XXVIII. *On the Nervous System of Molluscos Animals.* By ROBERT GARNER,
Esq., F.L.S.

Read November 4th, and December 16th, 1834.

THOUGH in this paper the author originally included the nervous system of the *Radiata*, yet he now, upon more mature consideration, determines to confine his observations to Molluscos animals, convinced that he can add little of importance to the recent labours of the German anatomists* in this department, who have shown the errors of their predecessors, and themselves discovered the true nervous system of Radiated animals.

In the *Tunicata* the nervous system consists of a ganglion and nerves (TAB. XXIV. fig. 1. A, *a*, *b*.), generally very visible on slitting the cartilaginous covering. In *Phallusia intestinalis*, Sav., we discover this single, yellowish ganglion, lying upon the muscular coat between its two orifices. In other species we see the ganglion nearly divided. One set (*a*.) of filaments surround the branchial orifice, and give nerves to its tentacula, and appear to meet on the opposite side, forming in the *Phallusia* a nerve which seems to run along the edge of the elongated branchial fold. The other set (*b*.) supply the muscular tunic, and also the mantle, and go towards the mouth. In *Cynthia*, and those *Tunicata*, which have thick muscular tunics, the ganglion is not visible external to the muscular sac, it being situated in its interior. The above-described ganglion is, according to Cuvier, analogous to the posterior or branchial ganglion of *Conchifera*. In the figure are shown two minute bodies (G.) seen on the intestine of *Phallusia*, which Meckel suspects may be ganglia, but which as probably may be traces of a second ovary.

* More particularly Tiedemann and Ehrenberg. Spix appears to have been mistaken in his account of the ganglia and nerves of the *Actinia*, as he certainly was in that of the nervous system of the *Asterias*. The author's observations agree with those of Leuchart, Rapp, and Meckel in this respect. The nerves of *Radiata* are exceedingly minute and difficult to discover; in preparations the vessels are often shown for them.

In the *Tunicata* are no lips, no foot, nor valvular muscles, and therefore the ganglia which supply those parts in *Conchifera* are absent. Their single ganglion evidently presides over the functions by which the water, &c. is drawn in and expelled.

The only correct description of the nerves of a Bivalve animal is that given by Mangili of the nerves of the *Anodonta*. In all Bivalves, with the exception of those entirely destitute of a foot, we find three ganglia, each of which is composed of two others. In *Ostrea*, which has no trace of a foot, there is no inferior or pedal ganglion, but only a few scattered filaments in its situation. The posterior ganglion is always situated at the posterior muscle between the branchiæ. That it is chiefly a branchial ganglion is proved by its being regulated in its disposition by the situation of those organs. Thus in *Ostrea*, *Cardium*, *Unio*, *Anomia*, *Venus*, *Pholas*, *Teredo*, *Solen*, *Mya*, *Mactra*, &c., in which the branchiæ are united together, the two ganglia which compose it form but one. But in *Mytilus*, *Modiola*, *Pecten*, &c., in which the branchiæ are separated, and at a distance from each other, the two ganglia are more or less separated, always, however, united by a transverse chord. This ganglion (TAB. XXIV. fig. 2, 3, 4, 5, 6 & 7, A.) gives off anteriorly two nerves (*a.*), by which it is joined to the anterior or labial ganglia (B.). Besides these, the posterior ganglion gives nerves to the branchiæ (*b.*), large branches to the respiratory siphons (*c.*), minute visceral filaments (*d.*) to the posterior parts of the viscera (the labial ganglia sometimes giving a filament or two to the anterior parts), twigs (*e.*) to the posterior muscle, and branches to the mantle (*f.*). These ganglia and nerves are much developed in *Conchifera*, which, like the *Pholas*, have their branchiæ and siphons large. The anterior or labial ganglia (B.) are never in conjunction, but always united by a transverse filament (*g.*), which arches over the mouth. In *Mytilus* and *Modiola* they are of a lengthened form, and situated a little behind the mouth. In the *Pectines* they are much more posterior. In *Mactra*, however, they have advanced forwards, and nearly meet over the mouth; and perhaps these *Conchifera* show more locomotive activity than any others. Besides the nerves which they receive posteriorly, and the connecting filament between the two, each gives off one or two nerves (*h.*) to the mantle, tentacular branches (*i.*), and muscular filaments (*j.*). Each ganglion likewise sends down a nerve (*k.*), which meets its fellow, and

forms a ganglion (C.) in the substance of the foot, giving many branches to this organ. This ganglion in Bivalves is never divided: that it chiefly belongs to the foot, and not to the viscera, is proved by its being regulated in size by the development of the foot, and being absent when that organ has disappeared. The author could never trace any filaments from it to the viscera. It is large in *Solen*, *Mactra*, *Unio*, &c., small in *Pecten*, *Mya* and *Anomia*, and absent in *Ostrea*. It is generally, as in *Mactra*, situated between the muscular tissue and the viscera; more forwards in *Cardium echinatum*; in *Pecten* at the anterior part of the base; in *Pholas* superficially at the point.

