

# PHILOSOPHICAL TRANSACTIONS.

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XIII. *On the Anatomy of Doris.* By ALBANY HANCOCK and DENNIS EMBLETON, M.D., F.R.C.S.E., Lecturer on Anatomy and Physiology in the Newcastle-upon-Tyne College of Medicine in connection with the University of Durham. Communicated by Prof. EDWARD FORBES, F.R.S.

Received November 27, 1851,—Read March 4, 1852.

WHILST engaged in arranging the materials for their Monograph on the Nudi-branchiate Mollusks now in course of publication by the Ray Society, it became evident to Messrs. ALDER and HANCOCK, that not only the external characters, but also the internal structure, of this interesting group of animals, should be fully investigated. Since then the writers of the following paper have taken up the anatomical part of the subject, and have already been enabled to publish in the 'Annals of Natural History' an account of the anatomy of one genus, *Eolis*; another genus, *Doris*, forms the subject of the present communication.

On entering on the present investigation, we were naturally anxious to avail ourselves of the stock of knowledge already collected by our predecessors in this walk of science.

CUVIER, the great master of Comparative Anatomy, had dissected and studied the genus *Doris*, and had left a considerable amount of information for those who might follow in his steps: indeed his memoir contains a more complete account of the anatomy of *Doris* than any yet published. Within the last few years Herr HEINRICH MECKEL has described the generative organs in MÜLLER's Archiv, 1844, and more recently Messrs. MILNE-EDWARDS and BLANCHARD have given accounts of the circulatory and nervous systems of *Doris*. We will not here dilate upon the works of these authors, but shall refer to them in the course of our description of the various organs.

Since the reading of our paper on the subject before us at the Edinburgh Meeting of the British Association in 1850, we have gone more fully into the details of the anatomy of *Doris* than it had been in our power up to that time to do, and having verified our observations in many particulars, and thrown additional light on our

results by comparative dissections, we feel more confidence in placing on record an extended account of our researches.

Before we commence the anatomical description, we may premise that for examination, we have selected *D. tuberculata*, not only as the species most highly typical of the genus, but as that which, on our coast, is the most abundant and the largest, and therefore in all respects most convenient for our purpose. We have not however confined ourselves to this single species, but have examined several others, with a view of obtaining a more accurate knowledge of the anatomy of the genus. Of these latter we may mention *D. pilosa* and *D. bilamellata*, as representing very fairly, with *D. tuberculata*, the three great divisions which have been characterized in the Monograph on the British Nudibranchiata, now in course of publication by the Ray Society.

*D. tuberculata* is 2 or 3 inches long, pretty regularly oval, rather depressed, arched above, with the mantle extending over the whole back, concealing the head and foot, and covered with numerous obtuse, spiculose tubercles of various sizes; the dorsal tentacles are retractile within cavities, of a clavate form, with the upper portion laminated: the mouth projects a little in front between the foot and mantle; on each side is a small depressed, obtuse, angular tentacle: there are nine branchial plumes united at the base, and retractile within a cavity; they form a circle on the median line of the back near the posterior extremity, enclosing the anal and renal orifices: the foot is broad, truncated in front, and rounded behind: the genital orifice is situated towards the anterior extremity, on the right side, between the mantle and foot.

*D. pilosa* differs from *D. tuberculata* chiefly in having the back more elevated, and in being clothed with soft conical papillæ; the oral tentacles too are fused into a veil, which is at either side expanded into a leaf-like process, and the branchial plumes are non-retractile, being merely contractile. This species is about 1 inch long.

*D. bilamellata* is not more than three-quarters of an inch in length, and is considerably depressed, having the mantle covered with large, spiculose tubercles: branchiæ of about twenty, simply pinnate, non-retractile plumes, set separately in an open circle: head furnished with a semicircular veil. In other respects this does not differ materially from the above species.

*Digestive System.*—On removing the skin of the back, the viscera, including the buccal apparatus, are seen bound down and completely covered by a transparent fibrous membrane, which is fixed on each side to the inner surface of the skin just above the track of its great lateral venous canals, and to the circumference of the pericardium. For want of a better name we call this membrane the peritonæum. It has been removed to show the viscera\*. The mouth opens on the inferior surface of the body between the cloak and the foot; it is surrounded by a protuberant, fleshy, outer lip divided below on the median line. The channel to the buccal cavity is very

\* Plate XI. fig. 4, and Plate XII. fig. 1.

short, and provided with a thin projecting inner lip. Immediately behind this is the buccal mass, which is strong and muscular, of considerable size, somewhat ovate, with the small end forwards; it is continuous with the channel of the mouth, and the œsophagus leads away from its upper and posterior part.

There are two sets of retractor muscles for the buccal apparatus\*; one composed of radiating bands, three or four on each side, inserted into the channel to the mouth in front, and attached to the skin at the sides of the body behind; the other consists of only two large strong straps, one on each side, having their insertions at the sides of the posterior part of the buccal mass by means of a band which there encircles that body, and running a good way backwards to be fixed to the fleshy foot. These two sets of muscles acting together will pull backwards the buccal mass, and mouth channel, with the external orifice; if they act separately, of course they will retract the parts into which they are respectively inserted.

A thin layer of numerous delicate parallel muscular bands coats the lateral parts of the buccal mass. These bands are attached in front to the channel of the mouth, mingling with other fibres of that part, and behind to the circular band that receives the attachment of the buccal retractors. When the channel of the mouth is fixed, these layers of muscle will advance the buccal mass towards the external orifice.

The remaining muscles, which are proper to and form nearly the whole of the buccal mass, are for the movements of the tongue and the buccal lip, and enclose, immediately, the cavity of the mouth.

On opening the buccal mass† from above, by cutting through the buccal lip and a strong layer of transverse bundles forming the posterior part of the roof of the buccal cavity, and therefore assisting in prehension and deglutition, we see projecting upwards and forwards from the floor of the cavity a broad conical mass surmounted by rows of teeth, and placed directly in front of the opening of the œsophagus; this mass is that of the lingual muscles supporting and moving the spiny tongue. In advance of this mass is a powerful sphincter or circular belt of muscle commanding the entrance to the mouth; this we propose to call the third or buccal lip, for reasons to be afterwards given.

The tongue consists of a tubular, dentigerous membrane, the upper or anterior portion of which is partly enclosed within, and partly expanded upon, the conical mass of lingual muscles; the lower or posterior portion is continued downwards and backwards, through the centre of the mass, into a delicate pouch which projects beyond the posterior and under part of the buccal organ. This spiny tongue‡ is easily detached from the muscular mass to which it is connected, and can be drawn out of the tube in which it is lodged; and it can then be observed that the part of the muscular mass§ which has been covered by the tongue is composed of numerous parallel transverse plates or flakes corresponding apparently in number and direction to the rows of teeth. These flakes are bound together by a thin layer of fibres which crosses

\* Plate XIII. fig. 1.    † Plate XIII. fig. 2.    ‡ Plate XIII. fig. 3.    § Plate XIII. figs. 4 and 5.

them at right angles. The transversely placed muscular plates above mentioned are most highly developed around the posterior lateral parts of the central cavity, and towards the front of the cavity show as a layer on each side, gradually decreasing in thickness, and in front are continuous with each other, completing at that part the cavity containing the dentigerous membrane. This cavity is a laterally compressed tube, somewhat elongated from above downwards, and has projecting from the whole length of its posterior wall, almost as far as the front of the cavity, a fleshy lamina, in transverse section, wedge-shaped above, fusiform below. This, which we shall call the cuneiform lamina, is not only connected with the posterior wall of the cavity, but also with the bottom of it,—the pouch at the lower and back part of the buccal mass; its anterior border and upper end are both free. It divides the cavity into two nearly equal lateral parts. A further notice of it will find place in the description of the teeth and their development.

If the upper portion of the above muscular conical mass be cut away, we find exposed on each side, a flattened dense substance\* placed vertically, and being made up for the most part of indistinct transversely fibrous texture, and partially enclosed by the transverse muscular flakes before named. In front, the inner opposed surfaces only of these bodies or nuclei are clothed by the muscular flakes, which there form a thin layer, and their fibres are short, extending from the lower to the upper border of the nuclei; further back the muscular coating is thicker and the fibres longer; these being continued gradually more and more over the upper border of the nuclei, and then by degrees down the external surface, till at length they enclose the posterior end of the nucleus altogether, which is then free as it were in a muscular cavity, and the muscular flakes being then attached to the lower border only of the nucleus, but by one end to the inner and the other to the outer edge, play round the upper border somewhat like a belt over a pulley.

By the action of this apparatus the tongue is not only partially everted from its tube, bringing numerous rows of spiny teeth to bear upon the food, but is retracted again into its previous position.

Something similar to this perfect arrangement we have elsewhere described in *Eolis*, only there the lingual mass is single, whereas in *Doris* it is divided into two lateral halves.

On the earliest approach of decomposition the dentigerous membrane† can be easily removed; it is then seen as an incomplete tube, being quite open at the bottom, behind, and at the part corresponding to the cuneiform lamina, but retaining its original form. On looking into this tube, a fine membrane, continuous with the dentigerous, is seen stretched transversely across; and if the tube be replaced in its cavity, that membrane is found to fit upon, and clothe the top of, the cuneiform lamina. Thus we find that the tube of the tongue is divided into two unequal parts by this membranous septum, which occurs about the end of the upper or anterior third of the tube. The lower two-thirds of the tube thus constitute a large follicle, in which

\* Plate XIII. fig. 6.

† Plate XIII. fig. 3.



are formed and developed the spiny teeth in regular rank and file; the upper third contains the mature teeth, which can all more or less readily be used in prehension.

*Development of Teeth.*—If we make a transverse section of that lower part of the tube\* which projects obliquely behind from the buccal mass, and examine it, we find in the centre, the cuneiform lamina having a somewhat pyriform shape, the base forwards, the apex backwards and attached to the muscular envelope of the pouch. Except at this point the lamina is free and lies in a cavity bounded by two parallel membranes, between which are developed the rows of teeth; the outer of these is the dentigerous layer, which rests upon the mucous membrane lining the muscular envelope of the tube. If we make another section† lower down, and obliquely through the end of the pouch, we find the cuneiform lamina fixed at both ends, the free edge has ceased, and the lamina is found attached along the median line of the fundus of the tube. Along each side of this attachment is found an enlargement of the mucous membrane, which must be of glandular nature, as from it seem to originate the two parallel membranes mentioned in noticing the former section just above.

Between these membranes, as already stated, the teeth are formed. These organs can be observed at a very early period of their growth. They may be discerned upon the newly-secreted edge of the outer or dentigerous layer as delicate rows of elongated and attenuated, soft and colourless cells. At the distance of a row or two further on they assume the exact form and size of the mature teeth, still, however, retaining their soft cell-like character. The next rows seem orange-coloured, and have put on some of the hardness and of the other characters of perfect teeth, which are however somewhat paler. The teeth examined just below the transverse membrane that closes in the teeth follicle above, are found to have attained all that extreme hardness and temper which characterize them when in use, and possess the most perfect pellucidity and polish.

The space between the two parallel membranes is packed with a soft matter which is derived from the inner layer, and which, when placed in spirit, becomes flocculent; in this matter the teeth are imbedded. These two membranes may not inaptly be compared to the pulp and enamel membranes of the teeth of the Vertebrata, though the denticles themselves, as far as we have been able to observe, are quite homogeneous in structure. We are inclined to think the denticles are siliceous in composition, as they resist the action of the stronger mineral acids, as do those of *Eolis*, which, although they possess the same hardness, transparency and polish, are in some measure affected by hydrofluoric acid.

Those teeth which are placed upon the top of the lingual mass, and are actually engaged in the act of prehension, become gradually blunted, broken or wholly detached, and that the more rapidly the more they lie away from the median line: hence the whole apparatus is worn to a point in front and on the median line. This continual wear and tear of the dental rows necessitates a fresh supply of them, and this is constantly being provided by the secretion of dentigerous membrane at the

\* Plate XIV. figs. 1 and 3.

† Plate XIV. fig. 2.

bottom of the follicle above described. The advance upwards of the teeth is assisted, in all probability, by the secretion of some matter supplementary to the dentigerous membrane by the surface of the tube in which it is contained. This surface is formed by a fine membrane, which in the follicle below is visible enough, but in the more muscular part of the tube above is not so easily demonstrated. This membrane, which is continuously spread over the whole of the buccal cavity, is analogous to the mucous membrane of the mouth of higher animals; the tube formed by it, and the pouch which terminates it, compose a follicle, the secretion of which is the dentigerous membrane beset with ranks of denticles, the analogues of epithelium and teeth. The inner of the two parallel membranes, and the flocculent matter in which the teeth are at first imbedded, gradually become detached and fall off, leaving the teeth bare as they reach their field of action.

The mode of growth of the spiny tongue of *Doris* is thus evidently quite analogous to the growth and advance of the teeth of Rays, Sharks, &c., or of the hoofs or nails of Mammalia.

In *D. tuberculata* the number of rows of denticles is forty-three or forty-four, eighteen of which are situated above the transverse septum or top of the follicle, and each contains 140 denticles; in this species therefore there are 6160 little teeth. These are not all of the same size, but diminish from near the ends of each row towards the centre, where the row is slightly interrupted, there being no central tooth\*. The five or six external denticles also rapidly decrease in size towards the end of the row. Each denticle† is expanded broadly at the base, and is well arched backwards and sharp pointed, somewhat resembling the spines of the dog-rose.

In *D. verrucosa* and *D. tuberculata*, VERANY, the buccal organ and tongue are constructed after the above model.

In *D. Johnstoni* the buccal and lingual apparatus follow the same arrangement, the rows of denticles being twenty-four in number, of which eleven are used in prehension. There are about fifty denticles to each row; the five outermost at the ends of the rows are much attenuated, being nearly linear‡.

In *D. coccinea* the above parts are after the same type; the external attenuated teeth of each row being much more numerous than in the last-named species.

In *D. repanda* we have the buccal mass and the tongue resembling those of *D. tuberculata*. There are sixty-eight rows of toothlets, and thirty-six toothlets in each row, but they are of more elaborate character, having their edges serrated: in each row there is a centre toothlet bearing four cusps§. Three or four of the little teeth on each side of the centre one are short and robust, those further out are much more produced.

In addition to the above lingual organ, we find superadded in this species a collar of crowded minute bifid spines arranged on the anterior surface of the buccal lip; to this curious organ we shall again shortly refer.

In *D. bilamellata* we have a very interesting modification of the buccal apparatus.

\* Plate XII. fig. 8.    † Plate XII. fig. 9.    ‡ Plate XII. fig. 10.    § Plate XII. figs. 11, 12 and 13.

