.

a commissural trunk. Here an impression made *equally* upon the afferent nerves of *all* the ganglia, will produce a consentaneous action. Thus, M. Dugès relates* that, if the stigmata on one side of a decapitated Scolopendra be exposed to an irritating vapour, the body will be immediately flexed in the opposite direction; and that, if the stigmata of the other side be then similarly irritated, a contrary movement will occur. But different actions may be excited in different parts of the cord, by the proper disposition of the irritating cause. In the higher classes, however, where the ganglia of the locomotive organs are much concentrated, the same irritation will produce consentaneous motions in several members, similar to those which the unmutilated animal performs. Thus, the *Mantis religiosa* customarily places itself in a very curious position, especially when threatened or attacked, resting upon its two posterior pairs of legs, and elevating its thorax and the anterior pair which are armed with powerful claws; the resemblance fancied to exist between this attitude and that of prayer has occasioned the specific name of the animal, but it is rather an attitude of resistance. If the anterior segment of the thorax with its attached members be removed, the posterior part of the body will still remain balanced upon the four legs which belong to it, resisting any attempts to overthrow it, recovering its position when disturbed, and performing the same agitated movements of the wings and elytra as when the unmutilated animal is irritated. On the other hand, the detached portion of the thorax, which contains a ganglion, will, when separated from the head, set in motion its long arms, and impress their hooks on the fingers which hold it. These facts prove unequivocally that the instinctive movements of

* Op. Cit. tom. I. p. 162.

these parts, which are performed in direct respondence to external impressions, require only for their stimulation the ganglionic centre with which the nerves that excite them are immediately connected.

81. Another instance, related by Burmeister, is still more satisfactory in regard to the manner in which these movements are excited. A specimen of the *Dytiscus sulcatus*, from which the cephalic ganglia had been removed, executed the usual swimming motions, when cast into water, with great energy and rapidity, striking all its comrades to one side by its violence, and persisting in this for half an hour; but, whilst previously lying with its abdomen on a dry surface, no such actions were excited.

82. We shall now enquire how far these views are applicable to the remainder of the Articulated classes; and we shall commence by examining in detail the nervous system of INSECTS, of which the general characters only have yet been adverted to. In their *larva* state, we find it consisting of a chain of ganglia disposed along the ventral surface, similar to each other in every respect, and one of them appertaining to each segment; with a cephalic ganglion, more or less developed, according to the perfection of the sensory organs connected with it. In this condition, therefore, the nervous system of Insects perfectly repeats that which is characteristic of the Annelida; and the varieties of both correspond in the most interesting manner, (Fig. 20.) Besides the nervous trunks given off from the cord at its ganglionic enlargements, (and which consist, as in former instances, of two portions derived from its ganglionic and fibrous tracts), we find, as in the lower classes, a series of nerves, given off at intermediate points, without any apparent swelling at their points of divergence. It is not easy to ascertain the true connections of these, except in the thoracic region,

where the ganglionic columns usually diverge laterally, especially when the metamorphosis is taking place into the pupa state. It is then seen (Fig. 21,) that a third column exists on the superior or visceral aspect of the ventral cord ; and that these nerves are given off from minute ganglionic enlargements upon it, which are much more distinctly seen, however, in the perfect Insect.

83. Although these nerves communicate with those of the symmetrical system, they have a separate distribution, being transmitted especially to the tracheæ, on the parietes of which they ramify minutely, and also to the muscles concerned in the respiratory movements. The latter, however, being a part of the general locomotive apparatus, are also supplied from the ganglionic column. These transverse or superadded nerves do *not* supply the muscles which open and close the stigmata or external orifices of the tracheæ ; and this might be thought inconsistent with the supposition that they are especially concerned in the respiratory function, if it were not recollected that the closure of the stigmata is an action more connected with the voluntary movements of the animal than with the mechanism of its aeration, it being in this manner that it prepares itself for flight, or for any other powerful exertion. These nerves, then, would seem analogous to those of the gills and mantle in the Mollusca, and may be regarded as corresponding with the pneumonic portion of the par vagum in Vertetrata, which is in like manner distributed on the air-passages, and with its associated motor nerves. It is to be recollected that the respiratory apparatus of Insects is diffused throughout the whole body, so that its presiding system of nerves must be proportionably extended ; and we here seem to have the *branchial* ganglion of the Mollusca repeated, like the *pedal*, in each segment. The enlargement of the ganglionic mass during

the metamorphosis, is a very interesting fact in relation to the increased activity of the respiratory function in the perfect Insect.