In *Conchifera* then the mouth is surrounded by a ring, of which the lower part is double. This ring is, however, very wide, other organs besides the mouth being within it. Generally the nervous system is symmetrical; but when the animal, as *Ostrea*, is inequivalve, the nerves going to the branchiæ and mantle in the deeper valve are lengthened and disarranged. In *Anomia* the anterior ganglia are displaced, and the inferior become lateral, from the change in the position of the mantle and foot. The ganglia of *Conchifera* are of an orange colour; in those, however, of which the tissues are transparent, they are whiter.

The anterior and posterior ganglia are figured by Poli in many Bivalves; in no instance has he described the inferior one. It is well known that he considered these nerves to be lacteals, and the ganglia receptacula chyli, from the possibility of injecting their sheaths.

That the anterior ganglia are the cerebral or sentient lobes of the animal appears from this, that the other pairs communicate with them, and not with each other. The separate ganglia of each pair are conjoined that their action may be consentaneous. The pedal, from its supplying the foot, may be correctly termed the ganglion of locomotion; whilst the posterior, supplying the branchiæ and siphons, may be termed respiratory: but as each pair supplies likewise other parts, their functions cannot be purely so limited, though it is probable that the subordinate function is derived from twigs they receive from the others, incorporated in the connecting nerves. The anterior ganglia in the *Pecten* (fig. 5, B.) are seen to be composed of two portions, one coloured and soft, the other fibrous, composed of filaments passing through the ganglia.

In *Pecten*, *Spondylus* and *Ostrea* we find small, brilliant, emerald-like ocelli, which, from their structure, having each a minute nerve, a pupil, a pigmentum, a striated body, and a lens, and from their situation at the edge of the mantle, where alone such organs could be useful, and also placed, as in *Gasteropoda*, with the tentacles, must be organs of vision.

The *Gasteropoda* offering much variety in form, present likewise corresponding differences in the nervous system; for in all animals the disposition of the latter is chiefly determined by the shape of the body; keeping it, however, in mind, that as we ascend, we find an inclination in the several ganglia to become concentrated and ascend towards the head. With the exception of the *Tunicata*, we find in all *Mollusca* the centre of the nervous system to be a ring around the commencement of the digestive tube, more narrowly embracing it as we get higher in the orders of animals. Its exact situation varies with circumstances; thus it will be found around the very commencement of the alimentary canal, close to the lips, in *Helix*; in *Eolida* behind the muscular pharynx; some distance down the œsophagus in *Buccinum*; whilst in one species of *Purpura* it is generally behind the stomach. In these latter animals it is fixed itself, but the œsophagus has free motion through it, as the proboscis is more or less protruded.

The nervous system of *Patella* (TAB. XXV. fig. 3.) shows, on the one hand, the resemblance of this system in the *Gasteropoda* to that of the *Conchifera*; and on the other to that of the *Cephalopoda*. We have the cerebral or sentient ganglia (A, A.) at the base of the tentacles and eyes, which are here present, supplying principally those organs, and receiving a filament (*b.*) on each side from the pedal ganglion (B.), and another (*a.*) from the branchial ganglion (C.), as in *Conchifera*. The ganglia of both these pairs are connected that their action may be combined, the connecting filament of the branchial passing in its course through the two pedal ganglia. The pedal ganglion supplies the foot, the branchial or respiratory ganglion the branchiæ and mantle, also giving lesser filaments (*f.*) to the viscera, and others (*e.*) to the shell muscles. That this last is a branchial ganglion is proved by this: the author has observed that in *Fissurella* (an animal differing from *Patella* in having the branchiæ removed to the back of the neck, and in which animal Cuvier notices the deficiency of the two external ganglia,) they exist, but in a dif-

