

under the microscope to be composed of two distinct, though connate carpels; the ovules are few, horizontally attached, or somewhat pendulous from narrow axile placentæ attached to the twofold dissepiment. These are characters that seem to correspond in great measure with the *Bruniaceæ*, with which the habit of *Lonchostoma* does not ill accord. These are merely hasty indications, as it would be foreign to the object of the present investigation to pursue such inquiries farther.

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XIX.—*On the Anatomy of Eolis, a genus of Mollusks of the order Nudibranchiata.* By ALBANY HANCOCK and DENNIS EMBLETON, M.D.

[Continued from vol. i. 2nd Series, p. 105.]

[With two Plates.]

*Nervous System.*

THIS is made up of central masses or ganglia united by commissures, and of nerves. The ganglia are five or six pairs, four of which are symmetrically arranged with regard to the median line, and together with their commissures surround the commencement of the œsophagus lying upon the upper and posterior surface of the buccal mass, vol. xv. Pl. V. fig. 16 *b* and Pl. V. fig. 1 of present paper. Two pairs are supra-œsophageal and two infra-œsophageal. The former exceed the latter many times in size. The masses are of a pale yellowish flesh-colour, and appear to be filled with globular vesicles of various sizes.

First, of the supra-œsophageal or cerebral ganglia, the median pair, Pl. V. fig. 1 *a a*, largest of all, are irregularly ovate, flattened above and below, and somewhat constricted about the middle as if composed of two parts; their anterior ends, which are the larger and truncated, are united across the median line by a short broad commissure. The second or lateral pair, *b b*, lie rather behind the first and on the sides of the œsophagus; they are irregularly spheroidal, smaller than the first and flattened like them, and intimately connected to their external posterior margin. The two pairs of infra-œsophageal ganglia are of very unequal size: the first or buccal, or larger pair, *c c*, are elliptical, their long diameters placed transversely one on each side of the median line, across which a short thick commissure unites their contiguous ends; from the under surface of these, at their outer and anterior part, spring two short pedicles, supporting the second pair of ganglia, *d d*, the gastro-œsophageal, very small, not one-fourth the size of the last, but of the same form. In

addition to these, there is a pair of ganglia, *ee*, at the base of the dorsal tentacles, which we call olfactory; and we have seen what we take to be other ganglia, but of these we shall speak further on.

The nervous centres intercommunicate by the following commissures. A short broad one, *f*, unites the first pair of supra-oesophageal, and a similar though smaller, *g*, the first pair of infra-oesophageal; these have been already noticed; then the lateral supra-oesophageal are united to the first or anterior or cerebral by a broad flat band, *h*, so short that the ganglia appear to be continuous with each other. Next we have three nervous bands or collars, concentrically arranged, inclosing the oesophagus, and serving to complete the connexions of the supra-oesophageal ganglia with each other, and to bring them into association with the infra-oesophageal. First, the innermost or thickest collar, *i*, lies close to the oesophageal wall, and is composed of four or five distinct nervous filaments running parallel to each other, and connecting together the posterior borders of the two lateral supra-oesophageal masses. Second, a slender, delicate collar, *j*, lies next outside, much wider than the former, and uniting the posterior and outer parts of the first pair of supra-oesophageal ganglia, it comes out from the under surface of these bodies and runs under the second or lateral ganglia. The existence of this collar or commissure between the posterior parts of the median cerebral ganglia, whilst their anterior parts are united by the anterior median commissure, seems to confirm the impression we received at first sight, that the cerebral ganglia are each of them double centres. It will be observed that the two last-described oesophageal collars are not attached in any way to the infra-oesophageal ganglia. The third or outermost collar, *k*, however establishes a communication between the first or median supra-oesophageal and the first infra-oesophageal ganglia. This is a strong band, being little inferior in size to the first, of uniform texture, and lying just outside of the second collar, and in contact with it, it is the widest of the three. In front it is attached to the under part of the outer border of the first cerebral ganglia, considerably in advance of the coming off of the second collar; from this part it is traced backwards under the lateral supra-oesophageal into the external end of the buccal ganglia.

The nerves vary a good deal in size, and we have been able to trace thirty-three pairs; of these, twenty-one come off from the supra-oesophageal ganglia, six from the infra-oesophageal, and five from the commissures. There is also a large pair which comes out from the buccal mass from an obscure ganglion imbedded in the muscular tissue, and a small nerve, apparently single, that separates from the middle collar of the oesophagus,

and seems to present a small ganglionic enlargement. We have numbered them in the order in which they occur, commencing at the median line in front.

The first and second pairs, very minute, come out of the under surface of the anterior commissure of the first or cerebral ganglia, and pass to the skin on each side of the median line before and behind the dorsal tentacles.

The third pair, large nerves, come out of the first cerebral ganglia at their upper surface, and near the middle of their anterior border; they pass forwards, upwards and downwards to the roots of the dorsal tentacles, within which each suddenly swells out into a remarkable ganglion, *e*, of an irregularly oval form, which, at its upper end, divides into three or four processes, each giving off nerves to be distributed for the supply of the whole tentacle. This pair we look upon as the special nerves of smelling, for reasons which will be adduced hereafter, and as endowing the tentacle with the power of ordinary sensation likewise. If this view be correct, then the small branches passing from the ganglion to the sentient surface of the tentacles are properly to be designated olfactory nerves, and the thick pedicle supporting the ganglion and connecting it with the cerebral ganglion, olfactory tractus.

The fourth and fifth pairs, considerably less than the third, arise also from the anterior part but under surface of the same ganglia, close together, and just outside of the third. The fourth runs forward to the outer lip before giving off any branches; after that it divides and subdivides minutely, and goes to supply the outer lip above and below. The fifth runs forward and is distributed to the skin of the head and between the dorsal tentacles, but does not give off such numerous branches as the preceding nerve.

