

VI.—The Anatomy of a New Species of *Bathydoris*, and the Affinities of the Genus: Scottish National Antarctic Expedition. By T. J. EVANS, M.A. (Oxon.), Lecturer in Zoology in the University of Sheffield. Communicated by Dr J. H. ASHWORTH.

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[Plates XVII. and XVIII.]

INTRODUCTORY.

The genus *Bathydoris* was created by BERGH in 1884 in his Report on the Nudibranch Mollusca collected by the *Challenger*. In his account of the anatomy of the new genus BERGH draws attention to the anomalous combination of characters possessed by the animal, and gives it an annectent position between the Dorids and the Tritonids, but places it among the Dorids on account of the predominance of Dorid features. The single specimen of *Bathydoris abyssorum* was dredged off New South Wales in 2425 fathoms. A second specimen of this peculiar genus was obtained by the Danish *Ingolf* Expedition and described by BERGH in 1900. This specimen came from 1870 fathoms in Davis Strait, and resembled *B. abyssorum*, with specific variations. Thus *Bathydoris* came to be regarded as an isolated genus with the characters of a connecting link, and appropriately a denizen of deep water. Our anatomical knowledge of the animal is derived almost entirely from BERGH's accounts of the two species mentioned, and is moderately extensive, considering the rather imperfect state of preservation of the material and the fact that he was dependent on single specimens in each case.

Two more specimens were brought from the Antarctic by the *Discovery* and described by Sir CHARLES ELIOT in the *Report of the National Antarctic Expedition* published by the Natural History Museum in 1907. These constituted separate species resembling BERGH's, but their state of preservation was such that ELIOT was able to add little to our knowledge of the anatomy of *Bathydoris*. The discovery of one of ELIOT's species in 100 fathoms dispels the idea that the genus is confined to the great depths.

A specifically distinct specimen was also taken by the German Antarctic Expedition, but THIELE, in the Report on the Mollusca recently published, confines himself to a superficial description in order to retain the rare animal intact as a museum specimen.

It would seem to be the fate of polar expeditions to bring back single specific specimens of this genus; for the species which forms the subject of the present memoir is based on one specimen dredged in 1410 fathoms by the *Scotia* in March 1904. When the zoological material of the Scottish National Antarctic Expedition

was distributed for identification, the animal went astray, and Sir CHARLES ELIOT, who received the Nudibranchs, comments with surprise on the complete absence of Dorids.

Dr BRUCE has provided the following notes on the haul in which the animal was included: "Locality, 71° 22' S., 16° 34' W. Bottom temperature, 31°·9 F. Surface temperature, 29°·9 F. Depth, 1410 fathoms. Bottom, blue mud." The haul included specimens of nearly every group of animals from sponges to fishes.

It is proposed to name the new species *Bathydoris brownii*, in honour of Dr R. N. RUDMOSE BROWN, naturalist to the expedition. To him and to Dr BRUCE the author's thanks are due for permission to undertake the investigation of its anatomy.

The six known species of *Bathydoris* may be tabulated as follows:—

1. *B. abyssorum*, Bergh. 2425 fathoms, off New South Wales. "Challenger."
2. *B. ingolfiana*, Bergh. 1870 fathoms, in Davis Strait. "Ingolf."
3. *B. hodgsoni*, Eliot. 100 fathoms, off Coulman Island. "Discovery."
4. *B. inflata*, Eliot. Depth not stated, off Coulman Island. "Discovery."
5. *B. clavigera*, Thiele. Depth not stated, Gauss Station. "Gauss."
6. *B. brownii*, sp. nov. 1410 fathoms, off Coats Land. "Scotia."

The specimen was preserved in about 5 per cent. formaldehyde, and suffered very little distortion or contraction. The viscera were also in excellent condition for dissection, and even the histological preservation was found to be remarkably good when certain tissues were cut and stained for identification.

EXTERNAL FEATURES.

The animal, as preserved, was 75 mm. long, 40 mm. broad, and 35 mm. in height. A thin, flabby foot margin extended about 8 mm. beyond the body all round and was rather bluntly pointed behind, while anteriorly its thickened edge ran transversely across the body behind the head, and had a deep glandular furrow extending into the lateral margin for some distance. The contraction of the foot when the animal was killed probably accounts for the distension of the dorsal integument and the extruded condition of the genital organs, which were forced out to the extent usual among Dorids during copulation. The mouth lies entirely on the ventral aspect, and is surrounded by crinkled lips surmounted by a bulging forehead, which extends laterally into rather long cylindrical oral tentacles. Nearly a third of the length of the ventral surface is occupied by the buccal region, the enormous size of which is a striking feature of the genus. The arched dorsal surface is covered by an integument which is delimited all round the body by a slight fringe at a distance of 4 or 5 mm. from the foot. Laterally this fringe or reduced mantle edge is represented by little more than a linear thickening of the skin. The dorsal integument is thin, transparent, and destitute of spicules, but, as in *hodgsoni*, *inflata*, and *clavigera*, the whole surface seems to have been originally studded with papillæ. Those that remain on exposed parts