ferent position, but where one might expect to find them, at the base of the branchiæ on the back. Perhaps we might infer from Cuvier's description that the nervous system in *Halotis* is similarly disposed. In *Lottia*, which has a single branchial appendage over the neck, and a branchial circle besides around the mantle, the ganglia are unaltered in their position. Besides eyes, we have in *Gasteropoda* another important part more than we find in *Conchifera*, the pharynx or manducatory apparatus at the commencement of the œsophagus, consisting of a muscular cavity, with a curious spiniferous tongue at its floor, often supported by two or more cartilages, and sometimes furnished with one or two horny maxillæ. Either a transverse band or two ganglia supply this complicated apparatus with nerves, this band, or these ganglia being always subœsophageal, forming another ring around the digestive canal. In *Patella* this band (D.) is connected with two ganglia (E.), which supply the fleshy lip of the animal, and not with the cerebral ganglia. Thus the second part of the digestive canal has its ganglion connected with those supplying the nerves of the entrance, and through them with the brain; the functions of the parts appearing thus naturally combined. The *Patella* appears to be the only Gasteropodous animal where these labial ganglia exist separate from the superior or cerebral ganglia. In the *Cephalopoda*, however, there are distinct labial and pharyngeal ganglia, the latter, as in *Patella*, only connected to the superior ganglion through the former. These pharyngeal ganglia, besides supplying the pharynx, give origin to superior visceral or sympathetic nerves (*k, l*), very fine and delicate, ascending and descending on the œsophagus and getting upon the salivary ducts and glands.

In *Chiton* (fig. 1. & 2.), there being no eyes nor tentacles, the upper portion of the ring has no evident ganglia. The branchial (C.) and pedal ganglia (B.) are sometimes distinct, sometimes conjoined on the inferior portion of the ring. The pharyngeal ganglia are also developed on the ring.

In *Scyllæa* (fig. 4.), an animal not covered, like *Patella* and *Chiton*, with hard, insensible, testaceous parts, but with a delicate and sensible dorsal integument, bearing also the branchiæ (the muscular foot having almost disappeared), we find the brain entirely supræsophageal from the change above mentioned. It appears composed of four united ganglia (A.), probably the cerebral and branchial, which latter might be appropriately named

branchio-visceral. The foot has become too insignificant to require appropriate ganglia. Though there are in this animal, and in some species of *Doris*, no eyes, the author thinks he has found the rudiment of them in two minute black spots which he has noticed, one on each side the brain; and he infers that so unusual a circumstance must arise from the pigmentum nigrum existing on the brain before the external eye is developed. These spots mark the superior ganglia to be the cerebral, and we find the tentacles supplied from them. Externally the nerves are derived which supply the mantle, branchiæ, and viscera. In *Doris* and *Eolida* (fig. 5.) the same conformation exists. According to Cuvier the four ganglia are quite separate in *Tritonia*; and it would appear, from the observations of the same anatomist, that the nervous system of the genera *Phyllidia*, *Onchidium*, *Tethys*, *Testacella* and *Pleurobranchus* is more or less upon the same plan. The pharyngeal ganglia are often small, but exist as usual.

The nervous system of the *Aplysia*, which is not figured in the plates accompanying this paper because it is so minutely described by Cuvier, is particularly interesting. The cerebral or sentient ganglia, giving origin as usual to filaments forming the pharyngeal ganglia, are conjoined, as in other naked *Gasteropoda*, into one situated above the œsophagus. The two lateral ganglia give off internal filaments to the foot, and external ones to the mantle. It will be seen, as we ascend, that there are separate ganglia for the foot, mantle and branchiæ. In the *Aplysia* there is, besides, another ganglion,—the one supplying the branchiæ and visceral organs at the posterior part of the body. That each of the lateral ganglia is in reality composed of two, appears from its supplying the two parts above mentioned, which, in most of the *Gasteropoda* and in the *Cephalopoda*, have separate ganglia for each: besides, the fellow ganglia are connected together by two separate filaments, and between them the aorta passes, which in many of the higher *Gasteropoda* and in the *Cephalopoda* distinguishes by its course that part of the ring which supplies the foot from that which supplies the mantle and viscera. Lastly, each lateral ganglion is connected to the sentient lobe by three nerves, being those which it receives from the pedal and from the branchial ganglia, and from that of the mantle.

In *Bullæa* (fig. 9.) we find the pedal ganglia (B.) distinct from the two sup-

plying the mantle (C.). The branchial ganglion (H.), situated as in *Aplysia*, does not send its filament (*f.*) as a distinct nerve up to the brain, but it passes through the ganglion supplying the mantle. The two cerebral ganglia (A.) are here lateral. The pedal ganglia are connected both with the sentient lobes, and with those supplying the mantle, as will be found generally the case. A subœsophageal nerve completes the ring, and combines the pairs of ganglia; and the cerebral ganglia as usual give the nerves forming the pharyngeal ganglia.