The sixth, one of the largest nerves in the body, comes out of the external anterior angle of the ganglion, and after a short course outwards and forwards bifurcates. The two branches are about equal in size: one passes into the oral tentacle, divides into two branches which subdivide and supply the tentacle; the other runs forward, and then inclines inwards towards the median line, and subdivides into many twigs which are distributed upon the roof of the channel of the mouth.

The seventh and eighth are minute nerves which issue from the outer margin of the ganglion just behind the sixth. They take a straight course outward and pass into the skin of the side of the head.

The ninth is a large pair, coming out of the same ganglion just behind the preceding, and running outwards and forwards gives off a twig which goes to the muscles attaching the buccal

mass to the skin. It then passes forwards and inwards, and is lost upon the sides of the channel of the mouth.

The tenth and eleventh pairs are small, come off from the same ganglion still further back and just in front of the eye, and pass directly outwards into the skin.

The twelfth and thirteenth arise from the junction of the anterior and lateral cerebral ganglia, and passing outwards and downwards first, then incline downwards and backwards and run half-way down the body, one above the other, in the skin between the border of the foot, and the rows of branchial papillæ.

The fourteenth and fifteenth, very minute pairs, emerge from the line of union of the anterior and the lateral ganglia, and are then placed directly under the eye. The former of these nerves goes to the skin of the side of the head between the oral and the dorsal tentacles, the latter to the skin immediately behind the situation of the former.

The sixteenth or optic nerves are stout but very short, and have the organ of vision at their extremity. They are inclined forwards and upwards from the line of union of the anterior and lateral ganglia.

The seventeenth or auditory are mere rudiments of nerves, and are attached to the anterior ganglia quite close to the bases of the optic nerves, and immediately behind them. The auditory capsule and the eye will be described further on with the other organs of special sense.

The eighteenth pair, one of the largest, issues from the outer borders of the lateral ganglia, rather in front of the middle, passes outward and bifurcates very soon after; each of these branches again bifurcates and is distributed by many twigs to the muscles and skin of the foot, both anteriorly and posteriorly (the pedial nerve).

The nineteenth, also of considerable size, come out of the external borders of the lateral ganglia, behind the middle, separated by a considerable interval from the eighteenth, and passing slightly outwards take a backward course, and can be traced in the skin for a long way down the sides of the back, giving off chiefly externally numerous branches that supply the skin. This we presume is the respiratory nerve.

The twentieth are seen to come forth from the posterior margins of the anterior ganglia, and are of a size little inferior to the last. They can be traced in the skin of the back between the last-described nerve and the dorsal median line nearly as far as the tail, giving off twigs from their outer sides like the nineteenth pair to the skin.

The twenty-first, twenty-second and twenty-third pairs are all small nerves coming out successively from the posterior borders

of the anterior ganglia between the last-described nerve and the median line. They all pass a good way backwards to the dorsal skin on each side of the median line.

The origin, course and distribution of the six pairs of infra-oesophageal nerves are as follows:—

The first pair come from the upper surface of the roots of the pedicles that support the gastro-oesophageal, and close to the buccal ganglia. The nerves are rather small, run forwards and apply themselves to the oesophagus, along which they are conducted to the stomach, the greater part of which organ they supply with branches.

The second, third and fourth arise from the margins of the gastro-oesophageal ganglia, are very small nerves, but can be traced to the oesophagus and neighbouring parts of the stomach.

The fifth pair come out of the external ends of the buccal ganglia in conjunction with the third or outermost oesophageal collar, to which they are slightly inferior in size. The nerves and the collar separate at once; the nerves passing backwards and outwards give off each a branch that bends forwards and outwards and becomes lost among the muscles of the buccal mass external to the ganglion. The trunk then inclines towards an opening between the muscular bundles of the back part of the buccal mass, and enters that opening lying in contact with another large nerve that is observed to issue from the same.

It is difficult to follow the trunk far into the intermuscular aperture, but as far as we have been able to trace it, it appears to be destined for the buccal mass and tongue.

The sixth pair is given off from the posterior margin of the buccal ganglia, and shortly after becomes lost among the muscular bundles of the back part of the buccal mass.

Of the five pairs of nerves from the commissures, two have already been described, viz. the first and second supra-oesophageal; the three that remain come off from the oesophageal collars in the following manner.

The pair marked  $\alpha$  come off from the outer margin of the first or innermost collar near the median line. They are very minute nerves, and we have not succeeded in tracking them to their destination.

That marked  $\beta$  is the genital and probably the cardiac nerve, and is an offset from the middle or slender collar, which it nearly equals in size, at a short distance behind its attachment to the anterior cerebral ganglion. It runs from this origin backwards and outwards to the generative organs, guided partly by the anterior aorta, gains the fissure where the confluence of the ducts from the different parts of the generative apparatus exists, and

is then subdivided among the testis, the oviduct, the mucus-gland, &c. It seems more than probable that the penis receives a twig from this nerve, and that the spermatheca and ovarium are also supplied from it, though we have not traced branches so far. If any branches pass from this nerve to the heart, which we are inclined to believe is the case, they probably run along the anterior aorta.

We think it only right to remark, that not having traced this nerve with the same precision as the rest, we do not feel ourselves competent to speak so decidedly of its distribution as we could wish.

The nerve  $\gamma$  arises from the third or hindermost collar at the side, passes backwards to the aperture previously noticed as existing in the buccal mass, and therein is applied to the surface of the nerve that issues from the opening, and further we have been unable to follow it.

In addition to these we have the nerve marked  $\delta$ , which appears to be single; it comes off from the inner margin of the posterior segment of the middle slender collar near the median line, and has been traced to the under surface of the anterior portion of the stomach. There appears to be a small fusiform swelling on this nerve.