of the back are smallest; while round the dorsal tentacles and along the notæal margin they are much larger. They seem to be more numerous in *brownii* than in any of the other three species possessing them. They are undoubtedly caducous, and, as recorded by ELIOT, the points of attachment of detached papillæ are marked on bare places by small circles with a spot in the centre. The only other conspicuous features of the dorsal surface are the dorsal tentacles and the anal complex, consisting of the anus, the renal pore, and the branchiæ. The rhinophores are club-shaped and perfoliated all round. There is no trace of a pocket. The branchiæ are two in number, and are placed symmetrically in front of the prominent anal papilla. Both numerically and structurally the branchiæ appear to differ very considerably from those of all the other species of *Bathydoris*. Thus, *B. abyssorum* has five and *ingolfiana* ten arranged in a circle in front of the anus, while ELIOT's species have eight and five or six respectively similarly arranged. The two tufts in *B. brownii* are united by a ridge which, on dissection, is found to contain the afferent and efferent vessels of the branchiæ. As the structure of the gills will be described later, it is sufficient here to mention that they are not fine dendritic structures like the gill-plumes represented by BERGH. The anal papilla is much shorter than in the other species, but this is probably due to the relatively greater local distension of the hinder end of the specimen. The renal papilla is inconspicuous, and lies in the median line between the anus and the base of the gills.

The extruded genitalia stand out conspicuously on the right side between the notæal margin and the foot, and are thrown further back than in the Dorids by the great size of the buccal region.

ANATOMICAL DESCRIPTION.

The importance of *Bathydoris* in any discussion of the interrelationships and classification of the Nudibranchs was recognised by both BERGH and ELIOT, and, during the examination of the anatomical structure of the present species, this importance became increasingly impressive as system after system was considered. This was deemed to justify a more complete and detailed account of the anatomy than has hitherto been given, especially as facilities for such an account were amply provided in virtue of the excellent preservation of the specimen. In the course of this memoir it will be noted that the description disagrees with those of BERGH and ELIOT on matters the bearings of which are of great theoretical interest. These contradictions are sometimes so striking that the inclusion of the species in the genus *Bathydoris* seemed jeopardised. The points of agreement, however, form such convincing evidence of generic identity that the serious divergencies here given must be regarded as corrections, based on examination of a more favourable specimen, of observations partially frustrated by the poor condition of the material observed by previous workers.

The various systems will now be considered in order.

THE ALIMENTARY SYSTEM.

It will be seen in fig. 2 that the general plan of the alimentary system of *Bathydoris* resembles that of the typical Dorid, but a detailed examination shows that there are very important differences. The great size of the buccal mass (*b.m.*) was emphasised by BERGH as a characteristic feature of the genus. Indeed, BERGH claimed its supposed relationship with the Tritonids solely on the character of the buccal mass and the radula. The mouth is surrounded by two sets of lips, an outer and an inner. The outer lips are crinkled and fleshy, and leave a wide gape into which the inner lips project. These are merely the thickened rim of the outer integument limiting the buccal opening. The inner lips (*p.m.*, figs. 2 and 3) are a pair of lateral pads enclosing a relatively small opening leading into the buccal cavity. The pads have the consistency and appearance of hyaline cartilage. Histological examination shows that the hyaline substance is a cuticular secretion which is continued in varying thickness as a lining of the alimentary tube from the buccal rim to the stomach. The underlying epithelium consists throughout of tall slender columnar cells, and corresponding columns of the secreted matter are faintly visible in the cuticle.

The buccal cavity contains a pair of dark-brown horny jaws (*J.*, fig. 3) supported on muscular pads (*P.J.*, fig. 3) which separate them from the globular odontophore (*o.*) occupying the middle of the floor. The free edges of the jaws are quite blunt, and each is produced into a slight beak opposite the mouth; so that they are probably used as a prehensile organ. The mouth must be capable of far more extension than might be supposed from its preserved state in order to bring the jaws into action. The radula (*R.*) is narrow in front and broad behind where it enters the radula sac, and the sac is entirely contained in the substance of the odontophoral mass. The first row of teeth has three teeth on either side of the rhachidian tooth and the radula broadens to 90. 1. 90, the formula of the youngest row. The total number of rows is about 50. The rhachidian tooth (*Rh.*, fig. 4) has a broad base on which stands a backwardly directed cusp. The laterals (*L.¹* to *L.^v*) are formed on the same plan, but the cusp bends from the base towards the middle line. The first four laterals differ from the rest in having shorter and blunter cusps. Unlike those of the other species, the extreme laterals show little sign of reduction. The teeth are firmly fixed in the specially thick cuticular covering of the radula mass, which is itself bilobed with a deep median depression. The direction of the cusps and of the underlying muscles suggests that the radula is used for gripping the food during trituration. The approximation of the cusps of the first laterals thus entailed would also explain the broken and irregular appearance of the rhachidian cusps as well as the reduction in length of the cusps of the first few laterals. Comparison with the figures published by BERGH and ELIOT shows that the present species can be identified by its radula alone.