84. The *stomato-gastric* system obtains a high degree of development in Insects, and is usually as distinct in the Larva as in the Imago. It consists of two distinct parts. The first of these, which is situated in the median line, has been called the *recurrent* nerve. It is described by Mr. Newport in the *Sphinx ligustri*, as appearing to commence by two roots from the peduncles which connect the cephalic with the first thoracic ganglion (Fig. 22.) These converge, and meet in a ganglion situated on the palate, which is thus anterior and inferior to the cephalic mass. From this ganglion nerves proceed to the walls of the buccal cavity, to the mandibles, &c.; whilst the principal trunk passes backwards to the pharynx, and is distributed on the œsophagus and stomach. Mr. N. regards this ganglion as analogous to the enlargement which is found on the par vagum when passing through the foramen lacerum; but *that* is evidently of the nature of an intervertebral ganglion; and we shall have reason from analogy to regard this as the ganglionic *centre* of the system of nerves proceeding from it, and the filaments which connect it with the peduncles of the cephalic ganglia as merely cords of communication. Its position and connections fully point out its analogy with the pharyngeal ganglia of the Mollusca, which are undoubtedly independent centres. Besides this median system of nerves, there is another disposed laterally, which seems of a different character. In the Sphinx, we find two small ganglia behind the cephalic, which are connected with these, and also with the recurrent system, as well as with the respiratory nerves. Of the ultimate distribution of these filaments, Mr. N. does not give a very minute account; but further details will be pre-

sently given (§ 88,) in regard to the development of this system in the perfect Insect.

85. Without following in minute detail the changes which occur in the Nervous System during the metamorphosis, or describing the various forms which it assumes in the different orders of Insects in their perfect state, such particulars will be adduced as bear upon the objects of the present Essay. It will have been observed that the nervous system of the Larva is constructed in exact accordance with its means and extent of locomotion. Each segment (in general at least) possesses a pair of legs; and with each is associated a *pedal* ganglion. None of the movements of the animal (in those tribes which undergo a complete metamorphosis, to which this description more particularly applies,) are very energetic; simple and slow progression is all for which its structure is adapted; and the uniformity in the actions of its legs would render it easy to combine them at the will of the animal, even though their respective centres remain so much isolated from one another.

86. But, in the perfect Insect, the whole locomotive apparatus is concentrated in the thorax. The six legs (which are now all that remain) and the single or double pairs of wings, are all developed from its three segments; and a much greater variety of action is required, as well as more complete consentaneousness, on account of the increased number and velocity of the movements of the animal. We accordingly find that the ganglionic matter of the ventral cord of perfect Insects is more or less concentrated in the thoracic region; whilst the ganglia of the abdomen are usually few and small (Fig. 23); the nerves to its segments, however, being given off as before at regular intervals. Upon the hypothesis that the ganglionic cord corresponds with the sensory columns in Vertebrata, we should be obliged to sup-

pose that these parts of the body are destitute of sensation, whilst they retain their motor faculties. This would seem highly improbable, since these are the very parts in which the least active movements take place, whilst the ganglionic matter is carried on to those segments which give attachment to the members whose reflex actions are so remarkable (§ 80.)

87. The three tracts of which the ventral cord has been described as consisting, may be seen in most perfect Insects, especially in some of the Hemiptera. The ganglia of the transverse or the respiratory series are more apparent in this condition than previously to the metamorphosis. The nerves which supply the wings are found, in all the stages of the development of these organs, to have a double origin. One root arises from the fibrous tract alone, whilst the other takes its origin from both tracts at the point of enlargement. The wings are also supplied with nerves from the transverse system, of which scarcely any go to the legs; this will be readily understood when it is considered that the wings are developed, as it were, out of an extension of the respiratory apparatus,* and that its actions are closely connected with these movements. There is another interesting peculiarity to be noticed in regard to the distribution of the nerves of the wings. Where the ganglionic centres which supply the anterior and posterior pairs remain distinct, there is a curious plexiform arrangement of their nerves, more or less intricate, according as the wings are destined to act with greater or less consentaneous energy, and absent when the anterior pair serve only as *elytra*, and do not assist in flight.† This would remind us, therefore, of the circular

* See Princ. of Gen. and Comp. Phys. p. 165 and 308.

† All the *facts* relating to the Anatomy of Insects, detailed in the last six Sections, are given on the authority of Mr. Newport. See his papers in the Philosophical Transactions for 1832, 1834, and 1836.

filament which was seen to connect the nerves of the arms in the naked Cephalopoda.