The spiral *Gasteropoda* present considerable variety in their nervous system. It may be premised that in them we shall (with a few exceptions, where we only find two,) observe four nerves originating from the superior lobes, when the ganglia of the ring remain far separate, but from the posterior part of the inferior expanded portion of the ring in the higher *Gasteropoda*. The two external ones are the nerves of the mantle, analogous to those we shall see in the *Sepia* (and it is to be remembered that the mantle is an important part in respiration): the two internal ones are analogous to the branchio-visceral ones of the same animal. The branchiæ are sometimes supplied by one, sometimes by the other, and sometimes by both; but in the higher *Gasteropoda* entirely by the latter, as in *Cephalopoda*; and we shall therefore call the internal pair, arising from the posterior point of the inferior portion of the brain in the higher *Gasteropoda*, the branchio-visceral when the animal is aquatic, or pneumogastric when terrestrial. From these latter, filaments go to the viscera, and often form a ganglion at or near the stomach. The nerves of the mantle originate external to the preceding, and sometimes wholly or in part supply the branchiæ. From the shape of the spiral *Gasteropoda* these are more or less twisted in their course. They may be well termed external respiratory, as they supply the mantle, siphons, and roof and floor of the respiratory sac, and often the branchiæ more or less. The shell-muscles partly receive their nerves from one of these pairs, partly from the pedal ganglion.

The nervous system of *Ianthina* (fig. 7.) is one of the most simple of those of the spiral *Gasteropoda*. In it we have a lateral ganglion (A.) on each side, considerably removed from each other, giving origin to the nerves of the eyes and tentacles (*g.*) and lips (*i.*), and posteriorly each ganglion sends off three

filaments, one to complete the ring (*b.*), on the lower part of which two separate locomotive ganglia (*B.*) are formed; and two others on each side, one (*f.*) of which attains the visceral organs, meeting the filaments from the pharyngeal ganglia, and not in this case forming a visceral ganglion or plexus, the other pair being the nerves of the mantle (*o.*) and muscular cavity in which the branchiæ are found. The right one of these last crosses over the œsophagus, and forms a ganglion (*H.*) in the left side, the left one here not crossing under the digestive canal, as, however, it often does: the direction being reversed in sinistral shells. In the first case the right branchial appendage has mounted over the body of the animal, and is the one most developed; the corresponding nerve having accompanied it, and been developed into a ganglion. This is not the posterior ganglion of bivalves, that having become incorporated in the lateral ganglia of the brain.

In *Paludina* (fig. 6.) we see better the two lateral ganglia (*A.*) to be composed each of two others, and each portion is united to the pedal ganglion (*B.*) by a separate chord, the posterior chord being shown by analogy to be the nerve connecting the two ganglia, which are united to the cerebral, in consent with each other. The right is largest, giving nerves to the penis (*r.*) from near the optic. These ganglia supply as usual the eyes, tentacles and mouth; the pedal gives nerves to the foot (*d.*) and shell-muscles (*e.*). Two large nerves (*c.*) go from the superior ganglia to supply the mantle, branchiæ, viscera, and in part the shell-muscles.

In *Turbo* (fig. 8.) we have also the two sentient ganglia (*A.*) at a distance from each other, each composed of two others sending down two twigs (*b.*) to the pedal ganglion (*B.*). From the anterior part of the lateral ganglia the nerves of the eyes and tentacles (*g.*) and mouth are as usual derived. From the posterior part we have the branchio-visceral nerves, forming a small ganglion at the back of the branchial sac of the animal supplying the branchiæ and viscera,—and two external respiratory nerves (*o.*), each forming a ganglion (*H.*) in the flank, supplying the mantle, and in part the branchiæ, also the shell-muscles, as well as the lateral appendages, often developed in this genus. There are also a few filaments (*p.*) to the floor of the branchial sac and side of the animal. With the pharyngeal ganglia (*D.*), which it is needless any further to describe from their uniformity, there are

in this little animal eleven ganglia. The genus *Trochus* appears similar in its nervous system, as does *Cyclostoma**.

In *Neritina* (fig. 10 & 11.) we find the two branchial and pedal ganglia of *Patella* become quite united into a transverse oval mass (O.), which, therefore, as well as the foot, also supplies the nerves we have just seen going from the superior compound ganglia. The two connecting filaments remain distinct as they were in *Patella*.

The *Planorbis* (TAB. XXVI. fig. 7 & 8.) has a nervous system rather remarkable, as the animal itself is in other respects, being organized to respire both air and water. There is a branchial cavity with a wide anterior opening as usual, containing a long branchial appendage; a small opening leads out of this cavity into the pulmonary cavity. Near this opening is the rudiment of the other branchial appendage. Two filaments connect the separate lateral superior ganglia (A.) with the inferior part of the ring, where the four ganglia with their connecting nerves form a quadrangle. The branchial cavity would appear to be supplied from the two posterior ganglia of these. A filament from the right side mounts over the œsophagus, joining one from the left, and together they form a ganglion supplying the pulmonary cavity situated to the left. Some filaments (*e.*) likewise from the posterior part of the quadrangle and from the ganglion just described, supply the shell-muscles, and form a small ganglion (G.), supplying the branchial appendage and viscera.