The œsophagus (*œ.* and *cr.*, fig. 2) seems to differ from that of the other species in that it turns to the left, even at its origin from the buccal mass. It is a broad, sigmoid

tube with muscular walls lined, as already mentioned, by a thick cuticle. At its lower end it ends in a thin-walled sac, the stomach (*st.*, fig. 5), lying below the liver, and partially imbedded in its substance. The lining of the œsophagus is, throughout its length, thrown into twelve raised longitudinal bands (*b.o.*, fig. 5) which are covered with minute, blunt, brown cones of various sizes. As shown in fig. 6, the cones are partly imbedded in the cuticle of which they are specially resistant local modifications. The dark tint of the cuticle of the first half of the œsophagus and the extensive crinkling of its walls obscured the presence in it of the longitudinal bands which were only seen after clearing. ELIOT, who describes the denticulate bands in the second half of the œsophagus, may have overlooked them in the first half for the same reason. The same writer, in his account of *B. hodgsoni*, names the two regions of the œsophagus the first and second stomach—names which seem inappropriate for a thickly cuticularised tube which serves merely for the delivery of the food to the sac in which it is actually digested. The denticulate cuticle would, moreover, be quite ineffectual for the purpose of mastication, and probably serves as a protective layer against the coarse diet of mud, sponge, and small shells. The thin-walled stomach stands at the junction of œsophagus, intestine (*int.*, fig. 5), and main liver ducts (*l.t.*) into the expanded ends of which the food enters for some distance, as in Dorids generally. At its junction with the œsophagus the stomach has a small pocket (*s.r.*) like that of the Dorids, which was not seen in any of the other species. Its function is not known, though such inapplicable names as “pancreas” and “gall-bladder” have been applied to it by different authors.

It may be mentioned that the similar stomach recess in *Doris tuberculata* secretes a glassy, refringent substance which is also found as a granular deposit on the mucosa of the intestine and on the massed *Halichondria* spicules passing down that tube. This suggests a protective function for the organ, its secretion acting as a lubricant for the passage of spiculose excrement down the intestine. The liver (*l.*, figs. 2 and 5) is a bulky organ which is not invaded by gonad or kidney, and is unlobed except in so far as the intestine and the lower end of the œsophagus lie in furrows on its surface. The intestine is a rather broad, smooth tube making an arc round the pericardium and ending by a sphinctered opening on the anal papilla.

The alimentary tract contained one large piece of undigested sponge, and sponge spicules were present in all parts of the stomach and intestine. There were also found much mud, bits of old shells, small pebbles, and the spines of Echinids. The animal is therefore probably an omnivorous feeder, though the prevalence of sponge suggests that it has predilections for that group, like the Dorids.

The salivary glands (*s.g.*, fig. 2) are flocculent and voluminous, forming a mass on each side pressed against the wall of the œsophagus, and opening by stout ducts on the hinder wall of the buccal cavity. BERGH and ELIOT mistook them for the blood glands, but their histological structure puts their salivary nature beyond doubt. Moreover, the true blood glands were found elsewhere.

THE NERVOUS SYSTEM. (Fig. 7.)

The brain of *Bathydoris* broadly resembles that of the Dorids, but with much less concentration of the ganglia. It lies on the top of the buccal bulb, the cerebral, pleural, and pedal pairs being quite separate, but lying close together. As fig. 7 shows, the ganglia are asymmetrical in shape and disposition. Each cerebral ganglion (*c.g.*) gives off four nerves from its anterior edge which go to the lips and oral tentacles, dividing as they go into a number of smaller nerves. The last bifurcations have small ganglionic swellings at the point of division, as in some Tectibranchs. On the posterior edge of the dorsal surface of the cerebral ganglion stands a small, almost sessile, proximal rhinophoral ganglion (*p.rh.g.*) which sends a stout nerve (*rh.n.*) to the dorsal tentacle. A distal rhinophoral ganglion swelling (not shown) marks the point of subdivision of the rhinophoral nerve as it enters the tentacle. No sub-cerebral commissure was found, so that the cerebrals are connected together below the alimentary tube by the stomato-gastric loop (*s.g.l.*) only. The pedal ganglia (*ped.g.*) are connected by a stout pedal (*ped.com.*) and a slender parapedal commissure (*p.ped.com.*). In the notch between the pleural and pedal ganglia of the right side is placed a small genital ganglion (*gen.g.*) which is broadly united to the pedal and connected with the pleural by a band of fibres from its lower aspect. From it four nerves go to the genitalia, both male and female, over the surface of which they distribute themselves with a number of local ganglionations on their courses.