88. As an illustration of the stomato-gastric system in perfect Insects, we may advantageously select the highly-developed form in which it exists in the *Gryllotalpa vulgaris*,* (mole cricket.) The median system appears to originate in a small ganglion (*a*, Fig. 24.) situated, as in the Sphinx, anteriorly and inferiorly to the cephalic mass (A, A,) with which it communicates by a connecting branch on each side. Its principal trunk, the *recurrent* of authors, is sent backwards, beneath the pharynx; and on this a slight ganglionic enlargement is seen, where the connecting branches are given off which unite it with the lateral system. Its ramifications are distributed along the œsophageal tube and dorsal vessel; whilst the trunk passes downwards to the stomach, where its branches inosculate with those supplied by the lateral system, and seem to assist in forming a pair of small ganglia, (*d*,*d*,) from which most of the visceral nerves radiate.

89. The ganglia of the lateral system are two on each side, (*b*, *b*, and *c*, *c*,). The anterior pair are the largest and meet on the median line, just behind the cephalic ganglia with which they communicate. Posteriorly to these lie the second pair, which are in connection with them. Two cords pass backwards on each side, one derived from the anterior, the other from the posterior of these ganglia. They run along the sides of the œsophagus and dorsal vessel, and are finally distributed on the digestive viscera, where they assist in forming the ganglia already mentioned.

90. The concentration of the ganglia in the ventral cord is sometimes carried to a much greater extent than in the

* Brandt, loc. cit.

example already adduced. Thus, in the *Melolontha vulgaris* (cockchaffer) we find all the abdominal ganglia consolidated into one, which is situated almost immediately behind the thoracic, and sends two principal trunks directly backwards, and others diverging to supply the respective segments (Fig. 25). In the *Pentatoma Grisea* we observe this concentration extending to the thorax, as well as to the abdomen ; the sensori-motor system possessing, in all, but three ganglionic masses, appertaining to the head, thorax, and abdomen respectively (Fig. 26).

91. Upon a comparison of the nervous system of Insects with that of the higher Mollusca, it will be seen that they differ more in the relative proportions and in the management of their parts, than in their absolute character. In both, there is a cephalic division of the ganglionic centres, in which sensibility and voluntary power appear to reside more particularly if not entirely. In both there is a division specially appropriated to the locomotive apparatus ; differing only in the multiplication of the centres in Insects, conformably with the arrangement of the members they supply; and sometimes, as we have just seen, consolidated even in them into two ganglionic masses. In both we find also a division appropriated to the respiratory apparatus, in which there is a corresponding multiplication of centres in the Articulata, in harmony with the universal distribution of their tracheal system. And in both we find a separate system of nerves distributed to the alimentary apparatus, and supplying the organs of mastication (with the salivary glands), deglutition, and digestion. Into the character of this *stomato-gastric* system, we shall now inquire.

92. As a preliminary to this inquiry it is to be remarked that the *par vagum* of Vertebrata is distributed to *three* separate systems—the respiratory, the circulating, and the

digestive. As we know that the ultimate fibrils of nerves never anastomose, there can be no doubt that these branches might be traced separately back to their origins, and would be found to have distinct connections with their ganglionic centres. There is no difficulty, then, in understanding that the respiratory system of Insects and other Invertebrata may be analogous with the pnuemonic portion of the par vagum, although it bears no relation with the cardiac and gastric divisions of that nerve. Looking to the distribution of the *recurrent* nerve upon the dorsal vessel, œsophagus, and stomach, we can have little hesitation in pronouncing it to be the analogue of these divisions ; but its commencement in the anterior ganglion, which also supplies the mouth and pharynx, might seem to place it on a different footing. With what does this anterior ganglion correspond ?

93. It may be inferred from the situation and distribution of its nerves, that the *anterior ganglion* of Insects is analogous both to the *labial* and *pharyngeal* ganglia of the Sepia and Patella (§ 57 and 38). These would seem to form a division of the nervous system by which the actions *immediately* concerned in the prehension of food are performed, almost as independently of the cephalic ganglia as are those of respiration. There would seem, however, a greater tendency towards the union of *these* centres with the œsophageal collar, than of those presiding over the respiratory function, which is more independent of the will ; and accordingly we find the *labial* ganglia apparently united with the cephalic in most of the Gasteropoda, whilst the *pharyngeal* forms a part of the sub-œsophageal mass in the Nautilus. The division of the nervous system in Vertebrata with which this stomato-gastric system corresponds, is a question of more apparent difficulty ; but if we bring into comparison not only the highest but the lowest forms of the cerebro-