The last nerve to be mentioned, and which is designated  $\epsilon$ , is somewhat inferior in size to the fifth infra-œsophageal, and as before stated emerges from the aperture among the muscular bundles of the posterior part of the buccal mass. On attempting to follow this nerve more deeply, we find it to end in what seems to be a ganglionic swelling  $\zeta$ , from which nervous branches apparently radiate throughout the muscular tissue of the buccal mass. If this nerve be traced in the opposite direction from the intermuscular aperture, it is found to pass forwards, inclining at first inwards, and as it approaches the outermost collar receives obliquely from it, near the union of the collar with the buccal ganglion, a branch of communication,  $\eta$ ; it next runs under that collar, and then under the middle one; after this still passing forwards and approaching the posterior margin of the lateral supra-œsophageal ganglia, it turns outwards, hooking round over the two outer collars, but having no connexion with either at this part, and reaching the skin at the side of the buccal mass, it bifurcates, one branch passing forwards, the other backwards; they both send off numerous twigs which have been followed to the ramifications of the gastric system at the bases of the papillæ.

In *E. olivacea*, *E. coronata*, Pl. VI. fig. 1, and *E. Drummondi*, Pl. V. fig. 2, the central masses and the nerves emanating from

them, and the commissures, excepting the modifications to be presently mentioned, are pretty much the same, as far as we have been able to examine them, as they exist in *E. papillosa*.

In *E. coronata* the olfactory tractus are much shorter, and their ganglia more globular, and of much greater relative size than in *E. papillosa*, being indeed more than one-third the size of the lateral supra-œsophageal ganglia themselves. There is besides one principal nervous stem from the ganglion which runs up the central axis of the tentacle.

In *E. Drummondi* the relative size of these ganglia is still greater and their form elliptical. The existence of these ganglia we believe to be constant in all the species; we observed them in *E. pellucida*, *E. Farrani*, *E. alba*, *E. gracilis*, *E. picta*, *E. punctata*, &c.

The three nervous collars of the œsophagus can be observed easily in *E. Drummondi*, in which there appears to exist at the coming off of the genital nerve from the middle or slender collar a small ganglionic swelling  $\theta$ . A similar swelling occurs also in *E. coronata*.

When viewed attentively with the naked eye, the cerebral ganglia, and particularly the first or median pair, present a number of large globular vesicles inclosed within a transparent membranous envelope. When compressed and somewhat magnified, all the ganglia seem to be made up of masses of vesicles, as the view of a buccal ganglion, Pl. VI. fig. 2, will show. Under a higher power these vesicles or cells are found of very variable size, externally smooth, internally granular, and having one or more large distinct nuclei and nucleoli; some have only one large nucleus and a distinct nucleolus; the interior is filled with smaller cells of different dimensions and also nucleated; the smallest of all however are minute, clear, bright cells, probably nuclei or rather nucleoli of larger vesicles. Many of these last are found also lying in the intervals of the large cells intermixed with the tenacious semifluid matrix that imbeds the nervous vesicles, and in which no distinct forms can be discerned. On tearing up one of the cerebral ganglia and examining the contents of the membranous envelope in the compressor, under a high power (one-eighth object-glass), numbers of the cells of all sizes are seen under the form of pear-shaped, largely nucleated vesicles, Pl. VI. fig. 4, having a long pedicle attached; the nucleus, which is very large, has an evident and well-marked nucleolus, and the pedicle or stalk of the cell is in the interior very finely granular. Groups of these pedicled ovoid vesicles may be observed, such as that at Pl. VI. fig. 3, their pedicles all lying in the same direction, and tending either to unite or to run on parallel to each other, putting us strongly in mind of some of the simpler forms of glan-

dular apparatus. We cannot confidently say that we have traced groups of these pedicles into the nerves that issue from the ganglia, but we have seen what inclines us very strongly to the idea, that such is in reality the relation of these two parts of the nervous system. At Pl. VI. fig. 2, where a nerve *b* is shown coming off from a buccal ganglion *a*, parallel striæ are observed distinctly passing towards the nerve from the interior of the ganglion. Again, when the connexions of the nerves with the cerebral ganglia are examined, parallel striæ can be seen continued from the commencement of the nerve for some distance into the ganglion, becoming gradually more and more obscured by the vesicles of the ganglia and then lost altogether; but from the toughness of the enveloping membrane—the body of the Nudibranch having lain for some time in spirit and water—and the extraordinary delicacy of the contained parts, we have not been able to lay bare, and leave *in situ*, in one and the same specimen, the real connexion which we believe to exist between the nerves and the vesicular element of the central ganglia. But we hope that further observation will enable us to show that the pedicles of the nerve-corpuscles in *Eolis* are continuous with the nerves; and if this be so, then that it may be the means of illustrating more clearly the connexion that exists in the Vertebrata and in Man between the nerves and the white and the gray matter of the brain and the rest of the centres of the nervous system. It is highly probable, however, that all the cells of the ganglia possess a pedicle or stalk in their perfect state, and that the apparent absence of a pedicle or pedicles in some cells or groups of cells may be owing either to the unfavourable aspect under which they are presented to the eye—they being so placed that the pedicle is either very much foreshortened or hidden altogether by the cell itself, or else to the pedicle having been broken off during the manipulation of the specimen, or again to the magnifying power in some cases not being sufficient to make them discernible, or lastly to their imperfect state of development.

These cells or vesicles of the nervous ganglia of *Eolis*, although they show only one cauda or prolonged pedicle, are doubtless analogous to those caudate vesicles or nerve-corpuscles which are characteristic of the gray matter of the cerebro-spinal and sympathetic ganglia of the higher animals.

The nerves themselves appear to have none of the cells above noticed, but to consist of series of parallel granular lines or fibrillæ, which on tearing the nerve across often remain detached from each other, and which are all in their perfect state enveloped in a strong common sheath continuous with the membranous capsules of the ganglia. Where a nerve gives off branches, lines of granular matter, probably the fibrillæ just mentioned, are

separated from the main stem and become inclosed in a sheath of their own, and this mode of division appears to be carried on to a very minute degree. We have not been able to detect the manner in which the nerves actually terminate; certainly we have seen nothing to warrant the description and the figures of M. de Quatrefages relative to this particular.