In *Carocolla* (TAB. XXV. fig. 12.), *Helix*, *Limax*, *Partula*, *Achatina*, and *Bulimus* (fig. 13.) the author finds little difference in the form of the nervous system. The brain when cut across over the œsophagus appears of a diamond form, a branch of the aorta dividing the anterior pedal portion below from the posterior part. From the anterior part below arise the numerous nerves of the foot (*d.*), others for the shell-muscles, and a few (*p.*) for the flanks of the animal: from the posterior portion in the centre proceed the visceral nerves (*f.*), often forming a sympathetic ganglion (G.) on the stomach, and sometimes another in the right side, which appears rather to belong to the generative organs than to the mantle: the posterior portion also gives origin, a little without the last, to the nerves of the mantle, which here do not cross. The

* Berkeley, Zool. Journ.

pharyngeal ganglia (D.) send down distinct filaments to the salivary ducts and towards the ganglion on the stomach; the retractor muscles of the pharynx being supplied with nerves (g.) from a point close to those which arise to form them (in these animals midway between the superior and inferior portions). We shall see in *Cephalopoda* that the pharyngeal ganglia through the labial receive a filament both from the superior and inferior portions of the ring; and in *Gasteropoda* it may often also be noticed that a filament runs back from the labial nerves (i.) to the nerve forming the pharyngeal ganglia. The nerves of the eye, tentacles and lips are given off, as usual, on each side superiorly, the part where they arise being sometimes more or less swollen into a ganglion on the ring.

In *Natica* (TAB. XXVI. fig. 6.), *Buccinum* (fig. 1, 2 & 3.), *Purpura* (fig. 10.), *Murex*, *Mitra* (fig. 11.), *Columbella** (fig. 12.), and *Oliva* (fig. 4 & 5.), all spiral, branchiferous, and carnivorous *Gasteropoda*, the nervous system is very similar in all. The brain is still principally subœsophageal, and it presents much resemblance to that of the *Sepia*. From the posterior part the branchio-visceral nerves (f.) arise, generally forming a ganglion or plexus (g.) at the back of the thoracic cavity, near the second stomach. The right nerve of the mantle (c.) crosses over the œsophagus, a ganglion (H.) being formed on it, near the brain, in *Buccinum* and *Purpura*. This nerve, and its fellow, which does not cross under the œsophagus, supply the margin of the branchial cavity and siphon. In *Natica* the right goes to the left over the œsophagus, and the left under it to the right, both forming a ganglion (H.). From the anterior part of the inferior portion the nerves of the foot (d.) are derived; also in part those of the retractor muscle of the animal into its shell: a few filaments (h.) arise on each side this part to the sides and integument of the neck. The nerves of the lips (i.), eyes, and tentacles (g.) arise as usual; the former in part supply the muscles of the proboscis, the other nerves supplying the organ more anteriorly, being from the pharyngeal nerve. The pharyngeal ganglia (D.) in *Purpura* and *Buccinum* are close to the brain, the nerves proceeding from them being very long, to allow of the extension of the proboscis; in *Natica* they are situated as usual on the pharynx, and are con-

* The author takes the liberty of introducing figures of *Mitra* and *Columbella*, though not bearing upon the subject of the paper, because he believes the animals have not been described.

ned by long nerves to the brain. In *Buccinum*, the two pharyngeal ganglia can be seen to have a root both from the superior and from the inferior portions of the brain. The penis in the male receives twigs (r.) from the cerebral portion near the optic.

The author need not add his testimony to that of Stiebel, Müller and Blainville as to the real dioptrical structure of the eyes of these animals, and consequently to their being real visual organs, and not (as has been argued by Home) organs of ordinary sensation. No acoustic organ has ever been shown to exist, though it appears probable from experiment that there are such, and that they might be discovered in large foreign species of *Gasteropoda*.

The author can only refer the reader for the description of the nervous system in the *Pteropoda* and *Heteropoda*, to the works of Cuvier and Poli; but he may observe, that in both these divisions it appears to be scarcely as perfect as that of some of the lower *Gasteropoda*, to which it offers most resemblance, being far below that of the *Cephalopoda*.