spinal apparatus, the chief difficulties will be removed. The analogies drawn from the distribution of the nervous branches would lead us to infer that the *third* division of the fifth pair (including its sensory and motor origins), the glosso-pharyngeal, and the gastric portion of the par vagum, would most nearly represent it. Now, when the fifth pair is traced back to its true origin, it is found to be not a cerebral but a spinal nerve ; and it is then seen to arise from the medulla oblongata in such close approximation with the par vagum and glosso-pharyngeal, as to show that, if this portion of the nervous centres were isolated from the rest, the nerves which proceed from it would form, anatomically as well as functionally, a natural group. The fifth pair, like other spinal nerves, may act in a simply reflex character ; although in man it is usually under the dominion of the will. In the lower animals we find these reflex actions bearing a much larger proportion to the voluntary, than in man ; and even in him we not unfrequently meet with cases in which the functions of the cerebral hemispheres seem suspended, whilst those of the spinal cord are unimpaired ; so that the prehension of food by the lips may take place without any effort of the will. A remarkable instance of this kind, in which the cerebral hemispheres were entirely absent, has already been mentioned (§ 69.) Further, the connection between the fifth pair and the par vagum is very intimate in Fishes—the class which approaches nearest in the character of its nervous system to the Invertebrata. We may reasonably infer, then, that the stomato-gastric ganglia are the centres of the reflex actions of the nerves which correspond to the third branch of the fifth pair, the glossopharyngeal, and the par vagum of Vertebrata ; whilst the branches which connect them with the cephalic ganglia bring them more or less under the influence of the latter (§ 100, XIII.)

94. This view is strengthened by the connection which these nerves have with the *sympathetic* system; a connection which is much more intimate in Fishes than in the higher Vertebrata, though even in these, according to Müller, filaments of the sympathetic may be abundantly detected in the fifth pair and par vagum. Now we have seen that, in the Mollusca, the sympathetic does not exist as a separate system, but would seem partly connected with the stomato-gastric, and partly with the branchio-visceral nerves. In Insects, the *lateral* ganglia of the stomato-gastric system appear to possess more particularly the characters of the *sympathetic;* especially in their connection with all the other systems, and in the share which their branches have in the formation of the cæliac ganglia.

95. It is scarcely necessary to extend this Essay to the detailed consideration of the Nervous Systems of the other groups of Articulata; since these will not supply us with any data which have not been already obtained from other sources. A very general outline of them will therefore suffice. The CRUSTACEA present to us a great variety of forms of this apparatus; some resembling the type characteristic of the Myriapoda, and corresponding with the equality in the segments and legs exhibited in the group; and others manifesting a degree of concentration even surpassing that of the highest Insects. Of the first type, the nervous system of the *Talitrus locusta* (Sandhopper) is an interesting example, from its exhibiting to us the lateral divisions, which are usually in close approximation, at a considerable distance from one another, (Fig. 27.) The transverse cords which unite each ganglion are evidently but prolonged forms of the fibres which have been formerly described (§ 76), as uniting the nerves of each side, where the ganglion appears to be single.

96. In the *Astacus marinus* (Lobster) we have an example of a form, which corresponds with that of Insects, in which the process of concentration has taken place but to a low degree. The thoracic ganglia remain distinct, and none of the abdominal ganglia are absent, although they are much smaller than the thoracic (Fig. 28.) The stomato-gastric system here presents us, however, with an interesting variety of conformation, which shows its tendency to approximate with the cerebro-spinal. That of the *Astacus fluviatilis* (Cray-fish) is represented in Fig. 29.* We here find no separate anterior ganglion existing; but it seems replaced by two small ganglionic enlargements of the cords or peduncles which unite the cephalic ganglia with the first thoracic. From these proceed the branches which supply the mouth and muscles of the jaw, as well as others that unite with a median branch proceeding from the cephalic ganglion to form the recurrent trunk, which is distributed upon the œsophagus and stomach, where it presents one or two minute ganglionic enlargements. It is evident that the small ganglia upon the peduncles of the cephalic mass correspond exactly with the division of the medulla oblongata from which the fifth pair and the par vagum are given off; so that the analogy which has been previously drawn would seem by this structure to be fully confirmed; and we shall be less inclined to adopt the opinion of Müller, who has described this stomato-gastric system in the light of a sympathetic.†

97. It is in the short-bodied Crabs, that the concentration of the ganglionic masses is most remarkable. Thus, in the *Maia squamado* we find but one large stellated ganglion in the trunk, from which the nerves radiate; a con-

* Brandt, loc. cit.

† Nova Acta, tom. xiv.

formation which evidently conducts us towards the Cephalopodous Mollusca (Fig. 30).