The pleural ganglia (*pl.g.*) give off two main lateral nerves on each side which supply the whole of the dorsal integument, with the exception of the anterior region which receives a number of very fine nerves from the pleurals not shown in the figure. The longer pair of pleural nerves pass back to the anal region, where they anastomose with each other and with a visceral nerve (*br.n.*) from the under surface of the right pleural ganglion. From the ganglia on this plexus the gills are supplied as in *Doris tuberculata*. The visceral ganglion, so obvious on the under side of the right pleural ganglion of *Doris*, is not represented as a discrete mass in *Bathydoris*. The visceral ganglion of *Doris* would appear to include the visceral centres as well as the penial centre usually associated with the pedal. In *Bathydoris*, however, the genital centres of the visceral seem to be segregated from the rest and to be associated with the penial centre on the pedal to form a special genital ganglion. The long, finely ganglionated visceral loop (*v.l.*, *v.l'*) about the middle of its course sends backwards the chief visceral nerve (*v.n.*), which, after giving a branch to the gastro-oesophageal anastomosis on the stomach and liver, continues its course as the reno-cardiac. Two delicate nerves from the pleuro-pedal angle (see diagram) supply the branches of the aorta. The stomato-gastric ganglia (*st.g.g.*) are relatively very large, but their size is not surprising when we remember the dimensions and muscular complexity of the buccal mechanism which they innervate. The inequality in length of the two cerebro-buccal connectives is probably the result of the sharp sinistral bend of the oesophagus. There are no separate

gastro-oesophageal ganglia, and the paired gastro-oesophageal nerves (*g.o.n.*) arise directly from the stomato-gastric ganglia. The paired nerves pass back in the connective-tissue investment of the oesophagus to the stomach, where they form a joint ganglionated anastomosis with the gastric branch of the visceral, as already described. From this plexus the stomach and liver receive their innervation, while the salivary glands are supplied from the gastro-oesophageals on their way down the oesophagus.

This compound system of gastro-hepatic ganglia is paralleled in the Dorids, where it was described by ALDER and HANCOCK, while DREYER has lately shown that an analogous arrangement is present in Aeolids and Tritonids.

Like the other species examined anatomically, *B. brownii* showed no trace of organs of sight, and otocysts could not be found by careful surface examination. They were, however, found on staining and clearing and also in sections of the brain. They are two small sacs placed close to the pleuro-pedal connectives on their lower aspect and partially imbedded in the connective-tissue capsule that surrounds the brain. The author has found small otocysts similarly placed in some of the Polyceratidæ. Otocysts were not found in the species examined by BERGH and by ELIOT.

THE EXCRETORY SYSTEM. (Fig. 8.)

The kidney of *Bathydoris* is unusually well developed. This was also noted by ELIOT, who described two fern-like organs lying over the liver as well as the renal syrinx. ELIOT, however, misconceived the nature of the renal organ, since he took the paired, fern-like structures to represent the main portion of the kidney, whereas they are merely outgrowths of its floor or ventral wall in the posterior half. The whole renal organ is a huge sac extending from almost the extreme posterior end of the body to within a short distance of the head, but narrowing in front on account of pressure between the alimentary canal and the genital mass. Posteriorly, its delicate dorsal wall is overlain by the pericardium, to which it is connected by fibres. Elsewhere it bulges free except where it is pinched by the intestinal loop (*int.*). This dorsal wall is throughout non-glandular, except at two points—namely, at its extreme anterior corner (*b.g.'*) and at a place in front of the pericardium (*b.g. "*) where a diverticulum of it lies as a flap across the intestine. These two points will be further mentioned in connection with the vascular system, because the two phagocytic or blood glands lie here adherent to the wall of the kidney. The glandular part of the kidney is therefore almost entirely confined to its ventral wall and to those parts of it which are folded inwards into the renal cavity as the two fern-like structures seen by ELIOT. These, however, are not two but six in number, the posterior pair being more fern-like than the other two which lie on the surface of the gonad (*h.g.*). These glandular regions coincide with the areas of distribution of great branches of the aorta, and the narrow strip-like folds forming the two anterior pairs may easily be mistaken for the arterial trunks themselves, which actually lie within them below the renal wall. The vascular

supply of the kidney is therefore purely arterial, and all the renal arteries arise from an aortic bulb (*a.c.*) opening into the ventricle at the point *o.v.* in fig. 8, and continuing forwards as the cephalic artery (*c.art.*). The extensions of the renal arteries into the gonad are not shown in fig. 8. The blood delivered by the renal arteries—which, as we have seen, occupy the crests of the glandular folds—passes on into venous lacunæ which lie deeper in the substance of the folds, and open into a great median venous space, lying between the kidney and liver behind, and between the gonad and liver in front. Into this median venous space also passes the blood that has traversed the gonad and liver.

The main collecting reservoir of the kidney lies behind the gonad, and in its hinder wall is seen the opening into the renal duct which leads to the exterior. In it originates the reno-pericardial duct (*r.p.d.*), consisting of a median tube opening in front by a funnel into the renal chamber, and a renal syrx (*r.s.*) opening on the floor of the pericardium. The syrx is a bulbous structure with a wide lumen which is almost filled with delicate laminate ingrowths of the epithelial lining. Sections of the floor of the kidney show that the gland cells lying in connection with the renal arteries contain concretions, often of large size, which stain faintly with basic dyes. The concretions collect in big vacuoles, which finally burst and liberate the excreted contents. The foliations of the wall of the syrx are covered with cells of two kinds. The distal part of a lamina—namely, the free edge towards the middle of the lumen—is covered by ciliated cells only, the cilia being extremely long. The proximal part—namely, that nearer the wall of the syrx—is glandular, and the cells contain fine granules of a substance which takes acid dyes. These cells are continued on to the wall of the pericardium. The renal organ of *Bathydoris* and its vascular supply are thus Dorid in type, the reno-pericardial duct, especially, being almost identical in structure with its homologue in *Doris*. The association with the blood glands, non-functional though that may be, the absence of ramifications into underlying organs, and its forward extension into the head region are features not paralleled among true Dorids.