It is small in proportion, and in general form has resemblance to that of *D. tuberculata*; but in addition there is the singular appendage of a lentil-shaped organ, having all the characters of a gizzard\*. This is attached by a short tubular pedicle to the upper part of the buccal mass, a little in front of the œsophagus. This buccal gizzard is not much inferior in size to the buccal mass itself: its walls are thick, its external surface on each side presents numerous muscular bundles radiating from a centre, and its peripheral margin is bounded by a strong belt of muscle. Its inner surface is smooth, but tough, and its cavity communicates with the mouth through the pedicle, which is itself muscular. There is nothing to discredit the idea that we have here an organ added to the buccal mass for the more perfect trituration of the food, and which may probably at the same time act in promoting deglutition, for there is along the roof of the mouth apparently a groove leading from the pedicle in the direction of the œsophagus.

In this species there is a modification of the tongue: it is here long and narrow; there are twenty-six or twenty-eight rows of toothlets, two only in each row; one toothlet is placed on each side of the median line. About eleven rows are engaged in prehension. The toothlets are long, stout, arched spines. There is likewise in this species a prehensile collar, which, instead of being denticulated, is roughened with transverse irregular rows of short minute papillæ. Moreover, there exists a minute pair of rudimentary jaws; but as both these parts exist also in *D. pilosa*, the description given under that head may suffice for *D. bilamellata* also.

*D. aspera*† and *D. depressa* have likewise the narrow tongue and buccal gizzard.

In *D. pilosa* the buccal mass‡ differs a good deal from the above forms. It is large, and the channel of the mouth opens into its under surface instead of in front, as in the other species. The difference of form is owing mainly to the apparent incorporation of a gizzard-like organ with the anterior part of the buccal mass. That organ has the radiating muscular fibres, and the peripheral belt observable in the gizzard of *D. bilamellata*. It is placed immediately in front of the œsophagus, and its connexion with deglutition is more evident. The tongue§ is of the same type as that of *D. bilamellata*, but the teeth have their margins denticulated.

The prehensile collar|| is present, and is different in form from that of *D. repanda*. It is divided into two lateral halves; its spines, which are directed inwards, are very densely crowded, being for the most part like bifid stumps. The two parts of the collar are broad below, where they are somewhat separated, and taper to fine points above. We have here, in addition to the prehensile collar, a pair of minute rudimentary triangular horny plates or jaws¶, which are situated between and immediately behind the lower separated ends of the collar. They are united in front for more than two-thirds of their length, and are imbedded in the lower part of the buccal lip, having only their free points exposed. Attached to the posterior border of each of these free parts of the plates is a thin transparent tough membrane, which

\* Plate XII. fig. 5.

† Plate XII. fig. 14.

‡ Plate XII. fig. 4.

§ Plate XII. figs. 6 and 7.

|| Plate XIII. figs. 7, 8, 9, 10 and 11.

¶ Plate XIII. fig. 12.

runs up the inner surface of the buccal lip, tapering away to nothing near the top. One edge of this membrane is attached to the buccal lip along the inner margin of the collar, the other is free, projecting into the aperture of the mouth. These rudimentary jaws and the prehensile collar are doubtless formed from the mucous membrane of the mouth, but we have not seen evidence to prove that they are, together or separately, the homologous parts or part to the horny jaws of *Eolis*, but they seem to be engaged in the same function, that of prehension.

*The œsophagus* in our typical species\* comes from the upper posterior part of the buccal mass, is somewhat dilated at first, and then pretty uniform in diameter, exceeds the stomach in length, is rather delicate in texture, and its interior is longitudinally plicated. It runs straight backwards, and opens freely into the posterior end of the stomach at the under part, and rather at the right side directly in advance of the great hepatic duct.

*The Salivary Glands* are a pair of long delicate tubes tapering backwards, where they lie against the liver, and open into the mouth on each side at the coming off of the œsophagus.

*The Stomach* is a large ovate membranous bag lying on the left side of the body, with its posterior end resting in a funnel-shaped depression in the anterior face of the liver. The great duct from the liver† opens into this posterior or cardiac end of the stomach so widely, that it is difficult to determine the line of demarcation between them. This duct, at its union with the stomach, lies above the cardia or entrance of the œsophagus, which is rather to the right; it lies also above the opening of a small duct from the pancreas, which is situated somewhat towards the left side. At the pyloric end, which is anterior in position, the stomach becomes rapidly constricted and converted into the intestine, which appears to come off from the under part, bends upwards to the right side, and then backwards, running along the right side of the stomach between it and the genitalia, inclining gradually towards the right; it then passes under the heart and right side of the pericardium, winds round and under the right side of the posterior end of the liver, and lastly, ascends behind the end of the liver to terminate at a projecting tubular anus in the centre of the branchial circle. The internal surface of the stomach is more or less closely and finely corrugated; the rugæ are most strongly marked at the upper posterior part of the organ in front of the hepatic duct.

*The Intestine*, which is of smaller diameter than the œsophagus, but pretty uniform in calibre throughout, has its internal surface longitudinally laminated.

*The Pancreas‡* is a somewhat elliptical pouch lying below and at the left side of the stomach. Its interior is divided by numerous projecting transverse folds of the lining membrane, strongly resembling valvulæ conniventes, and usually contains a dark brown matter. It opens very freely into the stomach. We have not examined microscopically the muscular coat of the alimentary canal, but on the external surface of the stomach and pancreas, after the aorta has been injected, can readily be

\* Plate XII. fig. 1.

† Plate XIII. fig. 13.

‡ Plate XVII. fig. 5.

seen a fine network or delicate arborescence of very minute vessels enveloping the organs. The whole alimentary canal, the pancreas and the great hepatic duct are likewise enveloped in the irregular meshes of the sympathetic system of nerves.

*Varieties.*—In *D. tuberculata*, VERANY, and *D. verrucosa*, CUV., we have the alimentary apparatus formed on the whole after the same type as that in the British *D. tuberculata*, only in *D. verrucosa*\* we have at the commencement of the œsophagus an extensive membranous pouch or crop projecting forwards, and the stomach is much reduced in size. The salivary glands are folliculated.

In *D. Johnstoni*†, we have extending from the buccal mass to the cleft of the liver, where it receives the hepatic duct, a simple tube dilated at its upper part; this dilatation may be looked upon as a sort of crop or anterior stomach. The intestine comes off upwardly immediately after the junction of the hepatic ducts, and though there is here no well-marked dilatation, we believe from analogy that the anterior part of what is here called intestine may perform the part of stomach; the salivary glands are very slender, almost linear, plain tubes.

In *D. pilosa*‡, at the commencement of the œsophagus, is an extensive membranous pouch; to this succeeds a much-contracted tube, which suddenly dilates into a fusiform sac like the crop or anterior stomach of *D. Johnstoni*. A tube from the opposite end of the sac plunges into the middle of the anterior surface of the liver, which is not cleft as in the previous species. The tube becomes dilated within the liver, and penetrates to about one-third the length of that organ, after which it curves upwards and slightly forwards, and emerges from its upper surface. After this the tube, still dilated, runs a little forward, and is then bent upon itself, at the same time becoming contracted in calibre, and having appended to it a small pancreas, assumes the usual course to the anus. That part of the tube enclosed within the substance of the liver receives three or four large hepatic ducts at the posterior and under part of the curve, and together with its continuation as far as the pancreas, must be regarded as the true stomach. The present species has its salivary glands curved and folliculated at the buccal end.

The alimentary tube of *D. bilamellata*§ is formed on the same plan as the last described; only the crop or anterior stomach differs somewhat in form, and has its walls folliculated. The salivary glands are here reduced to a small granulated body surrounding the commencement of the œsophagus.

In *D. repanda*, *D. coccinea*, *D. aspera*, and *D. depressa*, the alimentary canal appears to be cast in the same mould as the last-mentioned species. The inner surface of the stomach is plicated in all, and in all the intestine is rather wide, and plicated longitudinally throughout.

*The liver*|| is the largest organ in the body, and usually fills up more than the posterior half of the visceral cavity. It is of rather a conical form; the base, which is somewhat cleft above, and deeply hollowed out into the shape of a funnel, is

\* Plate XII. fig. 3. † Plate XII. fig. 2. ‡ Plate XII. fig. 4. § Plate XII. fig. 5. || Plate XIII. fig. 13.

placed forwards, and has the great ducts\* emerging from the apex of the funnel, and immediately joining the posterior end of the stomach which is lodged in the wider part of the concavity. From the cleft in the upper border of the base runs backward along the upper surface and median line of the organ, a considerable groove which lodges the trunk and the ramifications of the renal organ, and contains at its posterior part the trunk of the hepatic vein. The thin stratum of the ovarium lies spread out upon, and closely adherent to, the upper part and sides of the mass of the liver. The external surface of the liver itself is distinctly granular, and of a darkish brown colour, and together with the ovarium is overspread by the ramifications of the aorta which form a network upon these organs. Four or five principal ducts join together in the short wide common channel to the stomach, and if these ducts are traced into the substance of the liver, they are found to divide and subdivide very rapidly and minutely; and we believe, though we have not microscopically examined this, that the extreme branchlets end in the granules seen on the external surface of the organ. Owing to the number, size, and frequent division of the hepatic ducts, the interior of the liver has quite a spongy aspect; and there can be no doubt that, from the great size of the principal ducts, the food during digestion can easily enter them, as was remarked formerly by CUVIER, and as is the case in the Eolididæ.

*Varieties.*—The liver in *D. verrucosa*† is rounded in front, and less evidently cleft for the reception of the stomach, but is otherwise as in *D. tuberculata*.

In *D. Johnstoni*‡ the organ is deeply cleft, but the right lobe or side of the cleft is much reduced in size, whilst the left is larger in proportion than the corresponding part in *D. tuberculata*.

In *D. bilamellata*§ these modifications are carried to a much higher degree, so that the left lobe appears as a mere rudiment; and in *D. pilosa*|| that lobe is no longer distinguishable, the liver appearing as if truncated on that side, which is perforated by the œsophagus, as before mentioned.

The texture of the organ in all appears to be the same, though the colour varies somewhat, being greenish or yellowish, or even inclined to orange, and sometimes of a deep purple brown.

*Generative organs.*—The organs of this system are remarkable for their large size, high development, and complicated arrangement, being very analogous in their complex hermaphrodite character to those which we have elsewhere described in *Eolis*¶. They lie on the right side of the body (with the exception of the ovary, which is spread upon the liver), in front of the hepatic organ, behind the buccal apparatus, and on the right side of the œsophagus and stomach.

There is one common external aperture placed on the right side of the body, about a third of the way down from the head between the mouth and the foot. Imme-

\* Plate XII. fig. 1.

† Plate XII. fig. 3.

‡ Plate XII. fig. 2.

§ Plate XII. fig. 5.

|| Plate XII. fig. 4.

¶ Plate XI. figs. 1, 2, 3, 4; and Plate XII. fig. 1.

diately within this aperture is a very short common vestibule, on the inner wall of which are three orifices; an anterior, which admits of the exertion of the penis; a posterior, the vulva, leading to the female channel; and an upper, the vagina, leading to the androgynous apparatus, and receiving during coition the penis of the accoupled individual.

The organs are male, female, and androgynous.

*Male organs.*—These consist of, first, an intromittent organ, capable of being protruded from and retracted within the body; and secondly, a testis.

In *D. tuberculata*, in which these organs\* are most like those of *Eolis*, the penis lies in front of all the rest. When it is fully retracted within the body, we find a membranous pouch of a conical form attached by its base to the inner surface of the margin of the external opening for the passage of the penis; the pouch receives at its apex the external end of the testis. When laid open, there is found in it, continued from and through the apex, a small tube continuous with the testis; this tube runs down to be attached to the side of the apex of a smaller conical bag within, and about half the length of the other. The interspace between the cones is filled with a filamentous woolly-looking tissue, which fixes the inner cone and its attached tube in their position; the bases of the two cones are continuous with each other at the inner margin of the external orifice. When exertion takes place the inner cone is everted like the tentacle of a snail, forming the apparent external penis; whilst this is taking place the apex of the outer is drawn after that of the inner cone, by means of the tube by which they are connected; and the filamentous tissue connecting the two cones with a considerable portion of the outer cone, which becomes gradually everted as exertion proceeds, come at length to be contained within the body and base of the fully exerted penis. The process of exertion seems to be brought about by the contraction of the walls of the outer cone, in the first instance pressing upon the inner cone through the medium of the filamentous tissue between them, into which tissue some fluid, most likely the blood, may be rapidly introduced during venereal excitement.

*The testis* is a long, simple, pale flesh-coloured, convoluted tube, the coils loosely bound together with filamentous tissue; the bundle thus formed lies partly on the penis, and partly on the oviduct and anterior margin of the mucus-gland. The walls of the tube are firm, thick and muscular; and the interior, which is of very small calibre, lined with a glandular membrane, the inner surface of which is beset with minute cells. This tube is connected at the outer end with the apex of the cone described as the penis, and at the other it opens into the oviduct at a sudden turn, which that tube makes before entering into the channel of the mucus-gland, not far from the vulva, an arrangement identical with that in *Eolis*.

*Female organs.*—These are ovary, oviduct, mucus-gland, and channel leading to vulva.

\* Plate XIV. fig. 7.



When fully developed, the *ovarium* is spread over the liver as a thin layer of tubes and follicles. The tubes are ramified from the general oviduct, and end partly in anastomoses, and partly in free extremities, the ramifications being all studded with innumerable sessile follicles. This stratum in the breeding season is very conspicuous, but is scarcely discernible at other times, and extends over the whole liver, with the exception of a small space on the under surface along the median line. The main branches of the oviduct all tend towards the anterior and upper edge of the liver, along which the common trunk courses from left to right. The oviduct before leaving the liver dips somewhat downwards; it then quits that organ as a fine tube, which is at first free, and then becoming attached to the left side of the mucus-gland, is suddenly dilated; it then passes sinuously on as far as the front of the mucus-gland, where it is found somewhat diminished in size; it is then suddenly bent backwards, and again forwards, and at the second bend receives the inner end of the testis as above stated. It then sinks into a fissure in the opake portion of the mucus-gland, and being joined by the duct from the androgynous apparatus, debouches into the female channel.

The mucus-gland is an irregular rounded compressed mass; the left side is flatter than the right, and shows most easily the connexions of the different portions of the generative organs; and here also it can be seen that the gland in question is composed of two parts, one semipellucid, formed of the convolutions of a large tube, the other opake, brownish red, imbedded in the former and made up of the closely compacted folds of a minute tube. There is a large channel in the interior of the gland communicating with the vulva externally,—the female channel; this receives the termination of the convoluted tube of the gland, and also of the oviduct, after it has been joined by the duct of the spermatheca.

The androgynous organs are two spermathecae and connecting channels; one channel, the vagina, is large, longitudinally plicated within, leads from the common external vestibule, and opens freely into the principal spermatheca; this is a globular sac of a purple brown colour, owing to its contents, and lies between the male and female parts. Just where the vagina opens into the spermatheca a small duct leaves it, which is soon joined by one, still smaller, from the accessory spermatheca, and then opens into the oviduct, where it dips into the opake part of the mucus-gland. The accessory is a much smaller sac than the principal spermatheca; it lies against the vagina, is of lighter colour than the other, and its duct is very short.