98. The distribution of the nervous system in the ARACHNIDA is not dissimilar to that of the Crustacea—the spiders of the sea. In the long-bodied *Scorpions* there is a large mass surrounding the œsophagus, formed by the union of the cephalic with the first thoracic or infra-œsophageal ganglion, from which the nerves of the five pairs of legs are given off; and posteriorly to this are seven small ganglia disposed at regular intervals along the trunk. In the *Spiders* (Fig. 31), on the other hand, we find the cephalic ganglia distinct but small; and these communicate with a large stellate mass in the front of the thorax, which appears to be formed by the union of at least four pairs of ganglia, and which sends off nerves to the legs; from this proceeds a double cord which swells at its termination into an enlargement that gives off branches to other organs. The stomatogastric system of Arachnida, so far as it has been detected, seems more analogous to that of Crustacea than to that of Insects.

99. From the foregoing details regarding the nervous system of the Articulata, it would therefore appear that the inferences which were drawn from the examination of its character in the Mollusca are fully applicable to the physiological explanation of its structure in this division of the Animal Kingdom, and thus derive important confirmation from its phenomena; whilst the explanation usually adopted is neither consistent in itself, nor capable of being applied to the other Invertebrata. The study of the arrangement of the parts of the nervous system in Mollusca may be *most* advantageously pursued before that of the Articulata is entered upon; since the great variety in the disposition of the different systems in that group, the isolation of their nervous

centres, and the transposition and re-combination of these in so great a variety of ways, affords us the key to their real character, which may be effectually applied to the elucidation of the more complex apparatus of Articulata.

VI. GENERAL CONCLUSIONS.

100. A general review of the ground over which we have passed will enable us, we think, to draw the following conclusions with a high degree of probability.

I. That a nervous system, in the form of connected filaments with ganglia on certain parts of them, exists in all Animals (that is, in all beings endowed with any degree of sensibility and voluntary power), although its presence may not be detected by our means of observation.

II. That the actions most universally performed by a nervous system are those connected with the introduction of food into the digestive cavity.

III. That we have reason to regard this class of actions as everywhere independent of volition, and perhaps also of sensation;—the propulsion of food along the œsophagus in man being of this character.

IV. That, for the performance of any action of this nature, a nervous circle is requisite, consisting of an *afferent* nerve on the peripheral extremities of which an impression is made;—a ganglionic centre, where the white fibres of which that nerve consists terminate in grey matter, and those of the efferent nerve originate in like manner;—and an *efferent* trunk conducting to the contractile structure the motor impulse, which originates in some change in the relation between the grey and white matter.

V. That such actions may be regarded as the simplest of those which the nervous system performs, and most resemble the examples of contraction produced by the irritation of distant organs in Plants, (where an *impression* is mechanically conveyed by the circulating system,) of any which the Animal Kingdom affords.

VI. That in the lowest Animals such actions constitute nearly the entire function of the Nervous System; the amount of those involving sensation and volition being very small.

VII. That, as we ascend the scale, the evidence of the participation of true sensation in the actions necessary for the acquirement of food, as shown by the development of special sensory organs, is much greater; but that the movements *immediately* concerned with the introduction of food into the stomach remain under the control of a separate system of nerves and ganglia, to the action of which the influence of the cephalic ganglia,—the *special* if not the *only* seat of sensibility and volition,—is not essential.

VIII. That, in like manner, the active movements of respiration are controlled by a separate system of nerves and ganglia, and are not dependent upon that of sensation and volition, though capable of being influenced by it.

IX. That the centres of these systems are brought into closer structural relation with that of the sensori-volitional system as we ascend the scale of Invertebrated Animals; until they at last apparently become a part of it, as in Vertebrata, where, however, they still remain really separate, and may be artificially insulated.

X. That, whilst the actions of these systems are in the lower tribes almost entirely of a simply—reflex character, we find them, as we ascend, gradually becoming subordinated to the will; and that this is effected by the mixture of fibres proceeding directly from the cephalic ganglia with those arising from their own centres.

XI. That the locomotive organs, in like manner, have their own centres of reflex action, which are independent of the influence of volition, perhaps also of sensation.

XII. That the influence of the will is conveyed to them by separate nervous fibres, proceeding from the cephalic ganglia; and that similar fibres probably convey to the cephalic ganglia the impressions destined to produce sensations.

XIII. That the stomato-gastric, respiratory, and locomotive centres are all united in the spinal cord of Vertebrata, where they form one continuous ganglionic mass; and that the nerves connected with all these also receive fibres derived immediately from the cephalic ganglia.

XIV. That whenever peculiar consentaneousness of action is required between different organs, their ganglionic centres are united more or less closely; and that the trunks themselves are generally connected by bands of communication.

XV. That the sympathetic system does not exist in the lowest classes in a distinct form;—that the nervous system of the Invertebrata, taken as a whole, bears no analogy with it;—that, as the divisions of this become more specialised, some appearance of a separate sympathetic presents itself;—but that this is never so distinct as in Vertebrata.