On taking a review of the nervous system of *Eolis*, we are at once struck with the high grade of development, and with the symmetrical arrangement that obtains in it; the heterogangliate character applicable to many gasteropodous mollusks being, so far as our researches have led us, inapplicable to this more elevated being. The nervous centres are closely concentrated around the œsophagus, and there exists a sufficient correspondence between them and the same organs in the Cephalopoda to enable us confidently to compare them; indeed we have every reason to think that we recognise in them the homologues of the principal masses of the nervous centres of the Vertebrata.

If we turn to Professor Owen's memoir on the Pearly Nautilus, pl. 7. fig. 1, in which the nervous system is represented, we find that the supra-œsophageal mass or brain together with the attached optic lobes, taken in conjunction with the anterior œsophageal ring formed by the union of two ganglia, corresponds to the anterior supra-œsophageal ganglia of *Eolis* with the slender or middle collar round the œsophagus, since they give off nerves which go to supply analogous parts, viz. the eyes, tentacles, lips, &c. The posterior œsophageal ring of the Nautilus to a great extent represents in the same way the lateral supra-œsophageal ganglia of *Eolis*, united with all the infra-œsophageal ganglia and the two large collars or commissures together.

At fig. 3, same plate, Professor Owen gives a view of the nervous system of the *Sepia officinalis*; the homology is equally distinct as in the former case, only the parts are more concentrated; still they serve to lead us on more easily to compare the ganglia of *Eolis* with the several divisions of the more highly-developed nervous centres of the Vertebrata. In *Eolis* we see that certain nerves of relation—of special and common sensation, and their corresponding nerves of motion, voluntary or reflex—are in connexion only with the two pairs of supra-œsophageal ganglia. The olfactory and optic nerves, and numerous others to the lips, mouth, tentacles and side of head and back, are thus attached; hence we infer that the anterior part of the supra-œsophageal ganglia may be in some measure compared, though not perhaps quite accurately, to the cerebrum and optic lobes of the Vertebrata; at all events these are the only parts to which they correspond. The posterior parts of the median cerebral ganglia, and

the remaining ganglia together with their commissures and collars, are the representatives of the medulla oblongata and spinal cord of the higher animals.

We do not discern in *Eolis* anything at all analogous to the sympathetic system of the higher animals.

In the nervous system again we are sorry to be compelled to be at issue with M. de Quatrefages, who states in his paper that "toutes les grandes masses nerveuses sont réunies au-dessus de l'œsophage et d'elles seules émanent directement les nerfs qui se rendent dans toutes les parties du corps." Subsequently however he points out the presence of a single small ganglion below the œsophagus, from which small nervous twigs are given off to the mouth and digestive tube. The incorrectness of these and other observations we hope to have rectified. Further, M. de Quatrefages makes out only one nervous œsophageal ring; we have over and over again seen and verified the three represented in our plate. The nerves of vegetative life he derives from the same ganglia that give off the nerves of relation, and points this out as an interesting fact. The rule with two or three exceptions appears to be, that the two sets of nerves have two appropriately distinct sets of ganglionic centres, viz. the infra-œsophageal for vegetative life, and the supra-œsophageal for the life of relation, which is agreeable to analogy. With regard to the number and arrangement of the nerves, we find M. de Quatrefages to be again in confusion. His number is very far short of the full complement, and he has traced scarcely any to their proper destination. We observe that he gives to the optic nerves a ganglionic swelling which we have never seen, and omits the olfactory ganglion, which may be seen even during life in the more transparent species.

We do not understand M. de Nordmann's account of the nervous system. It is possible that in that section of the genus *Eolis* to which *Tergipes* belongs, the nervous system may differ from that of the other divisions, but we should be surprised to find it so different from that of those we have dissected, as it is represented in M. de Nordmann's paper.

#### *The Senses.*

The organs of the senses appear to be as highly developed in *Eolis* as in any other of the Gasteropods. The sense of touch is spread over the whole surface of the body, including the foot, the tentacles, and the branchial papillæ, which last are so extremely sensitive as to respond to the slightest undulations of the water around them. Many of the species indeed are so alive to such impressions, that it becomes a matter of difficulty to observe their habits, and even their natural form, since on the slightest

motion of the water they curl up their foot and fall to the bottom.

The oral tentacles, which are kept in perpetual action, seem to possess the sense of touch in an exquisite degree; so much so that we are led to conclude, that from this circumstance, and from their anterior position, they ought to be regarded as special organs of touch.

Taste, if present, most probably resides in the lining membrane of the buccal cavity, particularly in the folds at the back of the tongue (1st paper, Pl. I. fig. 8 *h*) and the cheek-mass, *ef*, and perhaps also in the laminæ at the commencement of the œsophagus.

When describing the third pair of nerves, we stated that we considered the dorsal tentacles to which these nerves pass to be distributed, as the olfactory organs, and for this opinion we now proceed to adduce reasons which appear to be sufficient.

That these tentacles are special and very important organs, a consideration of the internal anatomical arrangement of their nervous element and of the peculiarities of their external form, peculiarities susceptible of great variety, would seem to leave very little doubt in the unprejudiced mind.

First of all a large nerve, Pl. V. fig. 3, among the largest in the body, comes off from the front of the median cerebral ganglion; and secondly, this nerve, or more properly speaking, tractus, has superadded to it at the base of the tentacle a well-defined ganglionic swelling, *e*, of a size exactly proportioned to the extent of complexity in the external form of the tentacle. Thus in *E. papillosa*, in which the tentacle is smooth and in its simplest form, the ganglion is considerably less than in *E. coronata*, Pl. VI. fig. 6, and *E. Drummondi*, in both of which the tentacle has a surface of a far more complicated kind, being rendered much more extensive by the addition of numerous broad, circular laminæ; the ganglion being in these two species, as before noticed, upwards of one-third the size of the lateral supra-œsophageal ganglion itself, Pl. VI. fig. 1 *e*, and Pl. V. fig. 2 *e*.