Of the reproductive system of *Doris* there are two varieties, the most remarkable of which we shall now proceed to notice. In *D. bilamellata*\* the testis is considerably shorter and thicker than in *D. tuberculata*; it is suddenly much constricted at its junction with the oviduct, which is also suddenly and strikingly constricted a little way before it reaches the testis, and the whole of the twice bent part and its continuation into the opake portion of the mucus-gland is elongated, and of the

\* Plate XIV. fig. 8.

same minute size. The androgynous apparatus is modified in this species in the following way: the vagina and the channel, from the principal spermatheca to the oviduct, are united and communicate with that bag as a single tube; the channel to the oviduct is of considerable calibre, tortuous, and is continued into a blind dilated pouch, from the side of which comes off a short duct leading direct to the oviduct. The cæcum here mentioned may be regarded perhaps as an accessory spermatheca; it, as well as a portion of the dilated tube leading into it, is imbedded in the mucus-gland, which is not the case with the corresponding parts of *D. tuberculata*.

In *D. pilosa* the testis is shorter than in the last species, and somewhat stouter, but otherwise as in *D. tuberculata*. The vagina is very long and wide, and before reaching the spermatheca becomes constricted into a very fine tube, which a little before its entrance into the principal spermatheca, has appended to it a small accessory pouch with a delicate duct; between the junction of this duct and the principal spermatheca, and quite close to the latter, a very fine channel passes off nearly at right angles to join the oviduct at the usual point.

*D. repanda*\* has the testis reduced to a very short but wide tube, abruptly constricted at each end; at the outer end succeeds a narrow duct of nearly the same length as the testis itself, leading to the penis; this duct may be compared to the vas deferens. At the inner end, the constriction is in close contiguity to the junction of the testis with the bent part of the oviduct. The dilated portion of the oviduct is longer and wider than usual, and is suddenly constricted in front as in *D. bilamellata*; but in *D. repanda*, in which all these parts are remarkably open to observation, this constricted part of the oviduct is only once bent upon itself, where it is joined by the testis; a little further on it receives at another simple bend the channel from the androgynous apparatus, and as a small duct may be seen to enter the mucus-gland. The vagina is short, and soon receives a duct from the principal spermatheca; the tube then bends upon itself, becomes somewhat convoluted, and runs to terminate in the accessory spermatheca; the channel to the oviduct being given off as a very fine duct from the convoluted part, a little way in front of this last receptacle. The spermathecæ are more nearly of a size than in previous examples, and are both globular. The mucus-gland is here formed of the convolutions of a much larger tube than in any of the before mentioned species.

Hitherto we have noticed those species which possess a single loosely convoluted and comparatively short tube, which alone we have considered testis. We have now to call attention to another set of species, which are provided over and above with a dense fusiform mass bent upon itself, composed entirely of a very fine convoluted tube, the coils of which are compactly cemented together, forming a concentrated gland enclosed within a fine capsule.

Of this second set, *D. tuberculata*†, VERANY, is here first noticed, as it will lead us naturally to the rest; it has both the loosely convoluted tube and the fusiform gland

\* Plate XV. fig. 5.

† Plate XV. fig. 4.

largely developed. These two, at first sight dissimilar parts, we look upon as portions of the same gland, the testis. The looser part of the tube is much larger in calibre than that which is compacted in the fusiform mass, the latter tube being almost microscopic; the former is external, and at one end is in connexion with the penis by means of a much-attenuated and long duct, analogous to that which in *D. repanda* we have named vas deferens; at the other end it merges into the tube forming the spindle-shaped mass; the internal end of this latter tube opens into the oviduct, at the usual part at which the testis is received in the former category of species. The dilated part of the oviduct in this species is of unusual length, and the spermatheca of large size, as if in correspondence with the great elaboration of the testis. A small glandular sac, moreover, provided with a small duct, opens a little within the external orifice of the vagina, and this tube, which is short, communicates directly and separately with the spermatheca. The duct from that reservoir is short and delicate, comes off close to the junction of the vaginal tube, and shortly before it is united to the oviduct receives the duct of the accessory spermatheca.

In *D. coccinea*\* the testis is represented by the fusiform mass alone, which communicates by a very short simple duct with the penis at one end, and at the other, as usual, with the oviduct, which, as in some previously described examples, is here much constricted. The androgynous apparatus is arranged as in the last species, except that the vaginal gland is absent.

*D. verrucosa* has all the organs as last described, except the androgynous parts, which are in their connexions with each other slightly modified.

*D. Johnstoni*† has the fusiform gland composed of a very fine tube densely packed and connected at both ends, precisely as in *D. tuberculata*, VERANY, and *D. coccinea*, and the other organs are likewise disposed on the same plan as in those species.

In this species, however, and in *D. tomentosa*, VERANY, a closely allied species, we have the following addition to the already complicated male organs. There is an elongated hollow pouch, longer than the penis, placed in front of that organ, and opening alongside of it into the common vestibule. This pouch, into which projects, when the parts are quite retracted into the body, the finely-pointed end of a dart or stiletto, which in *D. Johnstoni* is straight, in *D. tomentosa* curved, is capable of being everted like the tentacle of a snail. To one side, and near the apex or internal end of this pouch, is attached by a short pedicle, a small ovate sac‡, from the side of which again a small twisted tube leads to a large, long, irregular, curved membranous bag, lying on the outer side of the mucus-gland. The stiletto mentioned above has its thicker end lodged in, and growing from the inner extremity of the ovate sac, whilst its shaft projects along the narrow pedicle of the sac into the hollow pouch beyond. This stiletto is evidently the production of the lining membrane of the ovate sac; that membrane forms also a sheath for a considerable portion of the stiletto, and projects with it into the pouch; here however we find it succeeded by a

\* Plate XV. fig. 3.

† Plate XIV. figs. 9 and 10.

‡ Plate XV. fig. 1.

horny layer, also of its own secreting, which sheathes the dart to the end\*, guarding its extremely fine point, but being open. The elongated pouch lying on the other genitalia is, we believe, of a glandular nature, and transmits along its tube or duct to the ovate sac its secretion. This fluid is necessarily therefore poured into the sheath of the stiletto. Now the pouch into which the stiletto projects, we have stated, is capable of undergoing eversion, and when this takes place, the ovate sac with the dart becomes thrust into the pouch, and is thus brought to the external orifice. This being effected, it is not difficult to conceive that, by successive longitudinal contractions and relaxations of the ovate sac, the dart may be projected and withdrawn by turns, and that the fluid which has been poured into the sheath of the dart will of necessity be driven out with the dart, and will therefore inevitably be shed into any punctured wound that the dart may have made in the soft body of a conjoined *Doris*.

The above apparatus is in all probability destined for the inoculation of another individual, previous to or during the act of congress, with a fluid of a stimulating or aphrodisiac character, the stiletto being analogous to the dart of the common Snail.

It is perhaps worthy of remark that the penis of *Limapontia* is pointed with a crystalline spur-like appendage; and we may be allowed to make the suggestion, founded on this circumstance, and on the above description of the genitalia of *D. Johnstoni* and *D. tomentosa*, that the two penis-like organs noticed in *Onchidium* by CUVIER in his 'Mémoires pour servir,' &c. as of doubtful character, are, one a penis with a hard spur-like end, the other a stiletto, such as has just been described.

In the latter set of species of *Doris* there is the same division of the mucus-gland into two parts as in the former, but these parts vary somewhat in proportionate size, and in the diameter of the tube, which is convoluted in them.

It will be found, from the foregoing description, that the reproductive organs do not differ essentially in *Doris* from those in *Eolis*, as given by us in the Annals and Magazine of Natural History for February 1848, and hence we infer that the two sets of observations and the results drawn from them support each other. At the above date we were not aware that Herr HEINRICH MECKEL had been engaged upon the sexual organs of the hermaphrodite Mollusks, as we have since learnt from the Report on Zoology for 1844, published by the Ray Society, and we are sorry that it has not been in our power to make ourselves acquainted with the full nature of the original memoir. From the Report, we find that MECKEL takes the same view as SIEBOLD, with regard to the organ seated upon the liver, namely, that it is androgynous, and has the vas deferens included in the oviduct. Since we became acquainted with the above views, we have examined the generative organs of *Helix*, *Limax*, *Onchidium* and *Aphysia*, and it would indeed appear that in these genera the part we call testis is insufficient for the function attributed to it; and in all of them we have detected spermatozoa in the ovary, as will shortly be seen we have found to

\* Plate XV. fig. 2.

be the case in *Doris*. We have failed to find the double sacculi and the inclusion of the vas deferens in the oviduct, at the same time we acknowledge that it is matter of great difficulty to determine the exact functions of the several parts of the apparatus.

But however the matter may be in the above Mollusks, as regards *Doris* we are still inclined to adhere to our own opinion founded on observation, namely, that the disputed organ attached to the liver is simply an ovarium; that there is no duct included in the oviduct, but that it is a simple tube, the function of the dilated portion of which is not merely to give passage to the ova, but to serve as a sort of reservoir for the seminal fluid, which is allowed to pass from the spermatheca along it, even as far as the ova in the ovarium. The testis and vas deferens, it will be seen, we recognize in that tube, of whatever length and however convoluted, which extends from the oviduct to the penis.

The position and arrangement of this testicular tube and its connection would seem of themselves to warrant this recognition; but when we find an almost microscopically convoluted tubular gland, almost the type of the mammalian testis, super-added, as in *D. tuberculata*, VERANY, and occupying part of the position of the larger or loosely convoluted tube of the true *D. tuberculata*, and that in some species, as in *D. repanda*, *D. verrucosa* and *D. coccinea*, there is a lengthened duct that may very aptly be compared to a vas deferens, leading as it does from the fusiform gland to the penis, then we must look upon our conclusions as in some degree warranted. It is true that this convoluted tubular testis joins the oviduct; but in this circumstance, instead of seeing anything that militates against our theory, we find a certain degree of confirmation of our views of the condition of hermaphroditism in which these creatures are placed. The connection with the oviduct we suppose is to provide the means of self-impregnation, when the extremely solitary habits of some of these mollusks render such necessary; and lastly, the evidence to be elicited from the contents of the testis and other genitalia would seem further to support what we have here advanced.

In *D. tuberculata* of our coasts, the testis, examined immediately after coitus, contains granular tenacious mucus, having imbedded in it numerous large granular vesicles, each having one or more clear cells developed in its interior. These vesicles\* appear to be spermatophora in an early stage of development. In the fusiform mass, making part of the testis in *D. tuberculata*, VERANY, the same kind of bodies has been observed. The same specimen of *D. tuberculata* of our coasts, the contents of whose testis have been just noticed, was examined as to its spermatheca; this was found to contain multitudes of minute elliptical cells, apparently enclosed in delicate fusiform membranous sacs, together with a few scattered spermatozoa. These sacs are the developed spermatophora†, and enclose cells,—spermatozoa in an incipient state. The spermatheca of other specimens taken during the breeding season, we found to be filled with large fusiform sacs, containing either simple cells,

\* Plate XV. fig. 6.

† Plate XV. fig. 7.

or these intermingled in various proportions with apparently fully developed spermatozoa. The accessory spermatheca, examined in season, is always found quite filled with perfectly developed spermatozoa arranged in parallel order, and in masses as if still surrounded by the membranes of the spermatophora, the simple cells having entirely disappeared. The spermatozoa\*, when fully developed, are elongated slender waved filaments, having at one end a small curved fusiform enlargement obliquely attached.

The dilated portion of the oviduct affords vast numbers of spermatozoa lying about without any obvious arrangement, though they have been seen on one occasion in bundles as if contained in spermatophora. Spermatozoa are also found abundantly, and also perfectly formed, in the ovarium itself; but we have never seen them having that exact relationship to the ova which is believed in by H. MECKEL, neither has anything like spermatophora been observed in the ovarium. If the observation and theory of this anatomist be correct with regard to *Doris*, then the development of the spermatozoa ought to proceed from the ovary in exactly the reverse order to that just described. In the ovarium young spermatophora ought to be found; these ought to burst either in the vas deferens or in the tube leading to the penis, where one ought naturally to expect to find the perfect zoosperms. These however we have never found therein; and indeed it would not appear correct to suppose that a thoroughly elaborated secretion, like the normal semen, should have to pass through such a minute and extensively convoluted tube as we find coiled up in the more solid part of the testicular apparatus of *D. tuberculata*, VERANY, *D. Johnstoni* and others; for this, from its composition, size and arrangement, is clearly itself an originator of secretion, and not merely the duct of a gland. Further, the spermatheca ought, for the same reason, to be filled with perfect spermatozoa always ready for fecundation; but we have always seen them here, with the exception of a few scattered accidentally about, still included in the spermatophora and in process of development. Indeed, the evidence we have already adduced, it will be perceived, strongly corroborates our view, namely, that the tube we call testis is really the secreting organ of a tenacious mucus-like semen, having imbedded in it numerous incipient spermatophora at the time of its emission; that this fluid is poured during coitus into the spermatheca of the conjoined individual; that there the spermatophora are matured and the spermatozoa within them; as these last are developed they are passed on in their spermatophora into the accessory spermatheca, thence to be shed into the oviduct as occasion may require. Along this tube they are gradually conveyed to the ovarium, where fecundation is in all probability effected. It may appear somewhat anomalous to state that the seminal fluid of one individual should have to be matured in the body of another, and yet from the contents of the different parts of the generative apparatus, and particularly of the spermatheca, we can adopt no other conclusion in the present state of our knowledge. We are aware, however, that, multiplied as our

\* Plate XV. fig. 8.

observations have been, the matter requires still more extended investigation before any very positive conclusion can be arrived at.

*Organs of Circulation and Respiration.*—These consist of central organs of propulsion, arteries, veins and sinuses, and of a plumose branchial organ arranged in a more or less complete circle.

First, we have the systemic heart\*, consisting of auricle and ventricle, inclosed within a membranous pericardium, of an oval form, best seen when distended, which is attached all round to the general peritoneal investment of the viscera, except at the entrance of the two lateral venous trunks from the skin and the vein from the branchiæ: there it is continued upon the veins themselves. On removing the heart, there may be seen, on each side on the floor, a number of small oblique perforations or pores.

The heart lies upon the upper surface of the posterior part of the liver-mass in front of the branchial circle, and the upper surface of the pericardium is in contact with the skin of the back. The heart, when distended†, almost fills the pericardium, the auricle being somewhat larger than the ventricle. The latter is very muscular, subtriangular in form, provided with numerous and strong carneæ columnæ, and having the auriculo-ventricular opening guarded by a double valve, the edges of which come together horizontally and project into the ventricular cavity. There is also a valve at the aortic opening. The walls of the auricle are much thinner and more delicate than those of the ventricle; the interior is lined with an irregular open network of much-attenuated fleshy columns, or rather threads.

The circulation appears pretty rapid in *Doris*; in *D. pilosa* there are seventy-two beats of the heart in a minute; in *D. tuberculata* upwards of fifty.