The nervous system of the *Cephalopoda*, on one side very similar to that of the *Gasteropoda*, approaches on the other that of some fishes. It may also be mentioned that the cartilaginous parts or skeleton offers a greater resemblance to the skeleton of a fish than has been supposed. In the *Sepia*, for instance, (excluding the shell of the back from our consideration,) we see a large cerebral cartilage surrounding the brain, supporting the eyes, and presenting a number of foramina for the passage of nerves and vessels. There are other cartilages dependent upon this, two articulated with each orbital process, and another at the base of the anterior feet. There are five lengthened cartilages, of which one is anterior to the liver, two lateral, descending from the cartilaginous disk at the back of the neck, and two others, external to the last, at the base of the fins. These, according to Cuvier, are a rudiment of a spine. In *Loligo* there is some appearance of this spinal rudiment being articulated; and it may be mentioned that the vertebræ of some fishes are more or less anchylosed. The structure of the fins offers considerable resemblance to that of those organs in cartilaginous fishes, in the skate, for instance. The muscular fibres are regularly interspersed by long slender cartilaginous laminæ, arising from a ridge on the longitudinal cartilage. There are other cartilaginous parts, which may be rudiments of shoulder-bones, if

the long cartilages mentioned above are not such, instead of spinal cartilages.

The brain of the *Sepia* (TAB. XXVII. fig. 2 & 3.) consists of several parts or ganglia conjoined into a ring around the œsophagus, (from which it is only separated by a sort of dura mater,) and enveloped by the large cerebral cartilage. Superiorly, upon the œsophagus, we find the ring expanded into a lobe (fig. 2 & 3, A.), cordate in shape, and giving in front four nerves (*a.*) to the labial ganglia (E.), and two bands (*b.*) descending to the anterior part (B.) of the lower division of the brain. The optic nerves (*c.*) arise from each side of this lobe, and then swell into two large ganglia (F.), which subdivide into numerous filaments, piercing the coats of the eye, and forming the retina. This lobe is also continuous with the posterior part (C.) of the inferior portion of the ring by the broad band (*c'*). The anterior part of the inferior portion gives its nerves to the feet, as it does in the *Gasteropoda* to the undivided locomotive foot of those animals. The anterior and posterior parts are connected together, but not quite so intimately as they are in some *Gasteropoda*. The anterior part, besides the pedal nerves (*d.*), sends a band (*e.*) to the labial ganglion, as we saw it did in the *Buccinum* to the ganglia, which in that animal gave off both the labial and pharyngeal branches. Here the labial and pharyngeal ganglia (D.) are distinct; the latter being connected to the former by two nervous bands (fig. 1, 2 & 3, *f.*), as we saw in *Patella*. The posterior part of the inferior portion gives off the two branchio-visceral nerves (*g.*); more outwardly the nerves of the mantle (*h.*), the great agent in drawing in the water to the branchiæ of the animal; more outwardly still, nerves (*i.*) which mount over the superior lobe and supply the retractor muscles: it also, in the *Sepia*, gives off here the two nerves which supply the respiratory valves. The nerves going to the mantle are distinct from those which supply the siphon or funnel (*j.*), nuchal valve (*k.*), &c. There are three nerves for the siphon, and two for the lateral valves. The aorta separates the part affording the branchio-visceral nerves, &c. from the more anterior half of this part, giving siphonic nerves*.

* The siphon is the expellent tube giving exit to the disaërated water, to the ink, fæces, and secretions. In respiration the *Cephalopoda*, with an inhaerent sac, and a valve in their siphon or funnel to prevent the entry of the water by the wrong opening, and also valves at the sides of the neck, and base of the siphon, to hinder its escape by the wide opening for its entry; having likewise protuberances on the inner surface of the sac, exactly fitting acetabula at the base of the siphon, for the

However, in other *Cephalopoda*, *Loligo* and *Octopus*, for instance, the two parts are not so distinct. In the midst of the nerves, which may be justly called the external nerves of respiration, arise the two acoustic nerves (*l.*); thus, as in vertebrated animals, connected at their origin with the nerves distributed to the respiratory tubes. The posterior portion is united to the anterior pedal portion, more or less intimately, in different genera. The aorta passes between them. The nerves supplying the external organs of generation do not arise from the brain, as in *Gasteropoda*, from their widely different situation. The pharyngeal ganglion (*D.*), quadrangular in *Sepia*, bilobed, as in *Gasteropoda*, in *Loligo*, is situated in its usual place, at the base of the tongue. Besides muscular and glandular branches (*m.*), it evidently sends down filaments (*n.*) upon the œsophagus. The labial ganglion, which gives two nerves to the pharyngeal, is large and round; it sends fifteen or twenty filaments (*o.*) to the lips situated around the maxillæ. As described above, it receives a nerve from the upper (sensitive), and another from the lower (motor) portion of the circle. A filament runs across from it, over the upper surface of the superior lobe, towards a round tubercle of nervous matter (*r.*), situated upon the optic nerve*. The upper surface of the superior cerebral lobe presents a division into an anterior and a posterior bilobed portion. As described above, it communicates by two chords on each side with the two divisions of the lower portion of the ring, the anterior band being in connexion with the band connecting the labial and pedal ganglia. The anterior division and band are larger in *Octopus* from the immense size of the feet†. The nervous

purpose of preventing any disarrangement of the parts; and, lastly, a funnel or siphon, through which the current is evacuated, conveying away the excretions, without their gaining access to and injuring the viscera: with such an apparatus these animals can have no need of vibratile cilia, so common in *Mollusca*; and the author has convinced himself that they want them, by examining the excised gills of the adult, and also the living animal of the *Sepioida* and *Sepia* just escaped from the ovum. We see the use of so many respiratory nerves from the complication of these organs.