If further evidence be required to illustrate the importance and special nature of these organs, we may go from the genus *Eolis* to the other members of the family *Eolididæ*, as for instance to *Eumenis marmorata*, in which we find the laminæ so closely set as to conceal the whole shaft of the tentacle, and moreover there exists a sheath at the base of the tentacle into which it can be retracted at the will of the animal. A sheath also exists in *Doto*, Pl. VI. fig. 7, into which the organ, though simple in form, is completely retractile. The same is found likewise in *Dendronotus arborescens*, Pl. VI. figs. 8 & 9, in which the tentacle is remarkable for highly developed laminæ; and here the

sheath, which is long, and into which the tentacle is quite retractile, is garnished around its extremity by a circle of arborescent filaments, by which the organ even, when extended, is to a great degree protected from injurious contact with surrounding objects.

Again, as if the laminated disposition of the tentacle were not sufficient for the purpose of the *Antiopa splendida*, Pl. VI. fig. 10, we have these organs, *aa*, standing out from the sides of a median crest, *b*, which is elevated above the surrounding skin, and crowned by a series of pinnate laminae. That this median crest is really a part of the olfactory organ, an addition to its complexity, is proved by the attendant modification of the nervous element, which is as follows. There is directly in front of and in contact with the median cerebral a pair of small ganglia, *cc*, each of which gives off two branches, one of which, *d*, goes to the tentacle, and the other, *e*, much thicker, goes to one half of the median crest.

We could easily adduce other examples from the *Dorididae*, if others were required, to show the importance and the speciality of these organs in the Nudibranchiata, but those we have brought forward seem enough for this purpose. Another circumstance bearing upon the special nature of these tentacles, and noticed by Joshua Alder, Esq., one of the authors of this paper, in a communication made to the British Association at the Cork meeting, is that the cilia on their surface vibrate in a direction contrary to that of those on the surface of the branchial papillae. On these the cilia move constantly from the body towards the extremity of the papilla; on those they act from the point of the tentacle towards the body; thus, in the former case, the water which has served for respiration is drawn from the body and thrown off from the apices of the papillae, whilst in the latter the fluid which we may suppose to contain odorous particles or qualities is attracted to the end of the tentacle, and made to pass down over the entire surface, and then thus to act upon the sentient nerve within.

Now it is a constant occurrence in the higher animals that the fluid to be tested by the olfactory organ is always brought to the nerve, and made to pass over the sensitive surface in the majority of instances by means of the agency of inspiration. In fishes however in which the nasal cavity is shut off from the mouth and throat, another agency than that of respiration is required; the olfactory plates however are freely supplied with cilia, and these probably act a part analogous to those of the laminated tentacles of *Eolis*. But the dorsal tentacles are not only, according to our view, important and special organs, but they are, further, organs of smell. Their laminated structure is one evidence of this. The

organs pointed out by Professor Owen in his memoir on the Pearly Nautilus, which "consist of series of soft membranous laminae compactly arranged in a longitudinal direction, and situated at the entry of the mouth, between the internal labial processes," are similarly constructed, and also supplied with nervous filaments from a pair of ganglia that are connected with the anterior cerebral or brain.

In fishes the olfactory organ consists of delicate membranous laminae, arranged in a manner not widely different from the disposition of those of *Eolis*; they are disposed, as in the *Dorididae*, in a pinnate manner, attached to a central stem: examples of this may be seen in the dace and in the burn trout, Pl. VI. fig. 12.

In the higher Vertebrata the laminated form is evident wherever we look. It may be objected to this argument, that in the case of *Eolis* the laminae are arranged on the exterior of the tentacle, and in the Vertebrata in the interior of a cavity; but if we can conceive of the tentacle of a *Dendronotus*, or of a *Doris coccinea*, Pl. VI. fig. 11, retracted within a sheath, we have then a very good representation of the olfactory organ of the fish.

Further, the ganglia of the tentacular nerves are in front of all the rest, and are attached by their tractus to the anterior part of the cerebral mass,—the anterior median ganglia, an arrangement which, together with the anterior superior position of the tentacles themselves, perfectly corresponds to that of the acknowledged olfactory apparatus in fishes and all other Vertebrata.

Lastly, if these tentacles be olfactory organs, we should expect, in tracing downwards the animal scale, that they would disappear before the tactile organs, the oral tentacles. That such is the rule even in the Mollusca we have the authority of Professor Owen. From what we have brought forward on this subject respecting the anatomical details, the external configuration, and the homology of the dorsal tentacles of *Eolis*, we feel justified in assigning to them the office of olfaction rather than in supposing them to be the seat of some new and hitherto undescribed and mysterious sense, or even of touch, as is generally believed. That they are not for touch seems to be indicated in some measure by their dorsal position, their direction upwards, and by their being in some instances defended from external mechanical injury by a fence of delicate processes, as in *Dendronotus arborescens*, Pl. VI. fig. 8.

The sense of vision is subserved by two minute organs somewhat inferior in development to those of the higher Gasteropods. They are situated beneath the skin, and are visible to the naked eye as two black dots immediately behind the dorsal tentacles; they are each supported by what appears to be a short thickish

pedicle, the optic nerve, Pl. V. figs. 1 & 2, no. 16, which comes off from the upper surface near the middle of the external border of the median cerebral ganglion, close to its connection with the lateral one. The nerve is directed forwards, outwards and upwards, and varies somewhat in length in different species; it is covered by a very delicate transparent sheath: the eye itself, Pl. V. fig. 3, has a wide external envelope—a delicate transparent capsule, *a*, continuous with the sheath of the nerve. This envelope holds the place of the cornea and sclerotica of more highly organized eyes. Within it is contained an irregularly-shaped cup, *b*, of black pigmentary matter, which embraces the posterior half of a spherical, colourless, highly refractive crystalline lens, *c*.