THE VASCULAR SYSTEM. (Figs. 9 and 10.)

In general, the vascular system of *Bathydoris* resembles that of the Dorids, but in several respects distinct affinities with the blood system of the Pleurobranchids are exhibited. It may be conveniently described under the following heads:—

(1) *The Heart.*

The most obvious feature of the heart and pericardium is their asymmetrical disposition, since the antero-posterior axis, unlike that of the true Dorids, lies at an angle to the long axis of the body. The pericardium is a spacious cavity lying posteriorly on the surface of the kidney, with the reno-pericardial opening in its extreme right-hand corner.

The asymmetry of position mentioned above is an insignificant matter compared with the structural asymmetry shown by the heart itself. The typical Dorid heart is roughly an isosceles triangle with three efferent ducts opening into its base, the efferent branchial in the middle and the two lateral integumental sinuses at the corners. The auricle of *Bathydoris*, on the contrary, receives but one efferent vessel, which enters it at the right-hand side, the efferent branchial vessel and the lateral sinuses being confluent outside the pericardium altogether, as in the Pleurobranchids. The left side of the auricle is fused for some distance with the pericardial wall, along which it sends a muscular wing. This asymmetry, as we shall see later, is only one of many pre-Dorid and ancestral opisthobranch features exhibited by *Bathydoris*.

(2) *The Arterial System.*

Although the arterial system possesses no striking feature, it is proposed to describe it somewhat fully, because no comprehensive account exists of the arterial system of any Dorid except HANCOCK and EMBLETON'S account of *Doris tuberculata* in their famous article in the *Philosophical Transactions of the Royal Society*. The ventricle (*v.*) is immediately followed by a large aortic bulb (*a.c.*) from which arise the renal arteries (see kidney), as well as vessels to the intestinal loop, the gonad and the periphery of the liver mass lying below. The aortic bulb is continued forwards as the main cephalic artery (*c.art.*) This gives off on the left the visceral artery (*v.art.*), running below the intestine and supplying the liver, stomach, and œsophagus. In fig. 9 the arterial trunks lying below the outlined viscera are dot-shaded. After giving off the genital arteries (*g.art.*) on the right, the cephalic artery bifurcates, one branch passing over the œsophagus to the left and the other below the buccal mass to the right. The left branch provides both salivary glands (*sal.g.*), the brain (*cer.art.*), and the buccal muscles of both sides, while the right branch goes direct into a spacious infra-pharyngeal lacuna (*lac.*), in which the left also ends. This lacuna was also found in *Doris tuberculata*. It should be noted that the cephalic artery forms a complete collar round the œsophagus and buccal bulb. From the central lacuna under the bulb arise a number of vessels. A median vessel passes straight up into the bulb (*buc.art.*); three run forward into the lips (*lab.art.*) and floor of the mouth, while a broad median vessel dips into the foot and bends backward in its substance, to continue throughout its length as a median pedal artery (*ped.art.*)

(3) *The General Hæmocœle.*

The irregular lacunar blood-space in which lie all the viscera is in *Bathydoris* nowhere spacious. It receives the blood that has passed through the tissues from the arteries, except the renal, gonadial, and hepatic blood, which is collected in another way already indicated in the description of the kidney. The hæmocœlic blood passes partly into the gills and partly into the dorsal integument, but the proportion of blood

that passes into the integument is much in excess of that in the Dorids. The thin skin, studded with papillæ, is conducive to this amplification of the tegumentary respiration in *Bathydoris*, while the thick, glandular, and spiculose skin of the Dorids has vitiated this system and necessitated the extension of the special gills. The dorsal wall of the hæmocœle is a membrane more or less bound to the underlying organs by conjunctive-tissue fibres. This membrane is separated from the dorsal integument by an empty space, but runs into it at the side of the body all round. Thus, when an incision is made through the dorsal body-wall, the space entered is not the hæmocœle, but this closed cavity between the body-wall and the dorsal wall of the hæmocœle. The same arrangement is present in the Dorids alone among Nudibranchs, though the shell-cavity of *Pleurobranchus* closely resembles the problematic dorsal cavity of the Dorids. Whatever be the nature of the cavity, HANCOCK and EMBLETON'S name—peritoneum—for its lining should not be perpetuated. The passage of blood from the underlying hæmocœle into the skin and its papillary outgrowths takes place below the level of the edge of the dorsal hæmocœlic wall all round. The blood that runs from the hæmocœle to the gills passes along two narrow conduits on the posterior aspect of the liver (*h.v.*, fig. 10). This must be regarded as of secondary importance in the afferent branchial system.

(4) *The Afferent Branchial System.* (Fig. 10.)