* This little body has been figured in the *Sepia* by Mr. Owen (*Anat. of the Pearly Nautilus*). It equally exists in *Loligo* and *Sepioida*.

† The *Octopus* creeps, as well as swims, by means of its feet; and these are the most general locomotive organs in these animals. Some, however, as *Sepioida*, swim, by means of the contraction of the sac, in repeated jerks, the head being posterior, using the fins merely as rudders. The *Sepia* swims entirely by means of these latter organs, and consequently uninterruptedly; commonly the head is posterior, but when it descends, it does so head foremost.

circle then is double inferiorly, as we saw so low in the scale as in *Conchifera*, and the anterior division supplies, as in them, the organs of locomotion, and the posterior, the branchiæ, &c. In conjunction with the siphonic nerves arises on each side a nerve (*y.*), which pierces the cranium and enters the orbit, supplying two small muscles of the eye, of which one unites with its fellow of the opposite organ, and the conjoined tendon slides backwards and forwards in a pulley on the anterior and superior part of the cartilage. The branchio-visceral nerves descend on each side of the vena cava, giving many nerves, and amongst others, many filaments (*t.*) to the œsophagus, joining those from the pharyngeal ganglia. It divides behind the rectum, a branch going outwards to the base of the gill (*u.*), forming there an oblong ganglion (F.), and supplying that organ, &c.; minute filaments go to the pericardium and heart; the remaining branches get upon the œsophagus (*o'*), and with those previously described, form a large ganglion (G.), in the *Sepia* a quarter of an inch in its long diameter, upon the stomach, between the cardiac and pyloric orifices. From this sympathetic ganglion filaments of a large size go to the cæcum (*v.*), intestine, ink-duct, penis and oviduct (*w.*), meeting filaments from the branchio-visceral. The nerve of the mantle gives a few nerves to the muscles, pierces the pillars supporting the head, divides into two branches, of which one forms the great ganglion (H.) of the mantle, from which nerves radiate in every direction to that part. The other continues to descend, receiving a large nerve from the ganglion, and then gets behind the large longitudinal cartilage, supporting the fin, where it subdivides, supplying that organ with large nerves (*z.*). Before it has pierced the muscle this nerve gives off fine filaments, which, running along the hepatic artery, get upon the œsophagus, and mix with its other filaments derived from other sources.

All the *Cephalopoda**, perhaps, have acoustic vestibules, containing a bag of fluid on which the nerve ramifies; also a small calcareous body, which in the *Sepia* has an accidental resemblance to the human incus.

In the eye there is a nervous coat or retina behind the pigmentum nigrum; and it has been a problem how it could be affected by light. The author is

* Not, however, according to Mr. Owen, in the *Nautilus*. The author has not seen them in the *Sepioida*, where the cranium is membranous; but probably it has been concealed, from its small size, in the latter.

convinced, however, that there is a retina internal to this pigment. By dropping dilute nitric acid on its internal surface, after removing the hyaloid, this retina is made apparent. It immediately becomes white and opaque, and is seen to be of considerable thickness, but, like the black coat itself, of the greatest softness and delicacy. It must, however, be confessed that no nerves are seen to go from the external retina to this; but their fineness may conceal them. The glandular mass at the bottom of the eye communicates externally by means of a duct which pierces the cartilage, deepening the edge of the orbit, and is seen to open externally beneath and behind the eye*. The external opening does not, as is supposed, admit the rays of light to the lens. In the living animal it is perfectly closed, and it ought to be considered as the excretory orifice of an anterior chamber. There is a round transparent part of the conjunctiva for the admittance of the light. The orifice is not in the axis of the lens; it is so small, that it is often difficult to discover; and it does not, in the living animal, prevent the existence of an aqueous humour before the lens†.

There are trifling differences in the nervous system of these *Cephalopoda*. Thus in *Loligo* the pedal ganglion is very anterior, whilst in *Octopus* it is scarcely separate from the rest of the brain. When there is no fin, as in the latter animal, the second division of the large nerves of the mantle is wanting. The author has not had an opportunity of examining *Octopus*, so that he cannot positively affirm that Cuvier has overlooked the labial, lingual‡, and sympathetic ganglia, but he may mention that he has seen them in *Sepia*, *Sepiola*, and in *Loligo communis* and *medius*.