The anterior border of this pigmentary or choroid coat appears to be free, and is irregularly crenate. Over the front of the lens, and separated from it by a narrow interval, is a transparent tunic, *d*, which is most aptly compared to the anterior capsule of the lens of the higher animals, though some may deem it the homologue of the cornea. The back part of the choroid coat seems to be pierced by the optic nerve, but from the minuteness of the organ and the opacity of the choroid, we have not been able to determine the exact relation of the retina to the pigmentary layer, nor the existence of a vitreous body.

The degree of vision enjoyed by these animals must be slight. They can distinguish light from darkness, and can probably appreciate imperfectly different degrees of light, and as the eyes are placed under the skin of the head, their perception of objects must be exceedingly faint and indistinct.

The auditory apparatus consists of a minute, elliptical, delicate, and transparent capsule, Pl. V. figs. 1 & 2. no. 17, less than the eye, directly behind which it is situated; it appears sessile upon the external border of the median cerebral ganglion, but there are faint indications of a pedicle or a nerve that enters the capsule at the front. The long diameter of the capsule lies in the antero-posterior direction; within this capsule, figs. 4 & 5 *a*, is another, *b*, still more delicate and much smaller. This latter contains numerous very minute, oval corpuscles or otolithes, fig. 4 *c*, smooth, transparent, and highly refractive of light. In the centre of each an obscure dot, fig. 6, occurs, which, when highly magnified, exhibits a distinct appearance of nucleus and nucleolus. They are seen as we have described them in *E. papillosa* and *E. coronata*; but in *E. aurantiaca* and *E. olivacea*, in *E. picta* and *E. exigua*, there is only one large spherical otolithe, fig. 5 *b*, which presents also indications on its surface of nucleus and nucleolus.

These capsules are specimens of the auditory organ in perhaps its simplest form, and as such are adapted for the most limited

perception of sonorous undulations. Since it has been ascertained that *E. punctata* and *Dendronotus arborescens* do emit sounds, it seems probable that these organs may be provided for the perception of such. These crystalline-looking bodies are stated to be calcareous, but on treating them with acetic acid we did not find after the lapse of some time that any material change had taken place.

In investigating the different organs of *Eolis*, we have endeavoured, as we at first proposed, to place their anatomy and physiology in as clear and correct a light as possible, and to show in what particulars we differ from M. de Quatrefages, and now in terminating this memoir we are in a position to state, that his anatomical details are with regard to every organ more or less erroneous.

We are very glad therefore to learn that he has been led to forgo his proposed order *Phlebenterata*, and we may express a hope that the whole hypothesis of Phlebenterism as applied to the Mollusca will soon be abandoned. This Phlebenterism, which was first brought to light by M. Milne-Edwards, and maintained by him and M. de Quatrefages and some of the most distinguished French naturalists, and which implies a fusion of the digestive and vascular systems by a marked degradation of the latter that reduces these Nudibranchiata almost to the condition of the Radiata, is, if we understand it at all, founded on the assumption that no veins or true auricle any more than a true intestine exists in the *Eolididæ* and other allied genera,—that the functions of respiration, chylication, and the secretion of bile are cumulated in the branchial papillæ, and that the ramifications of the digestive system in some way or other supply the deficiency which was supposed to exist at the venous part of the circulation, and also distributed the digested portions of aliment throughout the body. But on full consideration of what is put forth as Phlebenterism in the Mollusca by the French naturalists, we confess our inability to arrive at a precise understanding of what is meant by the term. We believe we have in our account of the anatomy of *Eolis* brought forward evidence enough to overthrow Phlebenterism, such as we conceive it to be as applied to these animals, and we will now in conclusion, and as briefly as we can, recapitulate what we have before advanced, adding some new observations which now occur to us.

First, we have demonstrated that the vascular system is not in that state of degradation supposed by the French savans. We have shown a well-formed heart, consisting of ventricle and auricle, inclosed in a pericardial sac, the ventricle giving off an aorta that branches away to supply the principal viscera and the foot. The

hepatic artery is wanting, but the fact of the liver being minutely divided among the branchial papillæ, and the divisions being thus placed in contact with aërated blood, explains this hiatus and necessitates it. The auricle receives three principal venous trunks, each of which is made up of several branches from the skin anteriorly and posteriorly. These trunks have been called branchio-cardiac by M. Milne-Edwards and his followers, under the conviction that the whole of the blood passes to the heart from the branchial papillæ by them. We find nothing in *Eolis* to favour the opinion that the whole of the blood is conducted by afferent vessels from the body or intervisceral lacunæ direct to the branchiæ, and thence exclusively by efferent vessels to the auricle. We see that the network of lacunæ in the thickness of the skin receives the blood from the interior of the body, and allows it to flow freely therein in all directions; part of it doubtless passes to the branchial papillæ, but part also must go at once along the veins to the auricular part of the heart. In other words, the veins draw their blood from the sinuses or lacunæ of the skin, and this suction, so to speak, attracts the vital fluid at one and the same time from the branchial papillæ and the lacunæ of the body, so that the veins, instead of being merely branchio-cardiac, are really both systemic and pulmonary together. We have likewise pointed out small veins going from one of the viscera, the ovarium, into the skin at the side of the body, and even a small vessel of similar character going from the ovarium into the posterior median trunk-vein; the latter of course are systemic veins. Again, we find corroboration of this view of the parts in *Eolis* if we look to *Doris*: here the auricle receives three branches, one from each side, and one from behind as in *Eolis*; this last branch in *Doris* is made up of veinlets from the respiratory organs alone, and hence may properly be called pulmonary or branchio-cardiac; the two lateral branches come not from the special respiratory organ at all, but directly from the skin. Now although the skin in *Doris* may have in some measure a function like that of the *Eolididæ*, it must from its peculiar nature perform that function in a most imperfect manner; hence we ought to look upon these lateral venous trunks in a corresponding inverse ratio as systemic veins. Thus both in *Doris* and in *Eolis* the blood enters the auricle in a state of only partial aëration, one portion reaching it from the respiratory organ, and another from the general system. In the Crustacea the blood in the great dorsal sinus is in the same state, a fact that John Hunter had long ago ascertained, and Professor Owen has more recently confirmed. Here surely there is not that degradation implied in the idea of Phleboterism; and according to M. Milne-Edwards' own showing, the

vascular system is at least as perfect in the *Eolididæ* as in the *Dorididæ*,—nay even as complete as in the majority of the Gasteropoda.