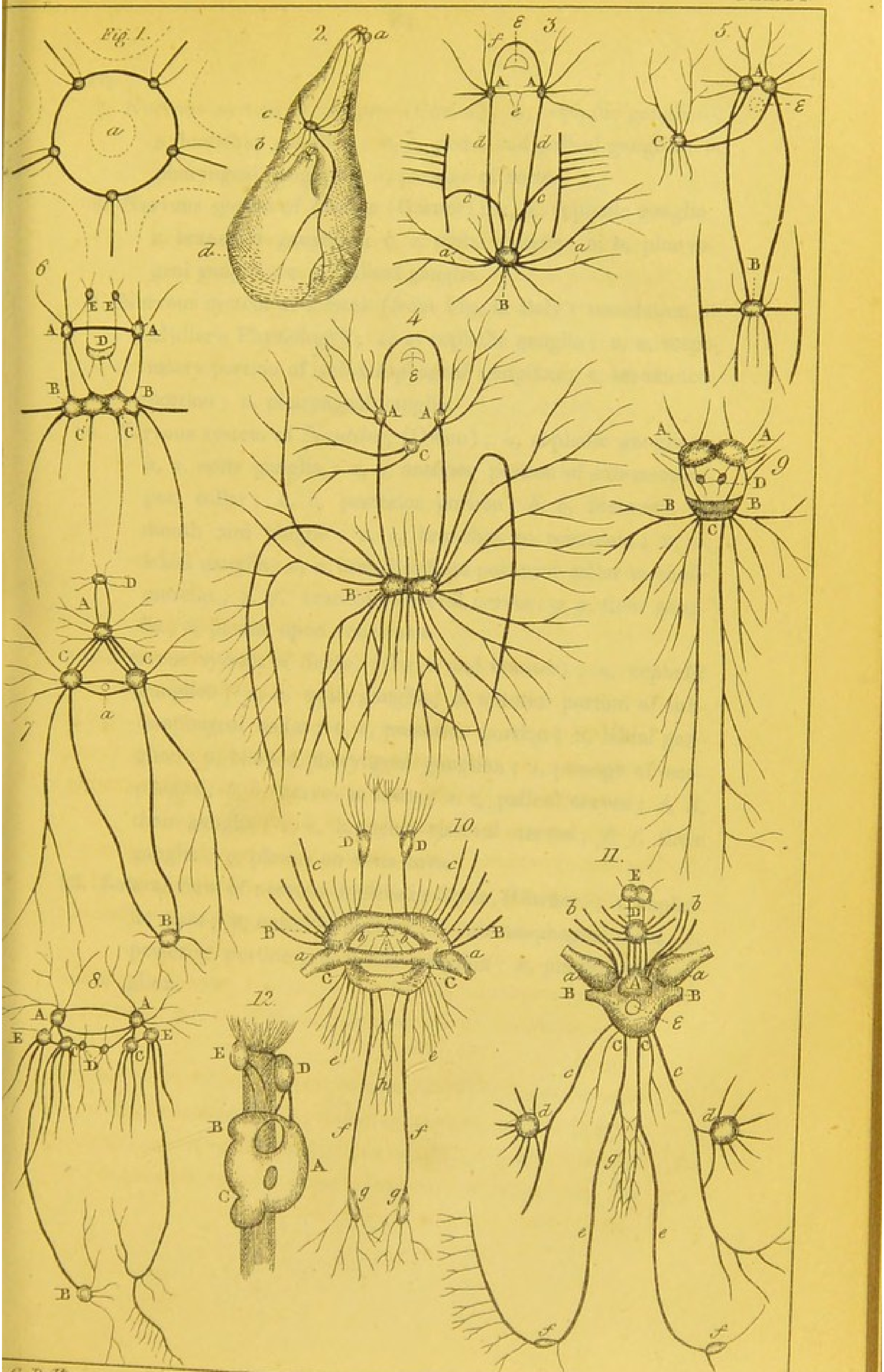
XVI. Hence it may be inferred that, as the sympathetic system is *not* developed in proportion to the predominant activity of the functions of organic life, but in proportion to the development of the higher division of the nervous system, its office is not to "preside over" the former, but to bring them into relation with the latter; so that the actions of the organs of Vegetative Life are not dependent upon it, but influenced by it in accordance with the operations of the system of Animal Life.

EXPLANATION OF THE FIGURES.

PLATE I.

Fig.