Secondly, we have lying under the pericardium and opening into it another propelling organ, which has not hitherto been noticed as such, of considerable interest, which shall be more fully described after we have traced the general course of the circulation. The general systemic artery‡ comes from the front or apex of the pyriform ventricle, and is almost at once divided into three principal trunks; of these, two are lateral and opposite; and each results in three branches, which ramify upon the upper surface of the sides and posterior part of the common mass of the liver and ovarium, dividing and subdividing into ramuscles of extreme tenuity, forming a network around the lobules of the ovarium and then plunging into the liver. The third or anterior trunk or aorta passes forwards on the right lobe of the liver, to which it gives several branches; it then gives off on the left side a strong branch, the gastric artery; after this another large tube passes off on the same side, supplying copiously a spongy glandular-looking organ, analogous perhaps to some of the vascular ductless glands of the Vertebrata, overlying the buccal mass. The same artery distributes branches to supply the supra-œsophageal ganglia of the nervous system. The aorta, soon after, gives off the genital artery from the right side; this supplies

\* Plate XI. figs. 1, 2 and 4.

† Plate XVI. fig. 2.

‡ Plate XII. fig. 1.



all the genitalia except the ovary, and a network of its fine ramifications, when injected, can be seen spread over the surface of the mucus-gland. The aorta next passes forward and gains the median line beneath the buccal mass, and is resolved into two branches, a buccal and a pedial, the former going to the buccal mass and channel of the mouth; the latter, dividing as it goes, runs backward on the floor of the visceral cavity, supplying the foot from end to end.

In the viscera, except in the liver and in the skin, after repeated injections and examinations, we have failed to discover veins, and must therefore conclude that the blood, after having passed through the network of arterial ramifications, falls into spaces or sinuses, among the tissues, between the viscera and in the general peritoneal cavity. We are unable as yet to say whether the spaces into which the blood thus escapes are or are not provided with a delicate proper lining membrane, as has been advanced by M. le Dr. ROBIN in his admirable 'Rapport à la Société de Biologie sur le Phlébentérisme, 1851.' The general peritoneal cavity communicates freely by many apertures with a network of canals or sinuses in the skin, but we have as yet found no veins leading from the general cavity of the body directly to the respiratory organ. The spongy network of sinuses in the skin opens freely and widely into a great trunk sinus, running backward on each side of the body at the angle of union of the mantle with the foot. These trunks, opposite the posterior angles of the auricle, turn suddenly inwards, perforate the inner surface of the skin, gaining the general cavity of the body; they then, in the form of distinct systemic veins, penetrate the pericardium and empty themselves into the auricular cavity. Thus the blood current which we have traced from the heart along the arterial system through the sinuses of the visceral cavity and the skin, is brought by venous canals through the skin back at once to the heart without having previously passed through the branchiæ.

How then, it will be asked, does the blood of *Doris* find its way to the branchiæ? It will be remembered we have accounted for the return to the heart of all the blood sent to the skin, and to the viscera, with the exception of the liver-mass; now it is that portion of the blood which has circulated through the liver-mass, and that only, which is made to traverse the specialized respiratory apparatus before reaching the heart. We before mentioned that the arteries distributed to the liver-mass can be seen to form on its exterior a delicate and minute network; we find by injection that the veins of this organ are similarly arranged, and that the principal branches of the arteries and veins run commonly side by side; moreover, we have succeeded in filling numerous arterial plexuses by injecting coloured fluid by the veins; here these sinuses or lacunæ must be reduced to their minimum, if indeed they exist at all. The principal venous branches of the liver converge and unite in a common hepatic trunk situated on the median line, at first concealed in the substance of the organ, and then in its backward course emerging at a groove at the posterior end of the liver. This trunk then turns upward and opens widely into the anterior limbus

of an internal or venous branchial circle\* which closely surrounds the anus. The blood from this circle passes on to traverse the branchial leaflets or plumes, by running up the inner side to the apex and then down the outer side to the base of the division, and then falls into a second, or external, or arterial circular canal at the base of the branchial crown. From the anterior limb of this outer circle a short wide trunk, the true branchio-cardiac or efferent vein of the branchiæ, opens forwards on the median line into the posterior border of the auricle of the heart. This efferent vein lies immediately over the hepatico-branchial or afferent vessel of the branchiæ. Thus it is that in the auricle of the heart, the blood from the liver-mass, having been aërated in the special respiratory organ, becomes mixed up with that from the other viscera, which has been returned through the general, though imperfect, respiratory surface of the skin, by the two great lateral systemic venous trunks before described.

Having now gone over the general course of the circulation, there remains to be noticed the additional blood-propelling organ situated, as before mentioned, beneath the pericardium. This is the organ which CUVIER calls a vesicle acting as a reservoir to a canal, which coming backward from the liver opens at the external orifice placed close to the anus. This canal and the vesicle act, according to the same high authority, as the agents for the production of an excrementitious fluid, which is prepared either by the liver itself in addition to the bile, or by some other gland, the lobes of which are so intimately interlaced with the lobes of the liver that the eye cannot distinguish one set from the other. M. MILNE-EDWARDS conjectures, we see, in his 'Observations sur la Circulation,' Article premier, in the *Annales des Sciences Naturelles*, 1845, "that the pore which exists by the side of the anus in *Doris* may be for the purpose of admitting water into the interior of the organism, there to be directly mixed with the blood."

We began the study of this organ impressed with a high idea of the labour which CUVIER had bestowed upon it, and with every disposition to believe in the accuracy of his results; but after repeated dissections, and injections, and careful observations, we find ourselves obliged, however reluctantly, to differ from the views that he and M. MILNE-EDWARDS have taken of these parts, and we therefore submit the following description, which we confidently believe will be found correct by those who will take the pains to examine into the matter with the minuteness it demands.

The vesicle, or heart† as we term it, is a hollow pyriform organ, lying somewhat transversely under the right side of the pericardium, with its base opening into that cavity just in advance of the posterior angle of the right side. The narrow end tapers to a tube, which after perforating the wall of the large sinus, to be presently mentioned, turns suddenly forwards along the median line of the liver, where it overlies the great hepatico-branchial vein, partially concealing it. In this course the tube

\* Plate XVI. figs. 2 and 6.

† Plate XI. figs. 1, 2, 3 and 4; Plate XII. figs. 1 and 5; Plate XVI. fig. 1.

gives off several offsets on both sides, and ends at the anterior border of the liver by dividing into several branches. The inner surface of the pyriform organ is, as CUVIER has pointed out, strongly plicated\*; the plicæ are arranged on an intricate plan, and so that they can act as a valvular apparatus to prevent the return of blood that has once passed through. The orifice is capable of being contracted like the mouth of a purse. This is the condition of the parts, as we have observed them, in *D. tuberculata*; but we have not yet seen how the branches of this tube terminate. In *D. repanda*, however, in which, as in the other species we have examined, the same organ, and branched tube proceeding from it, exist, and in which the tube does not extend so far forward as the anterior border of the liver, the terminal branches are lost among a minute network of twigs from the left side of the aorta, which are found to dip through the ovarium into the liver. In *D. bilamellata* also, we find that fresh light is thrown upon this curious apparatus†. The tube attached to the pyriform organ or heart, after passing forwards for about half the length of the liver, giving off numerous twigs, resolves itself into a multitude of other small branches. All these offsets go to form a very complete and close network lying over the hepatic vein in a superficial depression, and extending from one end to the other of the liver-mass; the sides of this plexus are united to a similar arrangement of numerous hepatic branches from both sides of the aorta. These branches, in *D. repanda*‡, are extremely numerous, and have a regular and very beautiful parallel arrangement; and the two lateral posterior branches in this species, as well as in *D. pilosa* and *D. bilamellata*, give off from their outer sides numerous much-ramified twigs. In these two species of *Doris*, therefore, the branches of the tube leading from the pyriform organ inosculate and form a network with those of the aorta; they therefore convey blood. This blood, coming as it does into the pericardium through the minute pores, already mentioned as existing on the floor of that organ and flowing through the vesicle or heart attached to it from the visceral cavity and intervisceral sinuses, is evidently venous; and our belief is that the vesicle of CUVIER is a ventricle, the office of which is to propel venous blood along its tube and branches, which are arterial in character, into the network formed by these branches and those of the aorta. This new apparatus then has a decidedly portal character.

The blood which has gone through the above network is conveyed through the liver to the hepatic vein, and we have satisfied ourselves that there is no channel of communication between this vesicle or heart and the external orifice near the anus; indeed, its office necessarily precludes the idea of such connection. The orifice near the anus is small, and leads into an extensive, more or less ramified cavity or sinus§, the trunk of which extends forwards along the upper surface and median line of the liver; its principal offsets follow the course of the chief arterial trunks, and appear to terminate on the surface of the liver.

\* Plate XVI. figs. 3, 4 and 5.

† Plate XI. fig. 3.

‡ Plate XII. fig. 5.

§ Plate XI. figs. 1, 2 and 3; Plate XII. fig. 1.

This cavity is circumscribed by a delicate membrane, which is found beneath the pericardium, and has the aorta running along its roof, and the great hepatic vein in the liver beneath it. It is intimately adherent to and undistinguishable from the capsule of the liver-mass. In the wall of the cavity lies the network from the two sources already named. The inner surface of the whole of this membrane is covered with a fine spongy-looking tissue\*, which is most abundant over the tracks of the blood-vessels; examined under the microscope, this tissue presents, particularly in *D. repanda*†, a remarkable honeycombed appearance, produced by slightly elevated lines of membrane, enclosing irregular five- or six-sided spaces, each holding a single, large, clear, globular vesicle, containing a few smaller cells of different sizes, together with some granules. In *D. tuberculata* a similar spongy tissue exists, but not so strongly marked. Considering that we have here a branched tube with a fine network of arterial and venous twigs on its wall, and the lining membrane evidently of a glandular nature, though of unusual form, there seems little room for doubt that this is an apparatus for the elaboration of some fluid from the blood; further, we find that this tube opens externally, and that the position of the orifice is close to the anus: hence we infer that this organ is one for excretion, and we have little hesitation in pointing it out as the renal organ of *Doris*. To return for a moment to the vesicle of CUVIER, it is now evident that it may with propriety be termed an accessory renal or hepatic heart; for its function is to propel venous blood, first to the renal and then to the hepatic organ; but if we may reason from what has been positively ascertained in the Vertebrata, we are inclined to consider it rather as belonging to the latter than to the former organ, particularly as we find the renal organ in *Doris* has not acquired that complete speciality and independence of other organs which it has attained in higher animals.

In recapitulation of what has been said, we will now endeavour to follow the course of the circulation in *Doris*. The principal or systemic heart propels a mixed stream of blood, which has come partly from the skin and partly from the branchial circle, and which therefore is not completely aërated, to all the viscera and the foot. This blood, with the exception of a small portion sent to the pericardium, passes from the viscera (except the liver, ovary and kidney) and from the foot through the inter-visceral sinuses, the common visceral cavity and the network of canals in the skin, by two lateral veins into the auricle. The liver, ovary and kidney are supplied with a current of blood brought to them, partly by the branches of the aorta, and partly by those of the portal heart, to which the pericardium acts as an auricle. This current, which on its passage to the liver acquires an additional venous character by traversing the walls of the renal sinus, penetrates the liver either through sinuses or capillary vessels, and is conveyed along a system of hepatic veins into the great hepatic-branchial trunk or afferent branchial vein; by this it reaches the branchiæ, whence, after having undergone the influence of the surrounding medium, it is returned to

\* Plate XIV. fig. 5.

† Plate XIV. fig. 6.

the auricle by a single trunk ; there it is mixed with the imperfectly aërated blood from the skin, and propelled again by the ventricle along the arteries as before.

Thus then we find here a systemic circulation divided into two portions, one general, the other partial ; the latter is combined with a portal circulation. It is from this hepatic course, in which the blood is most completely deteriorated, that it is sent to the branchiæ, and being returned thence to the heart, joins the current of the general portion of the circulation in the auricle. This part of the circulation seems not to have been hitherto noticed in the Nudibranchiata, and in 1845 we first pointed out the fact of the blood being returned to the heart, both from the skin and the branchiæ in *Doris*.

From what has been here said, it will be observed that we have assumed the skin in *Doris* to be to some extent an agent in respiration. That it is so, seems to be a fair inference from these facts following ; that a large quantity of blood traverses it on its way to the heart continually ; that although in most species the skin is stiffened by spicula, it is nevertheless sufficiently delicate to admit of the necessary changes taking place through it ; and that in some, as in *D. pilosa*, this membrane is very soft, and clothed with numerous soft and delicate papillæ, which, whilst they materially increase the extent of surface, are well adapted to the above purpose ; that in this last, as in the majority of the species, even the most spiculose, the whole of the mantle, and even the foot itself is covered with vibratile cilia. Moreover, if the skin be not a respiratory organ, the whole of the blood which supplies the viscera, with the exception of that sent to the liver-mass, must be returned to the heart unaërated, which is not likely.

In *Eolis* the skin in part performs the function of respiration, and in *Limapontia* entirely. Again, in *Terebratula* Professor OWEN has proved that the mantle alone is a respiratory organ ; and in *Lingula*, he has shown that there is the first appearance of a portion of that membrane becoming specialized as a gill ; and as we ascend in the scale of organization in the Mollusca, it is evident that this relationship between the gill and the mantle is always maintained, or in other words, the gill is a development of the mantle, and not of any of the internal membranes.

Thus, therefore, it is quite in accordance with what might have been expected, to find the blood partly aërated in the skin, and partly in the branchiæ ; and that such a state of things is no anomaly we learn from M. MILNE-EDWARDS, who states that in the Great Triton of the Mediterranean, in *Haliotis*, *Patella* and *Pinna*, the blood is returned to the heart in a mixed condition, part of it coming from the mantle, and part from the gill ; and from Mr. GARNER, who several years ago pointed out the same condition of parts and functions in the *Lamellibranchiata*. And when the whole subject shall have been fully investigated, it will probably be found that the above condition of the circulatory and respiratory organs predominates in the Molluscan type. If this should be so, then the conditions of the circulation in the Mollusca and the higher crustacea will be found to approximate more closely than has generally been thought ; inasmuch as, on the authority of JOHN HUNTER, and

more lately of Professor OWEN, it can be shown that a mixed stream of aërated and unaërated blood flows into the auricle of the heart.

Lastly, there remains to be described the special branchial organ\*. This is situated at the posterior part of the dorsal surface of the body, surrounding the anus and the renal orifice. It is composed of a variable number of plumes more or less divided or pectinated, and arranged in a more or less complete circle. In *D. tuberculata* they are three or four times pinnate. The plumes in some species, as in the last named and others, are retractile within a common cavity, the individual plumes being themselves contractile. In *D. pilosa*, *D. bilamellata*, &c., the plumes are merely contractile. Around the base of the plumes run two concentric canals† within the skin. The inner contains venous blood poured into it from the front by the hepatico-branchial or afferent vein, and communicates with as many channels as there are plumes. These channels run up the inner side of the stems of the plumes, and divide to apply themselves to their branches. At the ends of the branches these channels communicate with others corresponding to them on the outer side; the outer channels converge as they pass down to the stems of the plumes and debouch into the outer circle, which therefore receives aërated blood, and then transmits it to the branchio-cardiac or afferent vein, which opens into the posterior border of the auricle. In passing through these plumes, the blood follows the same course in all their subdivisions, running up the inner and down the outer surface; the main trunks of the plumes and all their offsets are clothed with vibratile cilia.