Blood enters the branchiæ from two sources: (*a*) from the hæmocœle by the small paired ducts (*h.v.*) already mentioned, and (*b*) from a great median venous space (*m.s.*) lying above the liver, which receives the blood from the kidney, liver, and gonad. Just before narrowing in order to enter the gills (*a.b.v.*), it receives the paired ducts from the hæmocœle (*a*). (See also the description of the kidney.) The afferent space at the base of the gills is not a circle, as in the Dorids, but a transverse expansion of the afferent vein from which ramifying tubes run up the branchiæ.

(5) *The Efferent Branchials.*

The afferent and efferent venules in the gill-leaflets form continuous loops from the afferent to the efferent side of a gill lobe, and the efferent veins from the two gills join together to form a transverse space at the base of the gills similar to the contiguous afferent space. This space is connected with the auricle by a tube (*e.b.v.*) running to the right and entering the auricle at its right-hand corner.

(6) *The Efferent Tegumentary System.*

The blood that enters the skin and its papillæ from the hæmocœle returns from all sides into a circular sinus (*c.s.*) running round the edge of the pericardium. The efferent tubules returning blood into the sinus were described by BERGH as renal tubules in *B. abyssorum*. The sinus opens behind into the efferent branchial vein just before

it reaches the right corner of the pericardium to empty itself into the auricle. The circular sinus is also represented in the Pleurobranchids, where it also opens into the efferent vessel, but takes a wider sweep round the body. In the Dorids it is represented by the two lateral sinuses, which there, however, enter the auricle separately and directly.

(7) *The Blood Glands.* (*b.g.'* and *b.g."* Figs. 8 and 9.)

The structures commonly called "blood glands" are characteristic of some Tectibranch families (Bullids and Pleurobranchids) and of the Dorids. They are lymphatic or phagocytic glands situated on the course of the cephalic artery and supplied by it. In the Dorids they lie in the head region near the brain, but in the Tectibranchs they are placed further back. In *Bathydoris* they form two separate masses united to the wall of the kidney. It is of some interest to note that in the Prosobranchs possessing them they are also associated with the kidney, so that in this, as in many other respects, *Bathydoris* presents features more primitive than the true Dorids, the equivalents of which are found among Tectibranchs rather than Nudibranchs. As already mentioned, BERGH and ELIOT confused the unusual salivary glands with the blood glands, the identity of which they did not recognise.

THE RESPIRATORY SYSTEM.

As already indicated in connection with the vascular system, the general pallial respiration is rendered more effective by the papillary outgrowths, and the blood so oxygenated returns into the circular sinus. The special respiratory organs or branchiæ are two tufts placed symmetrically on a transverse ridge in front of the anus. Each tuft stands on a broad base or stalk in such a way as to give the appearance of a roughly pinnate condition. The lobate units of the tuft resemble the pinnæ of the gill of *Pleurobranchæa*, being laminate on opposite faces of a wide rhachis, while the afferent and efferent vessels occupy its edges. The laminæ vary in size from mere ridges across the face of the rhachis to longish leaves which may themselves be provided with laminæ. In this way an irregular bipinnate condition is simulated. It will be seen that, by narrowing the rhachis so as to bring the ascending and descending vessels nearer together and regularising the pinnation, the Dorid plume would be produced. On the other hand, if the laminæ were equal in size and the tufts stretched along the ridge in a regular row, the sessile portion of a Pleurobranchid ctenidium would result. The gill of *Bathydoris brownii* would therefore appear to be in a condition intermediate between a typical Dorid rosette of plumes and a Tectibranch gill. There is, however, no indication of a circumanal circle either in the gill itself or in the underlying vessels, and though the tufts are provided with muscles capable of reducing their height, they cannot be retracted below the general level of the integument.

THE REPRODUCTIVE SYSTEM. (Fig. 12.)

No adequate description or figure of this system in a *Bathydoris* has hitherto been given, but both ELIOT and BERGH give a somewhat hesitating impression that it is constructed on the Dorid plan. Since the universal triality of known Dorids is one of their most striking characteristics, it is essential that on such a critical point our knowledge should be clear and definite.

The hermaphrodite gonad (*h.g.*) lies posteriorly below the kidney and above the liver within the arc made by the intestine. It is a yellowish, bi-convex lenticular body, truncated in front and with a minutely lobulated surface. The specimen was captured at the stage of male activity in the protandric cycle, since the male acini and ducts are full of sperms, while the eggs are small and lightly yolked. Its blood supply is an extension of the renal arterial system, branches from which pass through the lower wall of the kidney into its substance.

The common hermaphrodite duct (*c.h.d.*) leaves the gonad as a single slender tube. It is ampullated (*amp.*), as usual in Nudibranchs, but its extreme length escaped previous notice. After a short, slender portion beyond the ampulla, it divides into two tubes, the vas deferens (*v.d.*) and the oviduct (*o.d.*). The vas deferens is a comparatively short, coiled tube, expanded by the glands in its walls into a prostate for nearly the whole of its length. It enters the penis sac (*p.s.*) some distance from the end and runs a straight course to the tip of the everted penis imbedded in loose connective tissue and muscle fibres. The mode of extroversion of the penis, deducible from dissection of the everted organ, is represented in the section-diagrams (fig. 11, *a* and *b*), the dotted area representing loose fibrous tissue the perfusion of which with blood from the hæmocoel causes the extroversion. The penis is seen to be a partial introvert, since the end is retracted into the sac unchanged. This terminal portion (*p.*) presents a remarkable appearance on account of the sucker-like pits covering one side of it. It is possible that the pits, under control of the blood-pressure in the penis, really act as suckers on the smooth surface of the female atrial wall.