1. Nervous system of *Asterias* (after Tiedemann); *a,* oral orifice.
2. *Ascidia Mammillata,* with nervous system (Cuvier); *a,* branchial orifice; *b,* anal orifice; *c,* ganglion with radiating filaments; *d,* general surface of the sac.
3. Nervous system of *Oyster* (Garner); A, A, anterior ganglia; B, posterior ganglion; *a,* branches to mantle; *c, c,* branches to gills; *d, d,* connecting trunks; *e,* transverse filament uniting anterior ganglia; *f,* arch over œsophagus, E.
4. Nervous system of *Pecten* (Garner); A, A, anterior ganglia; B, posterior or branchial ganglion, bilobed; C, pedal ganglion.
5. Nervous system of *Mactra* (Garner); A, A, anterior ganglia nearly meeting over œsophagus, E; C, pedal ganglion.
6. Nervous system of *Patella* (Cuvier and Garner); A, A, cephalic ganglia; B, B, branchial ganglia; C, C, pedal ganglia; D, pharyngeal ganglion; E, E, labial ganglia.



C. Delt

Forrester's sculp

Fig.

7. Nervous system of *Aplysia* (Cuvier); A, cephalic ganglion; B, branchial ganglion; C, C, pedal and palleal ganglia; D, pharyngeal ganglion; *a*, passage of aorta.

8. Nervous system of *Bullæa* (Garner); A, A, cephalic ganglia; B, branchial ganglion; C, C, pedal ganglia; D, D, pharyngeal ganglia; E, E, palleal ganglia.

9. Nervous system of *Limax* (from Fig. in Baly's translation of Müller's Physiology); A, A, cephalic ganglia; B, B, respiratory portion of sub-œsophageal ganglion; C, locomotive portion; D, pharyngeal ganglia.

10. Nervous system of *Nautilus*, (Owen); A, cephalic ganglion; *a*, *a*, optic ganglia; B, B, anterior portion of sub-œsophageal collar; C, C, posterior portion; *b*, *b*, filaments to mouth and tongue; *c*, *c*, branches to tentacula; D, D, labial ganglia; *e*, *e*, branches from posterior collar to shell-muscles; *f*, *f*, branchio-visceral nerves; *g*, *g*, their ganglia; *h*, plexus upon vena cava.

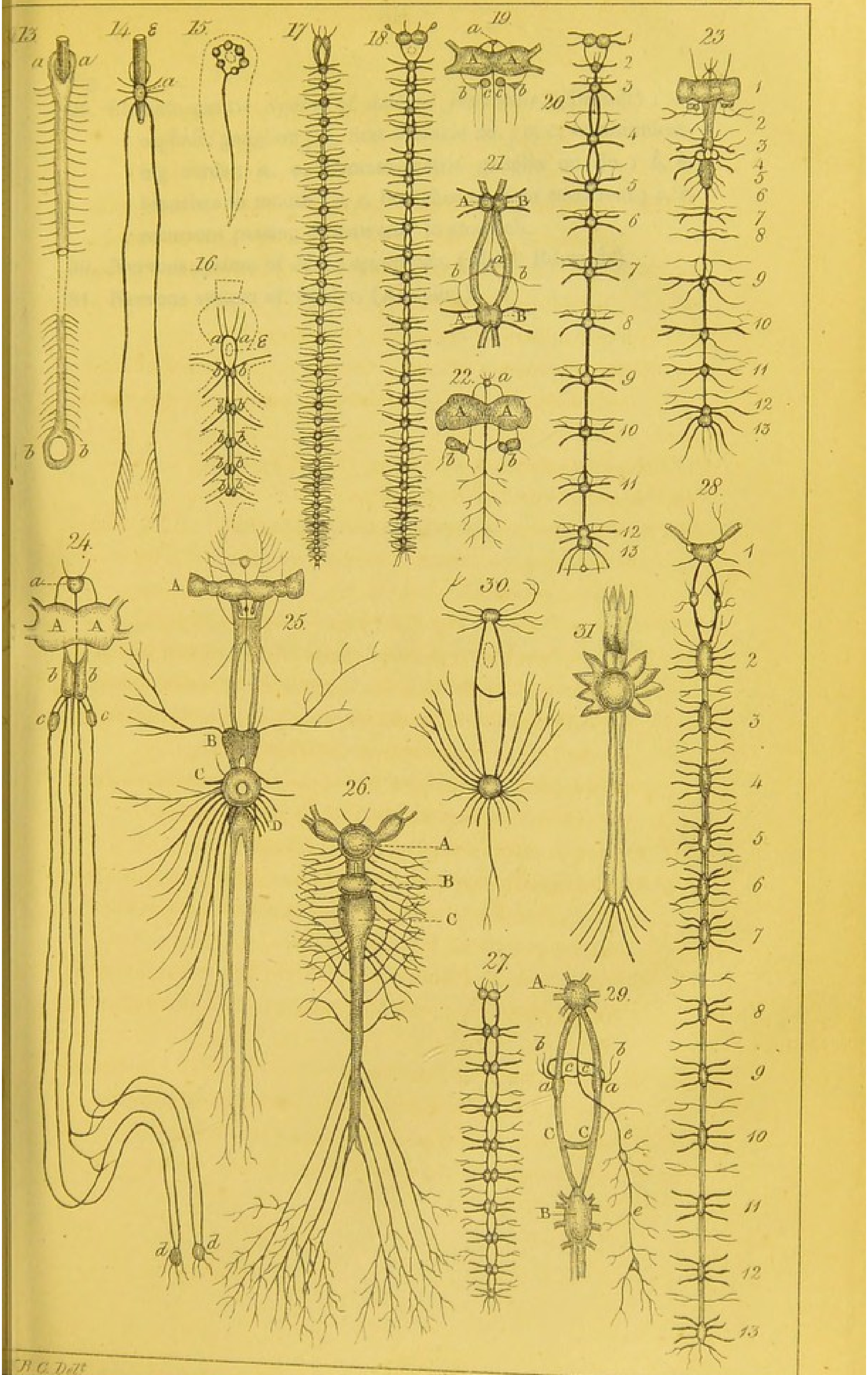
11. Nervous system of *Sepia*, (Owen and Garner); A, cephalic ganglion; *a*, *a*, optic ganglia; B, anterior portion of sub-œsophageal collar; C, C, posterior portion; D, labial ganglion; E, bilobed pharyngeal ganglion; ε, passage of œsophagus; *b*, *b*, nerves to arms; *c*, *c*, palleal nerves; *d*, *d*, their ganglia; *e*, *e*, branchio-visceral nerves; *f*, *f*, their ganglia; *g*, plexus on vena cava.