There is a peculiarity of structure in the branchial plumes of *D. pilosa*, the presence of which is indicated by their well-known white star-like centre. This appearance is owing to the existence of a double row in each plume stem of irregularly globular, hollow bodies‡, with elastic walls separating the inner and outer channels of the stem from each other. The function of this apparatus is somewhat doubtful; but we are inclined to believe that it is for the purpose of giving resilience to the breathing organ, and thus enabling the species in which it exists to continue its respiration for a time even out of water; and it is worthy of remark, that of all the species with which we are acquainted, the last-named enjoys the widest range of sea depth, being found from the coralline zone, to more than half-way between low and high-water marks. *D. tuberculata*, which is another species in which this apparatus is found, but in a less developed form, is to be taken both below and above low-water mark, and is frequently left dry among the crevices of the rocks.

*Nervous System.*—Of this there are two divisions; the first is made up of two series of ganglia, supra- and infra-oesophageal, interconnected by three commissures or collars. The former series is asymmetrical. These ganglia give off about twenty pairs of nerves, and four single nerves.

The second division consists of a complete and extensive network of minute ganglia and intercommunicating nerves spread out upon the viscera.

\* Plate XI. fig. 4.

† Plate XVI. figs. 2 and 6.

‡ Plate XVI. figs. 6 and 7.

The first division corresponds to the excito-motor, or indeed to the cerebro-spinal system, the second to the sympathetic system, of the Vertebrata. These two systems in *Doris* are at several points distinctly in connection with each other, and all the ganglia of the two systems are in *D. tuberculata* at least, from which the principal description of the nervous system is taken, of a bright orange colour.

The supra-oesophageal ganglia\* of the first system are five pairs and a single ganglion, the pairs being symmetrically placed with regard to each other, and to the median line; and the single ganglion, not hitherto described, and which we shall call the visceral, lies on the right side. Of these, three pairs predominate in size, the anterior of which, or sensorial, the cerebroid of M. BLANCHARD, lie next the median line, across which they are connected, and are of a somewhat conical shape, the base forwards. Springing from about the middle of the anterior border, and from the upper surface of these, is a pair of ganglia corresponding to the pedunculate pair, which in *Eolis* we have called olfactory. In *Doris* they are almost sessile, and though in size much inferior to the cerebroid, are nevertheless of notable dimensions. They give off each a large nerve to supply the dorsal tentacles, the first pair. The next three pairs of nerves come off from the under surface of the anterior border of the cerebroid ganglia, external to the attachment of the first pair. They run forward and supply the muscles and the skin at the side of the channel of the mouth and the lips: the second of these pass to the oral tentacles. The fifth pair comes off close after the fourth, passes forwards and downwards, and soon divides into two branches; one goes on to the under part of the channel of the mouth and lips, the other courses round under the buccal mass, and unites with the corresponding nerve of the opposite side, to form the first or anterior collar (*k*), which is slender and wide. External and close to, and of about the same size as the fifth pair, comes off a nervous trunk, which curving round the top of the oesophagus, joins the principal infra-oesophageal ganglion. This trunk, instead of being an ordinary nerve, constitutes with its fellow of the opposite side the second or middle collar (*l*) or commissure between the anterior supra-oesophageal and the larger infra-oesophageal ganglia, and for this reason we omit it in the enumeration of the nerves. The sixth pair are very short, and come off from two minute elliptical ganglia, almost sessile upon the external border of the anterior or cerebroid ganglia near their posterior end: these are the optic nerves and ganglia. The seventh pair of nerves appear to have no trunk, for the auditory capsule is sessile on the ganglia directly behind the optic nerve.

The posterior or branchial ganglia are broadly ovate, and connected in front with both the cerebroid and the other pair. The eighth, ninth and tenth pairs arise from these ganglia, and are distributed to the whole of the mantle; the two first of these pairs go to the anterior, and the last to the posterior portion, sending a branch of communication (10') to the branchial ganglia of the sympathetic system. The

\* Plate XVI. fig. 8.



eleventh and twelfth nerves arise also from these centres, and are distributed to the sides of the body between the mantle and the foot.

The lateral or pedial ganglia lie on a plane rather beneath the others, with both of which they are connected, and in shape and size are like the branchial. Three large nerves, the thirteenth, fourteenth and fifteenth pairs, are given off from these centres, and supply the whole foot.

The single supra-oesophageal or visceral ganglion\* is round, and about the size of the olfactory; it is sessile on the under surface of the anterior border of the right branchial ganglion, where this is in contact with the pedial. The nerves *g, h, i, j* issue from this ganglion; (*g*) the first in origin passes down by the side of the aorta, to which it gives branches; one of these has a small ganglion (*n*) in its course; the other, the larger, passes further on, and ends in two or three ganglia (*p*) placed at the root of the aorta, which send branches to the pericardium and heart. The trunk of the nerve passes down towards the branchiæ, and in so doing, gives off next another branch to the systemic heart, and then a large offset to the portal heart; after this the nerve comes into connection with the branchial ganglia and plexus (*q*) of the sympathetic system, and communicates with the renal plexus (*v*), apparently a dependence of the former or branchial. The next in order (*h*) runs backwards to the right side towards the base of the bag of the penis, where it merges into the principal sympathetic ganglion of the generative organs. The third nerve (*i*), smaller than the last, runs beneath the organs of reproduction and the stomach, and in its course distributes two or three branches to the mucus-gland, joining an open plexus (*s*), with a few small ganglia situated on that organ; the nerve then inclines towards the left side, presenting a small ganglionic swelling in its course; and shortly afterwards passes into the largest ganglion (*t*) of the gastro-hepatic plexus, that which receives the right par vagum nerve. The last nerve (*j*) runs straight backwards to the vicinity of the branchiæ, and after giving off two or three twigs apparently to the intestinal plexus (*w*), as it passes under the intestine, terminates in a small ganglion closely connected with the larger one, into which nerve (*g*) runs, both of these ganglia belonging to the branchial plexus (*q*).

We now come to the third, or posterior, or great oesophageal collar (*m*); it is stouter, more closely invests the oesophagus than the other two, and is composed of three parallel cords, two of which are attached to the under surface of the pedial ganglia; the third has one end in connection with the left branchial, and the other with the visceral ganglion.

The infra-oesophageal ganglia† are two pairs symmetrically disposed on the buccal mass; the larger or buccal, as we have seen, are connected by means of a collar with the cerebroid. They are elliptical, and are united by a short commissure. They give off laterally, and in union with the collar, two pairs of nerves, the sixteenth and seventeenth, which are distributed to the buccal mass. The eighteenth is a small

\* Plate XVII. fig. 1.

† Plate XVI. fig. 8.

pair which passes off backwards to the base of the tongue, and is joined by buccal filaments of the sympathetic. To the front of the buccal are attached the gastro-œsophageal ganglia, which are very small and give off three pairs of nerves. The smallest of these, the nineteenth pair, is given to the salivary gland. The twentieth supplies the top of the œsophagus, round which it curves on each side, communicating with the œsophageal sympathetic plexus. Lastly, the two nerves constituting the twenty-first pair, by far the largest of the three, are continued down on the under surface of the œsophagus, on each side of the median line, nearly parallel with each other, communicating by slender filaments with a fine open network of nerves and ganglia upon that tube, and unite with two of the largest ganglia of the sympathetic system of the stomach. This pair is the counterpart of the gastric portion of the par vagum of the higher animals, and is analogous to the nerves which in insects have been named stomato-gastric.

The principal varieties that have been observed in the cerebro-spinal nervous centres are as follows: in *D. pilosa*\* and *D. repanda*†, the first three pairs of ganglia are very distinct, and only slightly altered in relative position from those in *D. tuberculata*, the pedial becoming quite lateral as regards the œsophagus, and indeed almost meeting under that tube, the third collar being consequently of extreme brevity. In *D. Johnstoni*‡, *D. verrucosa*§, *D. coccinea*, *D. bilamellata*||, and *D. aspera*, the cerebroid and branchial are more or less fused into one mass, which in some of the species is elongated in the antero-posterior direction, and in others obliquely. In *D. Johnstoni*¶ the visceral ganglion is pedunculate; no material variation in the origin and distribution of the nerves has been observed. The visceral ganglion is present in all.

The two pairs of infra-œsophageal ganglia just described, have been noticed in the Annales des Sciences Naturelles for 1848, by M. EMILE BLANCHARD, in an article on the Opisthobranchiate Mollusks; the larger pair he names œsophageal, and gives all their branches to the alimentary apparatus; the smaller he calls *angéïens* or *aortiques*; these latter he announces as a new discovery, and states that they are placed on each side of the aorta to which they give filaments. The corresponding ganglia in *Eolis* were discovered by us in 1846, and are to be found described and figured in the third part of the Monograph on the Nudibranchiate Mollusca, published by the Ray Society in the following year. These branches have now been so often verified by us, both in *Eolis* and *Doris*, that we are quite satisfied of the truth of the account we have given of them. We cannot therefore see the propriety of the names that M. BLANCHARD has imposed upon these ganglia. Further, M. BLANCHARD looks upon the infra-œsophageal ganglia and nerves as the representatives of the splanchnic or sympathetic nervous system of the higher animals; and anatomists in general seem to have a confused idea that the œsophageal ganglia of the Mollusca,

\* Plate XVII. fig. 8.

† Plate XVII. fig. 9.

‡ Plate XVII. fig. 2.

§ Plate XVII. fig. 4.

|| Plate XVII. fig. 6.

¶ Plate XVII. fig. 3.

taken all together, represent not only the cerebro-spinal system of the Vertebrata, but their sympathetic system as well. We are now, however, we hope, prepared to show the error of such views, and to supply a desideratum in Comparative Anatomy, by pointing out the true sympathetic nervous system of the Mollusca. This system, it will be found, bears a very remarkable resemblance to, and correspondence with, its counterpart in the Vertebrata; and whilst its demonstration will, with the other new points which we have recorded in this paper, prove the very high degree of organization enjoyed by the Nudibranchs, it will also throw a clearer light upon the physiology of the whole of the ganglia surrounding the œsophagus than previously existed.

*The Sympathetic System\*.*—This exists, and is more or less demonstrable, in the skin, the buccal mass, and in all the internal organs. It consists of a vast number of minute distinct ganglia, varying in size and form, the larger quite visible to the naked eye, of a bright orange colour like the ganglia round the œsophagus, and interconnected by numerous delicate white nervous filaments, arranged in more or less open plexuses or networks. This beautiful system is in several points, as already indicated, connected with both sets of œsophageal ganglia.

In the skin the sympathetic system is not very easily detected, nor indeed have we much sought for it there; but we have seen enough to prove its presence in the fact of the existence of two or three ganglia in connection with filaments of the anterior branches of the branchial ganglion.

In the buccal mass this system is only a little more evident, and is very difficult of investigation; we have, however, succeeded in making out a few ganglia and nerves in the neighbourhood of the œsophagus. First, there is a nerve on the posterior surface of the buccal mass passing forward on each side of the infra-œsophageal ganglia, and having itself a small ganglion with other nerves at each of its ends imbedded in the buccal mass. This nerve runs within the second collar, communicating with it, and giving a twig to the salivary gland; it also furnishes a twig which joins the lingual nerve. This nerve is probably the rudimentary representative of that large nerve in *Eolis*, which passing from the same part of the buccal mass runs also within the corresponding collar with which it is in connection, and is distributed to the glands of the papillæ.

Around the œsophagus there is a fine open network † of very minute nerves and a few ganglia, frequently connected with both of the gastro-œsophageal nerves from the infra-œsophageal ganglia. This network at the top sends some offsets to the salivary glands, and others to the nerves and ganglia of the buccal mass. The œsophageal sympathetic plexus, with the gastro-œsophageal nerves, is continued down as far as the cardiac orifice of the stomach; at this part the gastro-œsophageal or vagi nerves pass into two comparatively large ganglia, situate under the cardia; and the œsophageal plexus, besides giving twigs to these ganglia, is continued into the gastro-hepatic

\* Plate XVII. fig. 1.

† Plate XVIII. fig. 3.

sympathetic plexus. Of these two great ganglia, the larger (*t*), that of the right side, receives likewise a distinct branch from nerve (*i*) of the visceral supra-oesophageal ganglion, and thus these gastro-hepatic centres are brought into relation with the cerebro-spinal centres. These two cardiac centres are the chief links of a complete chain or collar of ganglia\* and commissures that surround the posterior or cardiac end of the stomach, just behind the oesophagus, and at the entrance of the great duct of the liver. There are ten or twelve, or more centres in this collar, and from it, branches are given off on both sides, and chiefly from the centres; these pass forwards on the stomach, and backwards on the hepatic duct to the liver; the latter are fine, and form with small ganglia an intricate plexus on the duct; these have not been followed into the liver on account of the extreme delicacy of the parts; the former are larger, and four of them, which may be regarded as principal trunks, pass forwards upon the different aspects of the stomach, forming, with microscopic filaments and ganglia, a complete interlacement all over that organ, particularly on its under surface. The pancreas also is crowded with almost microscopic ganglia and filaments. We propose to denominate the whole of this very extensive and complicated network, of which the circular collar of ganglia may be considered as the centre, the gastro-hepatic plexus of the sympathetic system. Altogether it forms, with its almost countless orange-tinted ganglionic nodules of various forms and sizes, a novel anatomical spectacle of extraordinary beauty and interest. These nerves and ganglia are visible without much difficulty in a favourable specimen, and lie for the most part slightly imbedded on the external surface of the organs. Towards the pyloric end of the stomach the ganglia are thickly strewn, presenting the appearance of another collar or circle around that part: this may be called the pyloric plexus (*u*)†. From this there is a continuous minute and singularly beautiful plexus of nerves and ganglia, down the whole length of the intestinal canal to the anus. These ganglionic nodules are usually smaller on the whole than the gastric, varying less in size and in form, being mostly globular, and having the same orange colour. They are most numerous at the two extremities of the intestine; taken as a whole, they may very properly be called intestinal plexus (*w*, *w*)‡.

The branchial or branchio-cardiac portion, as far as we have observed, consists of a somewhat irregular chain of large orange ganglia and nerves lying across, and in front of the base of, the branchial crown, and over the hepatic vein. Twigs pass backwards from this to the branchial plumes, and forwards towards the heart, and two branches of communication (*g* and *j*) are received from the visceral supra-oesophageal ganglion. A twig reaching these ganglia laterally from the mantle nerve of each side keeps up a connection between them and the branchial supra-oesophageal centres.

An open network (*v*) with two ganglia has been observed on the floor of the renal organ, and over the hepatic vein; this is all we have found to represent a renal plexus,

\* Plate XVIII. fig. 1.