The oviduct soon enters the massive mucus-albumen gland complex (*m.g.* and *a.g.*), the structure of which could not be investigated on account of its stony hardness. The albumen gland could be recognised on the upper surface by its yellowish-brown colour and its granular consistency. The coils of the mucus gland end distally as the broad tube which opens into the female atrium. The atrium is turned out as in copulation: the first part of it has a highly crinkled surface, but inside this arise two leaf-like lips (*a.l.*), or folds of its surface, which between them enclose the entrance (*f.o.*) into the female channel. These valvular lips appear to be a characteristic feature of *Bathydoris*, because they are also partially shown in surface view in *B. clavigera* by THIELE. Within the valve on the posterior wall of the channel opens the vagina (*vg.*), which consists of a stout tube ending blindly in a globular recurved bursa copulatrix (*b.c.*).

There is no second sac on the course of the vagina, which is also the only connection between the bursa and the female channel. From this it follows that the hermaphrodite duct of *Bathydoris* divides but once—namely, into a male and a female duct. The Dorid duct bearing the so-called spermatocyst, and connecting the bursa with the region of fertilisation in the course of the oviduct, is totally unrepresented. In short, *Bathydoris brownii* is typically diaulic, like *Tritonia* and the Pleurobranchids.

Externally, the everted organs are surrounded by a rim representing the limit of the common genital vestibule of the male and female system.

SYNOPSIS OF SPECIFIC AND GENERIC CHARACTERS.

When we come to analyse the differences between the foregoing account and those of the two previous investigators of the genus, we encounter considerable difficulties in deciding which are specific differences and which may be put forward as corrections. To the latter category we may presume to relegate all differences in regard to which previous statements have been qualified or made with reservation.

The specific distinctness of *Bathydoris brownii* is undoubtedly more striking than that of any of the other recorded species, and, since the animal was mature, there can be no question of its being the young of any one of them. Among characters presumably not of generic rank which distinguish the species may be mentioned the following:—

- (1) The uniformity in size and shape of the lateral teeth of the radula.
- (2) The pitted pad on the glans penis.
- (3) The immediate sinistral bend of the œsophagus at its origin from the buccal mass and the unequal lengths of the cerebro-buccal connectives. The causal connection between these two features stamps them as true anatomical constants.
- (4) The two tufted gills placed on a transverse ridge symmetrically in front of the anus.

On the basis adopted above, it is likely that the following features in which the present account differs from those of BERGH and ELIOT may be regarded as of generic value:—

- (1) The diaulic of the reproductive system.
- (2) The circular canal embracing the pericardium and collecting blood from the dorsal integument.
- (3) The follicular nature and great size of the salivary glands.
- (4) The presence of two blood glands on the wall of the kidney (the structures described as such by BERGH and ELIOT turned out, on histological examination, to be the follicles of the salivary glands; the true blood glands were not seen by these authors).
- (5) The asymmetrical opening of the efferent vein into the auricle.
- (6) The great saccular kidney with its ventral wall thrown into folds.

- (7) The segregation of the genital elements of the visceral into a distinct ganglion on the surface of the brain.
- (8) The possession of a proximal and a distal rhinophorial ganglion.
- (9) The cuticularisation of the wall of the alimentary canal as far as the stomach (the horny cones imbedded in the cuticle were described by ELIOT for *B. hodgsoni*, but no armature was found by BERGH in *B. abyssorum* and *B. ingolfiana*; its systematic value cannot therefore be assigned).
- (10) The presence of a gastric cæcum.
- (11) The presence of small otocysts below the pleuro-pedal connective.

The genus may now be defined in the following terms, of which some are supplementary to BERGH's original definition:—

Body highly arched and elliptical in outline. The edge of the notæum slight or wanting. Dorsal papillæ present or absent. Rhinophores placed rather far back, non-retractile, perfoliated. Gills in front of the anal papilla, variable in number, non-retractile. Buccal mass very bulky. Radula sac not an appendage. Dental formula n. 1. n. Buccal cavity with a thick cuticle extending down the œsophagus. Powerful jaws present. Œsophagus may have horny cones. Liver massive and unlobed, not invaded by any other viscus. Salivary glands follicular, flattened, with a stout duct. Cerebral and pleural ganglia distinct. Stomatogastric loop very long. No gastro-œsophageal ganglia, but the long gastro-œsophageal loop arises from the buccals. Eyes absent. Kidney saccular with laminate ingrowths of its ventral wall. Branchial and pallial efferents join before entering the right side of the auricle. Penis unarmed and massive. Hermaphrodite gland a compact mass. Reproductive system diaulic.