12. Lateral view of nervous centres in *Sepia*, (Garner); A, cephalic mass; B, anterior portion of sub-œsophageal mass; C, posterior portion; D, labial ganglion; E, pharyngeal ganglion.

PLATE II.

Fig.

13. Nervous system of *Strongylus gigas,* (Owen) ; *a, a,* collar surrounding oral orifice ; *b, b,* similar collar around anus.
14. Nervous system of *Linguatula tænioides,* (Owen) ; *a,* ganglion beneath œsophagus, ε.
15. Nervous system of *Hydatina,* (Ehrenberg.)
16. Nervous system of *Anatifa,* (Cuvier) ; *a, a,* collar surrounding œsophagus, ε ; *b, b, b,* locomotive ganglia supplying members.
17. Nervous system of *Aphrodita,* (Milne Edwards.)
18. Nervous system of *Scolopendra.*
19. Stomato-gastric system of *Spirobolus,* (Brandt) ; A, A, cephalic ganglia ; *a,* anterior median ganglion ; *b, b,* and *c, c,* lateral ganglia.
20. Nervous system of *larva* of *Sphinx ligustri,* (Newport.)
21. Portion of cord from thoracic region of ditto, when just passing into the pupa state ; A, A, ganglia of regular system ; *a, a,* ganglia of respiratory nerves ; B, B, nerves of regular system ; *b, b,* transverse or respiratory nerves.
22. Stomato-gastric system of *Sphinx ;* A, A, cephalic ganglia ; *a,* anterior median ganglion ; *b, b,* lateral ganglia.
23. Nervous system of perfect Insect, (Newport.)
24. Stomato-gastric system of *Gryllotalpa,* (Brandt) ; A, A, cephalic ganglia ; *a,* anterior median ganglion ; *b, b,* and *c, c,* lateral ganglia ; *d, d,* cœliac ganglia.
25. Nervous system of *Melolontha vulgaris,* (Strauss) ; A, cephalic ganglion ; B, C, thoracic ganglia ; D, abdominal ganglion.
26. Nervous system of *Pentatoma grisea,* (Dufour) ; A, cephalic ganglion ; B, thoracic ganglion ; C, abdominal ganglion.
27. Nervous system of *Talistrus locusta,* (Milne Edwards).
28. Nervous system of *Astacus marinus,* (Milne Edwards).



B C Delt

Fig.

29. Stomato-gastric system of *Astacus fluviatilis*, (Brandt) ; A, cephalic ganglion ; B, first thoracic do. ; C, C, communicating cords ; *a*, *a*, stomato-gastric ganglia on do. ; *b*, *b*, branches to mouth ; *c*, *c*, branches to form recurrent ; *e*, *e*, recurrent passing downwards to stomach.

30. Nervous system of *Maia squamado*, (Milne Edwards).

31. Nervous system of Spider, (Audouin).