† Plate XVIII. fig. 2.

‡ Plate XVIII. fig. 4.

or it may more properly belong to the vascular system; the nerve (*g*) from the visceral ganglion also gives a twig to this plexus: this part of the sympathetic system will, however, require more close investigation than we have yet been able to bestow upon it.

The last portion of this system which now remains, is that belonging to the reproductive organs. Here at the under part of the base of the penis exists an intricate network of numerous nerves and ganglia of varying size; the largest of these centres (*r*) receives nerve (*h*) from the visceral ganglion of the cerebro-spinal system. The network is continued in a more open form over the whole sac of the penis, and prolonged also over the ovarian channel, and can also be traced upon the anterior part of the mucus-gland, where there are several ganglia; one or two ganglionic nodules have also been seen upon the oviduct. A slight network of nerves has been met with upon the posterior part of the mucus-gland, in connection with two or three twigs of nerve (*i*) from the visceral ganglion above mentioned.

The ganglia of the sympathetic system\* contain seldom more than a few nerve-globules; these are granular, nucleated and coloured, like those of the cerebro-spinal centres, but generally have two instead of one caudate prolongation. On account of the simplicity of the arrangement of the globules and nerve-tubes, the connection of these two elements may here be studied with great advantage. Various ganglia from the stomach have been submitted to the microscope, and what has usually presented itself to the eye is, that at the place where the ganglionic swelling occurs one or more nerve-tubes or fibres, according to the size and complexity of the ganglion, and the number of the globules contained, appear to dilate gradually or suddenly, and each to enclose a globule, the nerve-tube contracting again at the opposite pole of the globule, and resuming its former dimensions, the neurilemma also being bulged out to an extent correspondent with the size of the enclosed globule or globules.

The globules are generally more or less elliptical or fusiform, though some are pyriform: these last appear to be prolonged into a nerve-tube only at their apex. It is possible, however, that there may be, or may have been, another prolongation; but if so, it has certainly escaped us; at all events, as they have been observed, they remind us forcibly of the pyriform nucleated nerve-vesicles, formerly described by us as existing in the supra-oesophageal ganglia of *Eolis papillosa*. The globules vary greatly in size, are all provided with a large rounded or oval nucleus, having a distinct nucleolus; the whole globule is of a fine yellow colour, approaching orange, the nucleus being of a bright full orange; the nucleus and the whole cell are alike granular. The nerves of this system closely resemble those of the cerebro-spinal system, being semitransparent, pearly, and in showing parallel nerve-tubes enclosed in a common neurilemma. In spirit they become of an opaque white, and are then best seen and dissected. What we have seen in *Doris* touching the connection of

\* Plate XVIII. figs. 5, 6 and 7.

the nerve-tubes and nerve-vesicles, goes to confirm what we have elsewhere said respecting the corresponding parts in *Eolis*, and support the now almost universally received ideas on the subject of the relation of these parts to each other in the higher animals.

Extensive traces of the sympathetic system have been detected in several other species of *Doris* as well as *D. tuberculata*; and it is interesting to remark, that on the œsophagus, stomach and genitalia of *Eolis papillosa* ganglia and nerves of the same system have been observed. The same system has been seen in *Arion ater*, and there can be little doubt that it will be found in all the higher Mollusks.

It is worthy of notice, that in these Mollusks we have found no special relation between the nerves of the sympathetic system and the blood-vessels, such as are well known to exist in the Vertebrata, the only exception being that the nerve (*g*) from the visceral cerebro-spinal ganglion that goes to the branchial plexus, and to the two hearts, gives branches to the aorta and one of its divisions; on each of these branches appears a small ganglion. It is possible that on further and more minute scrutiny plexuses on the great vessels at least may be discovered.

After this detailed account of such a complicated system of visceral nerves, few perhaps will be disposed to doubt that we have here a true sympathetic nervous system. The fact, however, of the existence of ganglia and intercommunicating nerves forming plexuses, the mode of disposition of these networks upon the organs, their connections with the principal nervous centres grouped around the œsophagus, and lastly, the microscopic structure of both nerves and ganglia, all combine to prove the correctness of what we have advanced.

Assuming it, then, as proved that the system before us is a true sympathetic or splanchnic nervous system, let us now see what light this new fact is capable of throwing upon the physiology of the ganglia about the œsophagus. Although hitherto physiologists have seemed to concur in the belief that somehow or other the œsophageal centres preside at the same time over the functions of both animal and organic life, still there have been differences of opinion as to the mode of the assignment to the individual ganglia of functions apparently so different in nature as those of the cerebro-spinal and sympathetic systems. The principal theories to be met with are three; first, that all the ganglia, both those above and those below the œsophagus of the Mollusca, perform in some way or other the entire functions of cerebro-spinal and sympathetic systems; second, that the supra-œsophageal ganglia represent the cerebro-spinal, and the infra-œsophageal the sympathetic system of the Vertebrata; third, that whilst the two series of ganglia in the Mollusca are the counterparts of nearly all the cerebro-spinal in the Vertebrata, the nerves lying along the œsophagus and going to the stomach, represent the “par vagum” or the “sympathetic” or the “visceral nerves.”

The discovery of the true sympathetic nervous system not only proves that the third theory here noticed is that which most nearly approximates to the truth of

nature, but also supplies a point of analogy between the nervous system of the Mollusca and that of the Vertebrata, which was previously wanting. We are now free to compare the nervous centres and their offsets grouped round the œsophagus in the Mollusca, with those which constitute the cerebro-spinal system of the Vertebrata. This we shall now proceed to do; and it is highly interesting to find how remarkably close the analogy is, even to the details, between the sets of organs in the two Subkingdoms. But first let us take a brief review of the ganglia and their relation to each other in *Doris*, and then of the relation of the ganglia in *Doris* to those in other Mollusca. It has been believed by CUVIER and others that these ganglia are to a greater or less degree fused into one mass; but if in *D. tuberculata* the contents of the capsule\* or dura mater be pressed out completely, the true manner of the connection becomes evident. It is then seen that the communication between the ganglia is kept up through narrow apertures by means of small oval commissures, and that the masses are closely pressed as it were together, the opposed surfaces being flat. In such a preparation it can be observed that the cerebroid ganglia are divided by a strong septum, which is perforated by an oval opening; that the branchial are connected to both the cerebroid and the pedial ganglia by commissures somewhat similar; that the pedial are similarly united to the cerebroid; and lastly, that the visceral ganglion is joined to the branchial through a small aperture. The third or principal collar round the œsophagus is in such a preparation distinctly seen to be divided into three strands, two of which enter the pedial ganglia, the other passes from the left branchial to the visceral, which again, as above stated, is connected with the right branchial. From these intercommunications between the ganglia, and from the distributions of the nerves arising from them, a strict analogy may be drawn between the nervous centres of *Doris*, in which they have attained a high degree of concentration, and those of other Mollusks in which they are comparatively disjoined. We may take *Aplysia hybrida* as a fair specimen of the latter class. Here the cerebroid ganglia are slightly apart, being united by a short commissure. These, as in *Doris*, give their branches to the dorsal tentacles, the eyes, the channel of the mouth and lips. At a little distance behind these centres are the branchial, which are on the same plane, considerable in volume, rounded, and connected with the former by a stout commissure. The branchial ganglia supply the mantle, and are doubtless the homologues of the parts of the same name in *Doris*. Backwards from them pass two stout trunks, which go to two ganglia in the vicinity of the branchiæ; these ganglia are little inferior in size to the branchial, are united to each other by a distinct commissure, and send their nerves to the generative organs, heart and intestine; they are in some species fused into one, as we see in CUVIER's memoirs, and this he believed to have the office of a sympathetic system. These ganglia, or this ganglion, from its connections with the branchial, and from the distribution of its nerves, is undoubtedly the homologue of our single visceral ganglion in *Doris*. The

\* Plate XVI. fig. 9.



remaining supra-œsophageal ganglia are the pedial. These are placed on a plane below the branchial, on the side of the œsophagus, and are connected with the cerebroid and branchial by stout commissures of considerable length. Three large nerves are given to the foot from these ganglia. Thus we find that the homology of the parts is complete; and were the ganglia concentrated, we should find them connected in precisely the same manner as in *Doris*. There is moreover an exact correspondence as to the infra-œsophageal ganglia and their nerves in *Doris* and *Aplysia*.

The examination of the nervous centres of *Arion* and *Onchidium* strongly support the view we take of the functions of the different nervous ganglia in *Doris* and *Aplysia*. In both these instances we have the cerebroid ganglia giving their nerves to the organs of the senses, and to the channel of the mouth and lips, the branchial giving off their nerves to the mantle, and the pedial supplying the foot. *Arion* and *Onchidium*, however, differ from each other as regards the visceral ganglion; but this difference itself only corroborates our views of the functions of that organ. In *Arion* it is still formed, as in *Aplysia*, of two large centres; but these, instead of being placed at a distance and connected by long commissures with the branchial, are placed close between and united to them, and overlie the pedial. In *Onchidium* there is fusion of the pair into a single ganglion, which lies in the same position with regard to both branchial and pedial, and has the same connection with the branchial as in *Arion*. The nerves arising from this centre in *Onchidium*, and from this pair of centres in *Arion*, we have traced, though not quite perfectly, to all the viscera as in *Doris*. In *Onchidium* a little alteration in the relative position of the ganglia is all that is necessary to make the resemblance complete between its nervous centres and those of *Doris*.

Taking this view of things, we find ourselves at issue to some extent with M. E. BLANCHARD; for instance, the large posterior nerve from the branchial ganglion, the cervico-cardiac of this author, sends a branch of communication, as we have seen, to unite with the branchial sympathetic ganglia; these ganglia he takes to be the same as those in the posterior part of the body of *Aplysia*, and which we believe to be the homologues of our visceral ganglion; hence it is that he was led to consider the connectives between these ganglia and the supra-œsophageal centres to be the homologues of the great posterior nerve from the branchial ganglion; but in *Aplysia* we have the true representative of this nerve, which arises as in *Doris* from the branchial ganglion, and supplies the posterior part of the mantle. Moreover, we have discovered near the roots of the respiratory organ in *Aplysia* a minute ganglion and nerves, the real counterparts of the sympathetic branchial ganglion of *Doris*. We have therefore little or no doubt of the accuracy of our views on this point.

If we compare the nervous system of the higher Mollusks with that of the *Lamelli-branchiata*, we shall find that the principal centres are sufficiently well represented in the lower forms. In *Mya truncata* we have two large ganglia placed anteriorly at

the sides of the œsophagus, connected by a longish commissure; these, which are usually called the labial, answer to the cerebroid of *Doris*, and give branches to the anterior margins of the mantle, the seats of sensation; and the corresponding ganglia in some species are said to have the auditory capsules attached to them. From these centres run backward two commissures, one of which runs into a ganglion placed in the muscles of the foot, the pedial, the other passing further back enters a large ganglion situated on the posterior adductor muscle. This mass sends large nerves to the branchiæ, the siphonal tubes and the posterior portion of the mantle. This is the branchial ganglion of authors, and as the ganglia which we have so called in *Doris*, supply nerves to the mantle, and are brought into connection with the branchial ganglia of the sympathetic system; we believe them to be the homologues of the last-named ganglion of the *Lamellibranchiata*. It is worthy of note that we have discovered in *Mya truncata* two small elliptical ganglia attached to the anterior and underpart of the branchial, and united together by a commissure. These send filaments to the ovary, and ventricle of the heart, and therefore probably represent the visceral ganglia of *Doris*. Thus we have the representation of the nervous centres of *Doris* complete in *Mya*.

We shall now, then, return to the comparison of the nervous œsophageal ganglia in *Doris* with the ganglia making up the cerebro-spinal system of the Vertebrata. First, then, we have a small anterior pair of ganglia, which we have called olfactory, for reasons given in our anatomy of *Eolis*, and which it is perhaps unnecessary to repeat here. This is in position, and probably in function, the counterpart of the same organ in the Vertebrata, the rhinencephalon of Professor OWEN. Secondly, we have the large anterior supra-œsophageal or sensorial or cerebroid ganglia supplying the lips and channel of the mouth with both motor and sensitive nerves, and not only supplying the olfactory, but also the optic ganglia and the auditory capsules. This second pair is clearly comparable to either the hemispherical ganglia or the centres of sensation and volition, or to both these sets together, with a portion of the anterior extremity of the spinal cord, and probably also the cerebellum. They are analogous therefore to the prosencephalon, a portion of the mesencephalon and of the anterior end of the myelon, and possibly also of the epencephalon of the same high authority. Thirdly, we have the optic ganglia; these come the next in order in the Mollusca as in the Vertebrata, and in the former are to all appearance dependences of the sensorial or cerebroid. The optic ganglia from which the optic nerves arise, are analogous to the corpora quadrigemina, or a portion of the mesencephalon. Fourthly, come the branchial centres; these are next the median line, on the same plane as the cerebroid and posterior to them, and in several species, as we have seen, more or less joined with them into one mass. The nerves from these ganglia go to the respiratory organs, that is the skin or mantle, and to the ganglionic nervous centres of the branchiæ. The branchial ganglia correspond in function to the pneumonic portion of the pneumogastric apparatus of the medulla oblongata or macromyelon of the

higher animals. Fifthly, the visceral ganglion attached to the right branchial is the only evidence we have of the heterogangliate type in the œsophageal nervous centres of *Doris*. Its nerves go to the stomach, to the respiratory organs, to the circulatory and reproductive apparatus, being at these several viscera connected with their sympathetic ganglia. This single ganglion we take to be the representative in *Doris* of that part of the spinal cord in the Vertebrata which gives off a series of nervous branches, and communicates with either the chain of ganglia of the trunk of the great sympathetic or the plexuses more immediately attached to the several viscera. Sixthly, next in order come the pedial pair of ganglia, placed on a plane rather below the other two pairs and on the side of the sensorial. They subserve the locomotive organ, and hence represent those parts of the spinal cord of the higher animals, which also in them supply the organs of locomotion. Seventhly, the first infra-œsophageal or buccal ganglia supplying the buccal or lingual apparatus with sensation and motor power, and, as we suppose, with taste as well, answer to that part of the medulla oblongata from which the lingual and gustatory nerves arise. Eighthly, the second infra-œsophageal or gastro-œsophageal correspond to the gastric division of the pneumogastric ganglion of the medulla oblongata of vertebrate animals.

In *Doris*, then, we see the pneumogastric apparatus resolved into two parts; the pneumonic appears in the branchial ganglia, the cardiac is wanting, the gastric is seen in the gastro-œsophageal. These give off nerves, passing to the œsophagus and stomach, which are the counterparts of the pharyngeal branches of the glossopharyngeal, and of the pharyngeal, œsophageal and gastric portions of the par vagum of Vertebrata.

The sum of these comparisons is, that the whole of the ganglia arranged in *Doris* around the top of the œsophagus are analogous to the encephalon and a portion of the enrachidion of the Vertebrata.