Secondly, the nervous system has been shown to consist of ganglia well-developed and concentrated, and of numerous and large nerves; the eye, the ear, taste perhaps, certainly common sensibility exist, smell as well, and if our views be correct, to as high a degree as in any of the Mollusca; in short, the nervous system has reached a grade of organization higher than in the majority of the Gasteropods. This is most important evidence that the *Eolididæ* are not in the degraded state implied by Phlebenterism.

Thirdly, in these animals the respiratory system may be looked upon as somewhat less specialized than in other Gasteropoda, but it is sufficiently developed and specialized in the branchial papillæ to prevent us from attributing its function, even in part, to the prolongations of the digestive system.

Fourthly, we have pointed out the singular development and complexity of the genital organs, which are not in these respects inferior to many other Gasteropoda, and certainly similar to the genitalia of the *Dorididæ*, with the exception that in *Eolis* the ovarium is much more bulky.

Fifthly, from the certainly not lower state of development of those systems of organs we have enumerated, it ought not to be expected that there should be any degradation of the digestive system of *Eolis*, and accordingly we find fleshy sensitive lips with superadded tentacles, a strong muscular buccal mass with horny cutting jaws, and a spiny prehensile tongue, minute salivary apparatus, a constricted œsophagus, a well-marked stomachal sac, with the adjunct of a distinct intestine ending in a lateral anal nipple. So far we find no deviation from the Gasteropodous type; the liver however is as it were broken up into as many pieces as there are branchial papillæ, and which by a series of ducts of variable number communicate with the stomach. Why, it may be asked, does the hepatic organ not occupy its usual place in the body? The enormous development of the ovary we suppose necessitates the removal to the exterior which we observe, and the organ thus thrust out is divided among the papillæ, apparently for the purpose of ensuring its being constantly bathed with aërated blood, whilst at the same time by this arrangement the body of *Eolis* is kept of small dimensions, a condition probably rendered necessary by some peculiarities in the œconomy and habits of the creature with which we are unacquainted. By this arrangement also the hepatic artery becomes unnecessary.

Phlebenterism supposes that the chyle or nutritive part of the food passes into the blood-current of the system through the

ramifications as they are termed of the gastric cavity, which are prolonged into the papillæ. It cannot however be contended that the chyle is transuded through the granular or glandular part, such as occurs in many of the *Eolididæ* in the papillæ, since it is manifestly a secreting and not an absorbing surface, and the current must set from without inwards. Now in *E. despecta* the central duct or stem, and its accessory ducts, as well as their terminations in the papillæ, are granular throughout; therefore the fact of the whole apparatus being one for secretion precludes the idea that the products of digestion can pass into the system from this organ. This arrangement we see in a still more striking manner in several others of the *Eolididæ*, as in *Hermæa dendritica*, in which all parts of the much-branched hepatic organ are alike granular. In *Eumenis marmorata*, in which they are even follicular throughout, and in *Dendronotus arborescens*\*, the central duct is crowded with compound follicles, and all the branches are more or less follicular for a short distance, and then become simply granular; indeed in this genus the posterior part of the stomach and the intestine are the only parts which are free from the above granular character. We are therefore led to conclude that it is from the pyloric end of the stomach and from the intestine that exudation or absorption of the chyle takes place, and this conclusion is strengthened by the fact, that it is in the intestine that the contents first assume their faecal character. We may add also that in *Doto*, the intestine, which is short and wide, is in the interior longitudinally plicated, as if thus to increase the extent of the absorbing surface.

In conclusion then we hope to have shown, that not in any of the systems of organs is *Eolis* notably below the Nudibranchiate type; and we trust that this memoir, if it serve no other purpose, will at least assist in rescuing this genus, and

\* In this genus we see an intermediate link between those members of the Nudibranchiata which are provided with a concentrated internal hepatic organ and the *Eolididæ*, a fact which we pointed out two years ago. The central duct is in fact nothing else than a true liver reduced somewhat in bulk, but being diffused by its prolongations into the branchial papillæ. Another intermediate form and still more interesting link between the two extremes, as it exhibits the first step in the deviation of the liver from the typical state, is seen in *Scyllæa*, and which we noticed in a paper communicated to the Oxford meeting of the British Association. The liver in *Scyllæa* is broken up into several globular masses of convoluted tubes sending off minute branches that ramify in the skin and penetrate the branchial tufts. In a paper by M. E. Blanchard in the 'Annales des Sciences Naturelles' for March 1848, we observe that that gentleman has discovered in *Tethys* a similar arrangement of parts, and points this out as an excellent intermediate illustration of the affinities that exist among the different members of the Nudibranchiate group, and we are happy thus to find in his researches a corroboration of the fact which we had previously cited for the same end.

through it the *Eolididæ*, from the degradation which M. de Quatrefages and others from imperfect observations had too hastily imputed to them.

## EXPLANATION OF PLATES V. AND VI.

### PLATE V.

*Fig. 1.* Nervous system of *Eolis papillosa*: *a a*, median supra-œsophageal or cerebral ganglia; *b b*, lateral supra-œsophageal ditto; *c c*, buccal ditto; *d d*, gastro-œsophageal ditto; *e e*, olfactory ditto; *f*, anterior median commissure; *g*, posterior median ditto, or commissure of the buccal ganglia; *h h*, commissure between median and lateral supra-œsophageal ganglia; *i*, innermost or shortest œsophageal nervous collar; *j*, slender or middle ditto; *k*, outermost or widest ditto.