The author needs only notice Mr. Owen's beautiful "Monograph" to observe that the brain of the tetrabranchiate *Cephalopoda* must, from his description, be little different from that of the *Sepia*, though less perfect. The superior cerebral lobe is not developed; and in this and other respects it is more nearly allied to the brain of the higher *Gasteropoda*.

* The opening described by Blainville in the *Loligo* is probably the conjunctival pupil of Cuvier.

† There is much confusion and difference in the descriptions of Cuvier, Blainville, and Carus.

‡ This lingual or pharyngeal ganglion, however, though not described in the text, appears represented by his engraver without any mark of reference being attached. The author finds no mention of these different parts in Scarpa, Tilesius, or Swammerdam.

The nervous system of the *Cephalopoda*, then, has some resemblance to that of a fish. In one circumstance it differs from those of all vertebrate animals, viz. the brain has not yet entirely ascended over the œsophagus, but forms a ring around it. Without any stretch of fancy, the superior lobe may be compared to the optic lobes of a fish, or the corpora quadrigemina; and the anterior unlobed part of this ganglion is, perhaps, a rudiment of the hemispheres. But hence olfactory nerves ought to arise, as optic nerves do from the optic lobes, and form olfactory nerves. The nerves going hence form in fact a ganglion, which the author has called labial, but which gives a great number of nerves to two membranous parts around the maxillæ, the external one of which appears analogous to a membrane, which, in the *Nautilus*, Mr. Owen tells us, is of a structure identical with the olfactory laminæ of fishes, and to which he actually gives the name of olfactory organ. There is no rudiment of a cerebellum, which organ is, however, sometimes in a rudimentary state in reptiles. As we see in fishes large lobes developed on the olfactory nerves, we here see them on the optic. The eyes are as highly developed as those of many vertebrated animals, and hence the size of these lobes: to what parts of fishes, however, are they, and the little geniculata upon them, analogous? The pharyngeal ganglion and nerves supplying the jaws, tongue, maxillæ, salivary glands, muscles of deglutition, and forming the principal attachment or origin superiorly to the sympathetic, must be analogous to the ganglionic fifth nerve of higher animals. Its nerves of connexion are probably from two sources, two of those going from the anterior part of the superior lobe belonging to it, as well as the band of motor nerves from the pedal ganglion, going to it through the labial or olfactory ganglion; the fifth nerves here, as in other animals, being connected with the olfactory. The lower part of the cerebral circle evidently (with the exception of the pedal ganglion) gives off the same nerves as the medulla oblongata does in higher animals,—the external respiratory, acoustic, and branchio-visceral nerves. It receives from below two large columns, the position of which is similar to that of a spiral chord. External to these large nerves or columns is a large ganglion, which is connected to it by two separate bands: this ganglion gives its branches to the mantle, whilst the rest of the branches given by the nerve are distributed to the fin; all these nerves passing to their destination between cartilages, per-

haps bearing a resemblance to a spine. These two distant fasciæ offer but a poor resemblance to the spinal chord of many fishes: but in reality some of them, as *Lophius*, *Tetraodon* and *Petromyzon*, appear (from the description of authors*) to have that organ scarcely better developed; and a disjoined state is shown to be the normal condition of this organ in its first stage of development.

In concluding this paper, the author is conscious how much must be dry and uninteresting to many. As, however, he believes there are some new facts in it which may assist future inquirers, who may endeavour to show there is some meaning and method in these parts, and as he thinks he has proved the opposite to what another author† on the nervous system affirms of these organs in the Mollusca, viz. that they ought in every respect to be considered below those of insects, he will conclude by claiming the indulgence to which the difficulty of the subject entitles him.

* Des Moulins, *Système Nerveux*. Arsaky, *De Piscium Cerebro*.

† Serres, *Anat. Comp. du Cerveau*.

Fig. 3.

Macra, Stultorum.

Fig. 5.

Pecten maximus.

Fig. 4.

Modiola vulgaris.

Fig. 6.

Pholas dactylus.

Fig. 2.

Ostrea edulis.

Fig. 1.

Ciona intestinalis Flem.

Fig. 7.

Mya truncata.

Fig. 1.

Chiton fascicularis.

Fig. 5.

Eolida papillosa.

Fig. 9.

Duttha aperta.

Fig. 12.

Carocella albilabris.

Fig. 2.

Chit. marmoratus.

Fig. 6.

Patadina virgata.

Fig. 10.

Fig. 3.

Patella vulgaris.

Fig. 7.

Janthina fragilis.

Fig. 11.

Neritina canalis.

Fig. 4.

Scyllaea pelagica.

Fig. 8.

Turbo littoreus.

Fig. 13.

Palimnus hemastomus.

Sepia officinalis.