There seems great probability that the cerebral hemispheres and the cerebellum, with the seats of consciousness and volition, and also of emotion of the higher animals, are but very faintly shadowed forth in the cerebroid ganglia of the Mollusca.

*Organs of the Senses. The organs of Hearing.*—These are two very delicate, microscopic, ovoid capsules, sessile on the outer margin of the cerebroid ganglia immediately behind the eyes. When magnified considerably they show an inner and an outer capsule, enclosing fluid in which exists an agglomeration of minute otolithes. When these are more highly magnified their form is seen to be pretty accurately oval, presenting a central darkish spot or nucleus. When extracted with their capsule they present a continual vibratile motion.

In *Doris aspera* the number of otolithes was found to be upwards of forty. On account of the very rudimentary state of the organs and their depth from the surface, it is evident that their function must be excessively limited.

*The organs of Sight.*—These are placed immediately beneath the skin, behind the

dorsal tentacles, but in the adult animal are not visible (with the exception of the case of a single species, as far as we know,) from the exterior.

When the skin is removed, they are seen as minute black dots, placed at the outer sides of the supra-oesophageal ganglia. They are thereto attached by a minute pedicle of variable length, which is so short in some as to make the eyes appear sessile on the ganglia. On closer examination the pedicle is found to have at its base a roundish or oval ganglion, which we have in a former part of this paper called the optic.

The optic nerve emanating in a forward direction from this ganglion enters the base of a well-formed eyeball, consisting of, first, a delicate transparent investing membrane, within which rests a pretty regularly formed cup of black pigmentary matter, the choroid, having projecting from its mouth a globular, bright, crystalline lens, in front of which is a firm, transparent, well-arched membrane attached to the lips of the cup of pigment, the cornea, or perhaps the capsule of the lens. The eye of *Doris* is fully equal in development to that of *Eolis*; but in the former, as it cannot be seen through the skin, we infer that there is no perception of external objects, but that at most the creature can only distinguish between light and darkness. This appears to be the necessary extent of visual power for the preservation from external violence of the individual in animals of such limited locomotive powers, the tactile property of the oral tentacles, assisted by the lips, possibly the seat of taste, being all that is requisite for the selection of matters fitted for the sustentation of the organism.

*The organs of Smell.*—The dorsal tentacles, which have never been observed to be used as tactile organs, we believe to be the seat of the sense of smell; and this belief is strengthened when we reflect that these organs are most highly developed and minutely laminated; that they are most plentifully supplied with nerves from ganglia placed in front of all the rest of the cerebral masses; that they are externally covered with vibratile cilia, and so placed on the head as easily to receive impressions from any odorous particles that may be mingled with the circumambient water.

It is generally admitted now that snails have the sense of smell; and *Doris*, which is certainly not inferior to them in organization, can scarcely be denied the possession of that endowment, particularly as we find in it a highly developed, conspicuous, sensitive and therefore important organ, to which no other use can properly be assigned, but which appears to correspond, in arrangement of parts and position, to the laminated antennæ of insects, to which olfaction has been commonly attributed. In the Pearly Nautilus, certain laminæ within the oral sheath, plentifully supplied with ganglia and nerves, have been by Professor OWEN pointed out as the olfactory organ in that mollusk. It must be borne in mind that the laminated form of the organ of smell, and its supply of ganglia and nerves from the very front of the cerebro-spinal nervous centres, are universal in Fishes and the higher Vertebrata. In Fishes the organ presents, as is well known, a beautiful doubly laminated arrangement, the stem bearing the laminæ being fixed longitudinally to the bottom of the cavity of the nose.

In *Doris* we have a similar form, that of laminæ, attached to a central stem, which is ordinarily erect and exposed, but is capable in most species of being retracted within a cavity. These tentacles are placed on each side of the median line, at the anterior extremity of the body, over the head.

The subject of the nature and signification of the dorsal tentacles has been more fully discussed in our paper on *Eolis*, before alluded to; it is therefore perhaps unnecessary for us here to dwell more at length upon it.

*The organ of Taste.*—Is doubtful as to its existence; its use may be in some measure subserved by touch, it probably resides in the different lips and the passage to the buccal cavity, or may have its special seat in that cavity itself. The tongue, which is peculiarly a prehensile organ, seems very ill adapted for an organ of taste.

*The organ of Touch.*—This is the skin, over which the sense is universally diffused; but the faculty is undoubtedly specialized also in the oral appendages, whether these have the ordinary linear form of tentacles, or exist as a veil-like expansion partially encircling the mouth. The veil and the tentacles are alike the homologues of the oral tentacles of *Eolis*, and are supplied like them with nerves coming off from the anterior part of the cerebroid ganglia. The tentacles or veil are so placed that they can with perfect ease be applied to the surface of substances on which the animal crawls or seeks its food, and to the food itself; and there is every reason to believe that the sense of touch residing in these organs is exquisitely delicate.

We have not yet been able to examine with sufficient care the minute structure of the skin; at present we can only offer the following particulars. The skin in most species is tough and coriaceous, and is of a spongy or cellular structure within: the cloak, in all the British species examined, is stiffened with numerous imbedded spicula, having a more or less symmetrical arrangement. Spicula are also observed in the foot, in the tentacles, and in the roots of the branchial plumes. The under surface of the foot and the upper surface of the cloak, as before stated, are covered with vibratile cilia. The branchial plumes and dorsal tentacles are also furnished with them.

#### EXPLANATION OF THE PLATES.

#### PLATE XI.

Fig. 1. General view of viscera of *Doris pilosa* seen from above, the dorsal skin and peritoneal membrane having been laid open. *a*, buccal mass; *b*, upper surface of stomach; *c*, pancreas; *d*, intestine; *e, e*, liver; *f*, mucus-gland belonging to female organs; *g*, portion of testis; *h*, spermatheca; *i*, accessory spermatheca; *j*, pericardium, exhibiting through its transparent walls the ventricle and auricle; *k*, ventricle; *l*, auricle; *m, m*, two lateral venous

trunks passing from the skin to the auricle; *n*, efferent or branchio-cardiac vein; *o*, portal heart lying below pericardium, and seen through it; *p, p*, upper wall of renal organ, exhibiting, by the aid of injection, a fine network of arterial twigs in connection with the aorta; *q*, a gland-like body in connection with the vascular system, and overlying the cerebral ganglia; *r*, branchial plumes.

Fig. 2. Dorsal view of viscera of *Doris bilamellata*. *a*, buccal mass; *b*, buccal gizzard; *c*, portion of salivary gland; *d*, upper aspect of stomach; *e*, pancreas; *f*, intestine; *g, g*, liver; *h*, mucus-gland of female organs; *i*, spermatheca; *j, j*, testis; *k*, pericardium; *l*, ventricle; *m*, auricle; *n, n*, lateral vein from skin, entering auricle; *o*, portal heart; *p, p*, upper wall of renal organ, exhibiting a fine arterial network; *q*, branchial plumes; *r*, gland-like organ in connection with vascular system.

Fig. 3. Dorsal view of viscera of *Doris repanda*, the heart having been removed. *a*, buccal mass; *b*, upper aspect of stomach; *c*, pancreas; *d, d*, intestine; *e, e*, liver; *f, f*, renal organ, exhibiting a symmetrical arrangement of arterial twigs on its upper wall; *g*, aorta with apex of ventricle attached; *h*, portal heart appearing through the upper wall of renal organ; *i*, branchiæ; *j*, generative organs; *k*, glandular organ in connection with aorta, overlying supra-oesophageal ganglia, from which nerves may be seen to radiate.

Fig. 4. Dorsal view of viscera of *D. tuberculata*. *a*, buccal mass; *b*, stomach, upon which part of the gastric plexus of sympathetic nervous system is visible; *c*, intestine; *d, d*, liver with the principal arterial trunks of the renal organ seen on the surface; *e*, retracted penis; *f*, mucus-gland of female channel; *g*, spermatheca; *h*, vagina, leading to same from external orifice; *i*, pericardium; *j*, ventricle; *k*, auricle; *l, l*, lateral trunk veins from skin to auricle; *m*, efferent or branchio-cardiac vein; *n*, portal heart seen through the transparent membranes of heart; *o*, branchial plumes; *p*, glandular organ in connection with vascular system; *q*, supra-oesophageal ganglia with numerous nerves radiating from them; *r*, branchial ganglia of sympathetic system; *s*, retractor muscles of channel of mouth.

## PLATE XII.

Fig. 1. General view of viscera partially separated, arterial system injected, *D. tuberculata*. *a*, buccal mass; *b*, muscles for retracting channel of mouth; *c*, oesophagus; *d*, salivary glands; *e*, stomach; *f*, pancreas; *g*, hepatic duct; *h*, liver; *i, i*, intestine; *j*, anus; *k*, renal orifice, with a bristle passed through into renal cavity; *l*, renal organ having the hepatic arteries imbedded in its superior wall; *m*, portal heart, partially contained within renal organ; *n*, apex of ventricle, the heart having been removed; *o*, re-

tracted penis; *p, p*, mucus-gland in connection with female channel; *q*, spermatheca; *r*, vagina leading from external orifice to same; *s*, accessory spermatheca; *t*, supra-oesophageal ganglia giving off numerous nerves; *u*, gland-like body connected with vascular system.

Fig. 2. Alimentary system of *D. Johnstoni*. *a*, buccal mass; *b*, retractor muscles of channel of mouth; *c, c*, salivary glands; *d*, dilated portion of oesophagus; *e*, true stomach; *f*, intestine; *g*, liver.

Fig. 3. Portion of alimentary system, *D. verrucosa*. *a*, oesophagus; *b*, stomach; *c*, pancreas; *d*, hepatic duct; *e*, intestine; *f*, liver.

Fig. 4. Alimentary system, *D. pilosa*. *a*, channel of mouth; *b*, anterior or gizzard-like portion of buccal mass; *c*, crop at commencement of oesophagus; *e*, dilated portion of oesophagus; *f*, true stomach laid open, exposing on its interior surface the orifices of the hepatic duct; *g*, pancreas; *h, h*, intestine; *i*, anus; *k*, liver.

Fig. 5. Alimentary system, &c., *D. bilamellata*, exhibiting renal organ laid open. *a*, channel of mouth; *b*, buccal mass; *c*, gizzard, opening into same; *d*, salivary gland; *e*, tubular portion of tongue; *f*, dilated portion of oesophagus; *g*, liver; *h, h*, intestine; *i*, pancreas; *j*, anus; *k*, small orifice leading into renal cavity, a bristle is passed through this orifice into cavity; *l, l*, wall of renal organ laid open longitudinally, exhibiting a minute network of aortic twigs anastomosing with other branches from the portal trunk; *m*, ventricle; *n*, auricle; *o*, portal heart; *p*, portion of the floor of pericardium attached to same.

Fig. 6. Tongue of *D. pilosa* removed from muscular support. *a*, anterior or exposed portion; *b*, tubular portion.

Fig. 7. Portion of same more highly magnified.

Fig. 8. Central portion of two rows of spines from tongue of *D. tuberculata*.

Fig. 9. One of the spines from same tongue more highly magnified.

Fig. 10. Outer portion of a row of spines from tongue of *D. Johnstoni*.

Fig. 11. Central portion of two rows of spines from tongue of *D. repanda*. *a*, central, *b*, lateral spines.

Fig. 12. An outer spine of same.

Fig. 13. A spine next median line of same.

Fig. 14. Two spines from tongue of *D. aspera*.

### PLATE XIII.

Fig. 1. Side view of buccal mass, *D. tuberculata*. *a*, channel of mouth; *b*, buccal mass; *c*, oesophagus; *d*, lingual sac; *e, e*, salivary glands; *f, f*, muscles for retraction of channel of mouth; *g, g*, muscles for retraction of buccal mass; *g'*, belt to which these are attached; *h*, muscles for advancing buccal mass.

- Fig. 2. Buccal mass, *D. tuberculata*, laid open above. *a*, channel leading to mouth; *b*, exterior orifice; *c*, outer lip; *d*, inner lip; *e*, buccal lip; *f, f*, walls of buccal cavity; *g*, muscular support of tongue; *h*, tongue; *i*, fleshy septum passing down tubular portion of tongue, and supporting in front a membrane which divides anterior from posterior portion of lingual organ; *j*, œsophagus; *k, k*, retractor muscles of channel of mouth; *l, l*, retractor muscles of buccal mass.
- Fig. 3. Tongue of *D. tuberculata*, removed from its fleshy support. *a*, anterior exposed portion; *b*, posterior tubular portion with edges separated; *c*, membranous septum dividing the two portions; *d*, portion of mucous membrane of mouth.
- Fig. 4. Upper view of muscular apparatus of tongue. *a*, buccal lip, exhibiting circular and transverse muscles; *b*, œsophagus; *c*, lingual sac; *d, d*, exposed portion of firm central nucleus; *e, e*, radiating and circular muscles for moving the tongue; *f*, channel in continuity with lingual sac; *g*, fleshy septum passing down tubular portion of tongue; *h, h*, upper bundle of muscles; *i*, lower ditto for advancing and rotating muscular support of tongue.
- Fig. 5. Side view of muscular apparatus of tongue. *a*, buccal lip, composed principally of circular fibres; *b*, lingual sac; *c*, exposed portion of the firm central nucleus; *d*, radiating muscles for the eversion and retraction of the spinous membrane; *e*, circular muscle to assist in this action; *f*, upper muscles for advance of fleshy support of tongue; *g*, middle ditto to assist in this action; *h*, lower ditto, likewise for the same purpose.
- Fig. 6. Upper view of fleshy support of tongue, the upper part of one side being removed. *a*, channel through which tubular portion of tongue passes; *b*, fleshy septum passing to bottom of lingual sac; *c*, lingual sac; *d*, radiating muscles cut through; *e*, central nucleus; *f* and *g*, upper and middle bundles of muscles for advancing lingual support.
- Fig. 7. Cavity of buccal mass, *D. pilosa*, exposed from above. *a*, channel of mouth; *b*, outer lip; *c*, inner lip; *d*, wrinkling of mucous membrane; *e*, buccal lip; *f, f*, the two lateral portions of spinous collar with the rudimentary jaws between them; *g*, anterior gizzard-like portion of the buccal mass; *h*, œsophagus; *i*, crop at origin of same; *j*, tongue, resting on fleshy support; *k*, lingual sac.
- Fig. 8. Front view of spinous prehensile collar of *D. pilosa*, channel of mouth having been removed. *a, a*, buccal lip; *b*, prehensile collar; *c*, front portion of corneous jaws; *d*, membrane extending from same along margin of prehensile collar; *e, e*, portion of mucous membrane lining channel of mouth.
- Fig. 9. Portion of prehensile collar more highly magnified, showing the arrangement of spines.



Fig. 10. Group of spines from same, still more highly magnified.

Fig. 11. Two of same spines, yet more highly enlarged.

Fig. 12. Corneous jaws removed from buccal lip. *a*, anterior, free, exposed points; *b*, extremity buried in buccal lip.