Nerves from supra-œsophageal ganglia: Nos. 1 and 2, small nerves to skin of head; 3, olfactory tractus or nerves; 4, nerve to the outer lip; 5, ditto to skin of head between dorsal tentacles; 6, ditto to oral tentacles and roof of channel of mouth; 7 and 8, ditto to skin of side of head; 9, ditto to muscles attaching buccal mass to skin, and to sides of channel of mouth; 10 and 11, ditto to skin at side of head; 12 and 13, ditto to skin down side of body below the rows of papillæ; 14 and 15, ditto to skin of side of head near the tentacles; 16, optic nerves; 17, auditory ditto; 18, nerves to the foot; 19, ditto to skin down side of body to papillæ (respiratory nerve); 20, ditto to skin of back; 21, 22 and 23, ditto to skin of back near median line.

Nerves from infra-œsophageal ganglia: 1, small nerves to stomach; 2, 3 and 4, smaller ditto to œsophagus and stomach; 5, large ditto passing into the buccal mass; 6, small ditto to back part of buccal mass.

Nerves from œsophageal collars:  $\alpha$ , minute nerves from innermost collar, destination unknown;  $\beta$ , genital and probably cardiac nerves;  $\gamma$ , nerves from outermost collar passing into buccal mass;  $\delta$ , single nerve from middle collar, probably gastric;  $\epsilon$ , large nerve coming out of buccal mass from a ganglionic swelling, and passing to be distributed to glands of papillæ of skin;  $\zeta$ , the ganglionic swelling situated in buccal mass, from which the large nerve  $\epsilon$  comes off;  $\eta$ , branch of communication between the large nerve  $\epsilon$  and the outermost œsophageal collar.

*Fig. 2.* Nervous system of *E. Drummondii*. The letters correspond to those in last fig. except one,  $\theta$ , which marks a small ganglionic swelling in connexion with middle collar and genital nerve.

*Fig. 3.* Eye of *E. picta*: *a*, outer capsule; *b*, pigmentary cup; *c*, lens; *d*, capsule of ditto.

*Fig. 4.* Auditory capsule of *E. papillosa*: *a*, outer capsule; *b*, inner ditto; *c*, otolithes.

*Fig. 5.* Auditory capsule of *E. picta*: references as in last fig.

*Fig. 6.* Two otolithes from *E. papillosa* highly magnified ( $\frac{1}{8}$ th object-glass), showing nucleus and nucleolus.

### PLATE VI.

*Fig. 1.* Nervous system of *E. coronata*. Letters as in Plate V. figs. 1 & 2.

*Fig. 2.* *a*, buccal ganglion of *E. papillosa* slightly compressed and magnified to show the vesicular contents; *b*, nerve coming from same.

- Fig. 3. Group of pear-shaped nerve-globules with pedicles all lying in same direction, the globules showing large nuclei and nucleoli from cerebral ganglion of *E. papillosa*.  
 Fig. 4. Two isolated, pear-shaped, pedicled, nucleated nerve-corpuscles of large size from the same.  
 Fig. 5. Smallest cells, bright and transparent, probably nucleoli, from the same.  
 Fig. 6. Side view of dorsal tentacle of *E. coronata*: *a*, olfactory ganglion and nerve.  
 Fig. 7. Dorsal tentacle with sheath, *Doto fragilis*.  
 Fig. 8. Lateral view of ditto ditto, *Dendronotus arborescens*.  
 Fig. 9. Front view of ditto ditto ditto.  
 Fig. 10. Side view of dorsal tentacles and laminated crest of *Antiopa splendida*: *a a*, tentacles; *b*, laminated crest; *c*, ganglionic swelling in front of median cerebral ganglion; *d d*, tractus olfactorius to laminated crest; *e e*, ditto ditto to tentacle.  
 Fig. 11. Front view of dorsal tentacle of *Doris coccinea*, showing central stem and laminæ.  
 Fig. 12. Olfactory laminæ of Burn Trout, showing its resemblance to those of *Doris coccinea*: *a*, nostril; *b*, central stem; *c*, laminæ.

XX.—*Brief Notice of several Mammalia and Birds discovered by B. H. Hodgson, Esq., in Upper India.* By THOMAS HORSFIELD, M.D. &c.

DEAR SIR,

Library, East India House, Feb. 12, 1849.

B. H. HODGSON, Esq., late British resident at Nepal, who is now zealously pursuing his researches into the natural history of the upper provinces of India, has lately presented to the museum of the East India Company, a small collection of mammalia from the neighbourhood of Sikim and Darjeling, and two birds from Tibet; and (Mr. Hodgson) being desirous that a concise notice of them may be communicated to the public without delay, until he shall have an opportunity of publishing a more detailed description of the new species, I request you, in his name, to insert the following list, with a few remarks, into an early number of the 'Annals and Magazine of Natural History.'

Yours faithfully,

Richard Taylor, Esq.

THOMAS HORSFIELD.

*List of MAMMALIA from Sikim and Darjeling, near Nepal, in Upper India.*

Numbers 1 to 4 have already been described and published.

1. Genus PORCULA, Hodgson, Journal of the Asiatic Society of Bengal, vol. xvii. p. 423, with a figure.

Type *Porcula Salvania*\*, Hodgson.

\* *Salvania*, of or belonging to the Saul forest.



Hancock, Albany and Embleton, Dennis. 1849. "XIX.—On the anatomy of Eolis, a genus of mollusks of the order Nudibranchiata." *The Annals and magazine of natural history; zoology, botany, and geology* 3, 183–202.

<https://doi.org/10.1080/03745485909494620>.

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