Fig. 13. Stomach and hepatic duct of *D. tuberculata* laid open. *a*, stomach; *b*, œsophagus; *c*, pancreas; *d*, liver; *e*, great biliary duct laid open exposing numerous orifices leading into it from the liver; *f*, cardiac orifice; *g*, opening of pancreatic duct.

#### PLATE XIV.

Fig. 1. Lingual sac of *D. tuberculata* projecting from buccal mass behind. *a*, posterior extremity of same; *b*, line of section *b*; *c*, line of section *c*.

Fig. 2. Section *b* of lingual sac, explanatory of growth of spines. *a*, fleshy septum extending the whole length of tubular portion of tongue; *b*, membrane of sac; *c*, membrane supporting the spines; *d*, inner or lining membrane; *e*, the spines lying between the two last membranes and imbedded in a soft flocculent matter; *f*, point where septum joins bottom of sac; *g*, vacant space between lining membrane of tongue and fleshy septum.

Fig. 3. Section *c* of lingual sac. *a*, fleshy septum; *b*, muscles of buccal mass; *c*, membrane of sac; *d*, dentigerous membrane; *e*, teeth or spines; *f*, lining membrane; *g*, space between lining membrane and septum.

Fig. 4. A portion of membrane from root of renal organ, *D. pilosa*, exhibiting injected a fine arterial plexus.

Fig. 5. Inner surface of a portion of same membrane of renal organ, *D. repanda*, considerably magnified, exhibiting the tracks of the arterial branches thickly covered with a glandular substance.

Fig. 6. Portion of same membrane more highly magnified, showing the structure of the glandular substance, which is extended over it as well as over the vessels.

Fig. 7. Generative organs of *D. tuberculata* spread out to show the connection of the parts. *a*, inner sac of penis leading to external orifice; *b*, retracted penis; *c*, fine tube passing from testis to extremity of intromittent organ; *d*, testis; *e*, ovary spread over liver; *f*, oviduct; *g*, dilated portion of same; *h*, point where it is united to testis; *i*, point of its union with duct from spermatheca; *j*, female channel leading to external opening; *k*, opaque portion of mucus-gland; *l*, semipellucid portion of same; *m*, vagina leading from external orifice to spermatheca; *n*, duct from spermatheca to oviduct; *p*, accessory spermatheca connected to duct of spermatheca.

Fig. 8. Generative organs, *D. bilamellata*. *a*, retracted intromittent organ; *b*, testis; *c*, oviduct as it leaves ovary; *d*, dilated portion of oviduct; *e*, contracted

portion of same at the point where it receives duct from testis; *f*, opaque portion of mucus-gland connected with female channel; *g*, semipellucid portion of same gland; *h*, female channel leading to external orifice; *i*, vagina leading from external orifice to spermatheca; *j*, spermatheca; *k*, duct from the same, which after passing into the mucus-gland, is joined to oviduct.

Fig. 9. Generative organs, *D. Johnstoni*. *a*, testis; *b*, vas deferens; *c*, retracted penis; *d*, oviduct as it leaves ovary; *e*, dilated portion of oviduct; *f*, point where it receives duct from spermatheca; *g*, opaque portion of mucus-gland; *h*, semipellucid portion of same; *i*, female channel leading to external orifice; *j*, vagina leading from external orifice to spermatheca; *k*, spermatheca; *l*, duct from the same; *m*, accessory spermatheca connected with ditto.

Fig. 10. Generative organs, partially exserted, *D. Johnstoni*. *a*, lip of common orifice; *b*, male intromittent organ; *c*, orifice leading to female parts; *d*, vaginal orifice leading to spermatheca; *e*, large penis-like organ furnished with a stiletto; *f*, sac containing stiletto.

#### PLATE XV.

Fig. 1. Stiletto in its pouch, *D. Johnstoni*, seen in the compressor. *a*, portion of penis-like organ with which the pouch is connected; *b*, outer pouch of stiletto; *c*, inner pouch of same; *d*, stiletto; *e*, sheath of same; *f*, duct leading to large glandular sac in connection with stiletto.

Fig. 2. Extremity of penis-like organ with stiletto partially exserted. *a*, apex of penis-like organ; *b*, stiletto; *c*, *c*, sheath of same.

Fig. 3. Generative organs, *D. coccinea*. *a*, testis; *b*, vas deferens; *c*, retracted penis; *d*, oviduct as it leaves ovary; *e*, dilated portion of same; *f*, contracted portion of same where it is united to testis; *g*, point at which it is united to duct of spermatheca; *h*, opaque part of mucus-gland; *i*, semipellucid part of same; *j*, female channel leading to external orifice; *k*, vagina; *l*, spermatheca; *m*, duct from same; *n*, accessory spermatheca.

Fig. 4. Generative organs, *D. tuberculata*, VERANY. *a*, compact portion of testis; *b*, tubular portion of same; *c*, vas deferens; *d*, retracted penis; *e*, dilated portion of oviduct; *f*, the point of its union with duct from compact portion of testis, and near to which it likewise receives duct from androgynous organs; *g*, opaque portion of mucus-gland; *h*, semipellucid portion of same; *i*, female channel leading to external orifice; *j*, vagina leading from exterior to spermatheca; *l*; *m*, duct from spermatheca; *n*, accessory spermatheca.

Fig. 5. Generative organs, *D. repanda*. *a*, testis; *b*, vas deferens; *c*, retracted penis; *d*, oviduct as it leaves ovary; *e*, dilated portion of same; *f*, contracted

portion where it receives duct from testis; *g*, point where it receives duct from androgynous apparatus; *h*, opaque part of mucus-gland; *i*, semipellucid portion of same; *j*, female channel leading to external opening; *k*, vagina leading to spermatheca *l*; *m*, duct from same to accessory spermatheca *n*; *o*, duct from accessory spermatheca to oviduct.

Fig. 6. Supposed immature spermatophora from testis of *D. tuberculata*.

Fig. 7. Two spermatophora from spermatheca. *a*, one almost filled with irregularly-shaped cells; *b*, another in which the cells have nearly all disappeared, containing innumerable spermatozoa.

Fig. 8. Mature spermatozoa from spermatheca.

### PLATE XVI.

Fig. 1. Side view of contracted heart of *D. pilosa*. *a*, ventricle; *b*, auricle; *c*, upper or dorsal wall of pericardium; *d*, floor of same; *e*, aorta; *f*, branchio-cardiac or efferent branchial vein; *g*, portal heart.

Fig. 2. Upper view of heart inflated, *D. tuberculata*, the pericardium laid open, with diagram of branchial circulation appended. *a*, ventricle; *b*, auricle; *c, c*, walls of pericardium; *d*, aorta; *e, e*, two lateral veins coming from skin to auricle; *f*, branchio-cardiac or efferent branchial vein; *g*, outer or efferent circle, venous; *h*, inner or afferent circle, arterial, at root of branchiæ, within which latter circle are situated the anal and the renal orifices; *i*, vessel passing from liver to branchiæ; *j*, great efferent vessel from a branchial plume; *k*, afferent ditto; *l*, anal orifice; *m*, renal ditto.

Fig. 3. Portal heart laid open, *D. pilosa*, showing pectinated laminæ placed round the orifice leading to pericardium. *a*, lip of this orifice.

Fig. 4. Side view of a pectinated lamina.

Fig. 5. View of orifice leading into portal heart from pericardium, showing the inner margin beset with ends of pectinated laminæ.

Fig. 6. Side view of stem of branchial plume, *D. pilosa*. *a*, afferent branchial vessel; *b*, efferent ditto; *c*, peculiar apparatus for the purpose of giving elasticity to breathing organ; *d* and *e*, branchial leaflets. The arrows show the course of the blood.

Fig. 7. Front view of portion of branchial plume showing its peculiar central apparatus, the vessels having been removed.

Fig. 8. Cerebral nervous system, *D. tuberculata*. *a, a*, cerebroid ganglia; *b, b*, branchial; *c, c*, pedial; *d*, olfactory; *e*, buccal; *f*, gastro-œsophageal. 1, olfactory nerves; 2, nerves supplying upper portion of channel of mouth and lip; 3, those to oral tentacles; 4 and 5, to the sides and lower portions of channel of mouth and lip; 6, optic nerves, each having at its origin a small ganglion; 7, auditory capsules, the nerves being invisible; 8 and 9, nerves

supplying anterior portions of mantle; 10, nerves to posterior portions of same, sending a branch of communication; 10', to branchial ganglia of the sympathetic system; 11 and 12, nerves to side of body; 13, 14 and 15, to foot; 16 and 17, nerves to buccal mass; 18, to tongue; 19, to salivary glands; 20, to top of œsophagus; 21, nerves passing down that tube and united to two large ganglia of sympathetic system of stomach; *g, h, i, j*, four nerves arising from visceral ganglion which is attached to lower surface of branchial; these go to be united with ganglia of the sympathetic system of the various organs; *k*, first or anterior collar; *l*, middle or second collar or commissure uniting the supra- and infra-œsophageal ganglia; *m*, the third or posterior or great œsophageal collar.

Fig. 9. Transparent capsule of supra-œsophageal ganglia, *D. tuberculata*, exhibiting from below the perforated septa dividing them. *a, a*, cerebroid ganglia; *b, b*, branchial; *c, c*, pedial; *d*, visceral; *e, e*, the extremities of the great œsophageal collar.

Fig. 10. Eye, *D. repanda*. *a*, optic ganglion; *b*, optic nerve; *c*, choroid; *d*, lens; *e*, cornea; *f*, general capsule.

Fig. 11. Auditory capsule, *D. aspera*. *a*, outer capsule; *b*, inner capsule containing numerous otolithes.

Fig. 12. Two otolithes highly magnified showing central nucleus.

## PLATE XVII.

Fig. 1. View of under surface of cerebral ganglia showing their connections with the sympathetic system, *D. tuberculata*. *a, a*, cerebroid; *b, b*, branchial; *c, c*, pedial; *d*, olfactory; *e*, buccal; *f*, gastro-œsophageal; *g'*, visceral; *g*, anterior or first nerve from visceral ganglion giving twigs to aorta, to ganglia at apex of ventricle, to pericardium, to portal heart, to renal plexus, and terminating in a ganglion of branchial plexus; *h*, second nerve from visceral ganglion terminating in principal ganglion of genital plexus; *i*, third nerve from visceral ganglion giving branches to a plexus on female generative organs, and ending in the chief ganglion of gastro-hepatic plexus; *j*, fourth or last nerve from visceral ganglion passing to lower portion of intestine, to which it gives branches, most probably, to the ganglia thereon, and terminates in a ganglion of branchial plexus; *k*, first or anterior collar of cerebral system; *l*, second or middle ditto; *m*, third or great œsophageal ditto; 18, lingual nerves; 19, nerves to salivary glands; 20, to upper portion of œsophagus; 21, nerves (par vagum) passing down œsophagus, united with the plexus thereon, and terminating in two of the principal ganglia of gastro-hepatic plexus; 22, nerves in connection with ganglia and nerves on buccal mass; *n*, minute ganglion

on aorta; *o*, ditto on a branch from same; *p*, two ganglia at apex of ventricle; *q*, branchial plexus connected by branches with nerve 10 from branchial ganglia; *r*, principal ganglion of genital plexus; *s*, plexus of female organs; *t*, principal ganglion of gastro-hepatic plexus; *u*, pyloric; *v*, renal; *w*, *w*, intestinal plexus;  $\alpha$ , retracted penis;  $\beta$ , testis;  $\gamma$ , mucus-gland;  $\delta$ , stomach;  $\epsilon$ , hepatic duct;  $\zeta$ , pancreas;  $\eta$ , œsophagus;  $\theta$ , intestine;  $\iota$ , anus.

- Fig. 2. Cerebral ganglia, *D. Johnstoni*, seen from above. *a*, cerebroid, supporting optic ganglia and auditory capsules; *b*, *b*, branchial ganglia; *c*, *c*, pedial; *d*, olfactory; *e*, buccal; *f*, gastro-œsophageal; 1, nerves to dorsal tentacles; 2 and 3, to lips and channel of mouth; 4, 5 and 6, to mantle; 7, 8 and 9, supply the foot; 10, 11 and 12, visceral nerves; 13, pass down œsophagus; 14, supply salivary glands; 15, nerves to top of œsophagus, 16, to tongue.
- Fig. 3. Under view of one side of cerebral ganglia, *D. Johnstoni*. *a*, cerebroid; *b*, branchial; *c*, pedial; *e*, visceral, giving off visceral nerves, 10, 11, 12.
- Fig. 4. Dorsal view of cerebral ganglia, *D. verrucosa*, giving off nerves in the usual manner. *a*, *a*, cerebroid; *b*, *b*, branchial; *c*, pedial; *d*, olfactory; *e*, buccal; *f*, gastro-œsophageal.
- Fig. 5. Pancreas laid open, *D. tuberculata*, to show transverse laminæ.
- Fig. 6. Dorsal view of cerebral ganglia, *D. bilamellata*. *a*, *a*, cerebroid; *b*, *b*, branchial; *c*, *c*, pedial; *d*, olfactory; *e*, buccal; *f*, gastro-œsophageal; *g*, optic; 1, 2, 3, visceral nerves.
- Fig. 7. Under view of same ganglia. *a*, *a*, cerebroid; *b*, *b*, branchial; *c*, *c*, pedial; *d*, olfactory; *e*, visceral, giving off three visceral nerves.
- Fig. 8. Dorsal view of cerebral ganglia, *D. pilosa*. *a*, *a*, cerebroid; *b*, *b*, branchial; *c*, *c*, pedial; 1, 2, visceral nerves.
- Fig. 9. Dorsal view of cerebral ganglia, *D. repanda*: these ganglia are arranged as in the last species; 1, 2, visceral nerves; 2 exhibits a ganglionic swelling.

## PLATE XVIII.

- Fig. 1. View of cardiac or posterior portion of stomach, *D. tuberculata*, showing gastro-hepatic plexus, and collar or chain of ganglia of sympathetic nervous system. *a*, œsophagus; *b*, hepatic duct; *c*, pancreas; *d*, *d*, nerves of par vagum; *e*, third nerve (*i*) from visceral ganglion; *f*, *f*, great chain or collar of ganglia; *g*, principal ganglion of same; *h*, *h*, two of the principal nerves of gastric plexus connecting gastro-hepatic with pyloric plexus.
- Fig. 2. Pyloric extremity of stomach, and small portion of intestine displaying part of pyloric and intestinal plexuses of sympathetic system. *a*, *a*, pyloric plexus; *b*, commencement of intestinal ditto.

Fig. 3. Portion of œsophagus with network of nerves and ganglia of sympathetic system. *a, a*, the two nerves of par vagum. .

Fig. 4. Upper portion of intestine with intestinal sympathetic plexus.

Figs. 5, 6 and 7. Ganglia of sympathetic system from stomach highly magnified, demonstrating nerve-globules in relation with nerve-tubules. *a*, neurilemma containing tubules ; *b*, ganglionic enlargement containing nerve-globules.