THE AFFINITIES OF BATHYDORIS.

BERGH and ELIOT have invested *Bathydoris* with a certain importance as a type combining the features of the Dorids with certain Tritonid characters, with preponderating affinities to the Dorids. The Tritonid features accentuated by BERGH were the buccal apparatus and the unarmed penis, while ELIOT rightly passes over the latter resemblance unnoticed, since an armature of the penis may be present or absent among the species of some genera of Dorids. As to the buccal apparatus, even a superficial examination shows that, when reference has been made to the great size of the buccal muscles and the jaws, the sole resemblance has been stated in full. In *Tritonia* the odontophoral mass arises from the dorsal wall of the buccal cavity and bulges downwards, while in *Bathydoris* that organ arises from the floor of the buccal cavity and bulges upwards. The mandibles are also quite differently placed and used in the two animals, those of *Tritonia* having their long, finely serrulated cutting edges facing the floor of the mouth cavity below the radula mass, while the blunt beaks of the mandibles of *Bathydoris* jut into the mouth above the radula. Moreover, the œsophagus takes its origin on the hinder aspect of the globular buccal bulb of *Bathydoris*, while the

oesophagus of *Tritonia* rises out of the dorsal surface of the bulb and well forward, the main bulk of muscles being behind it. These and corresponding differences in the muscular mechanism suffice to make good the statement made above, that the supposed resemblances are confined to size and the presence of powerful jaws. It should be mentioned that BERGH refers specially to *Bornella* in assigning Tritonid features to *Bathydoris*; without discussing the problematic relationship of *Bornella* to the Tritonids, suffice it to state that the large buccal apparatus of that form differs from that of both *Tritonia* and *Bathydoris*.

It is indeed likely that these three cases of powerful and mandibulate mouth parts are examples of convergence in unrelated types. The only other reference to a non-Dorid affinity of *Bathydoris* is made by ELIOT when he compares the armature of the "stomach" with that found in *Bornella*. This comparison is strange, coming from an author who has since, in the Ray Society's monograph, separated the two genera in his first cleavage of the Nudibranchs. In any case the comparison is untenable, since the two armatures are totally unlike in structure and position, that of *Bornella* being situated in a region of the alimentary tube *posterior* to the point of entrance of the liver ducts. On the foregoing grounds we must regard the proposed Tritonid and Bornellid affinities of *Bathydoris* as inadmissible. It is, however, obvious that the investigation of this last species has brought out certain features of the genus which render necessary the reopening of the discussion of its affinities and, as we shall see later, those of the Dorids generally. It is no less certain that the genus presents a combination of characters far more significant than that considered by BERGH when he assigned its affinities—namely, a Dorid gill of a primitive form, an asymmetrical heart and efferent branchial system, blood glands placed far back on the course of the aorta, a thin integument with scattered branchiate outgrowths, a diaulic reproductive system, a liver distinct from the gonad and kidney, a brain with separate ganglia, a nerve collar embracing the buccal bulb and not the oesophagus, and finally, but perhaps least significant, a powerful buccal apparatus.

That *Bathydoris* must be definitely placed among doridiform animals follows from its possession of the following striking Dorid characteristics:—

(a) The collocation of the anus, renal pore, and gills in the median line posteriorly.

The gill is, however, more primitive than the typical rosette form common among Dorids, though primitive gills are also found in such types as *Trevelyana* and *Nembrotha*.

(b) With the exception of the buccal mass and the protected oesophagus, the alimentary canal is Dorid, even to the possession of a gastric cæcum, and those divergent features are adaptations to a coarser and more omnivorous diet. The enlargement of the salivary glands is probably due to the same cause.

(c) The kidney is a Dorid structure, the reno-pericardial tube and syrinx being practically identical with those of *Doris* as described by HANCOCK

and by HECHT. The absence of ramifications is, doubtless, a primitive character.

- (d) The blood system is built essentially on Dorid lines, but presents a greater number of primitive features than any other. Chief among them are the possession of but one auricular efferent opening, the union of the circular collecting canal of the integumental system with the efferent branchial, and the position of the blood glands. It is noteworthy that these primitive features are points of agreement with the Tectibranchs, especially the Pleurobranchids.
- (e) As to the reproductive system, its dialic condition makes it more primitive than that of any other known Dorid; but, apart from that very important divergence, it closely resembles that of *Doris*, since the separation of the gonad from the liver is found in a typical Dorid like *Alloiodoris*.
- (f) The nervous system, in spite of a close similarity to the Dorid type in most respects, differs from it in several important points. Of these, the length of the nerve collar and the position of the brain on the top of the buccal mass are paralleled in *Tritonia* and the Pleurobranchids, and should probably be regarded as primitive, while the distinctness of the ganglia of the brain and the absence of separate gastro-oesophageals, if primitive features, take us back to a condition earlier than that found in the Pleurobranchids and *Tritonia*. The fusion of the ganglia of the visceral loop with the pleurals is, on the other hand, a modern feature, as is the loss of eyes consequent on the adoption of a deep-water habitat.

We conclude, therefore, that *Bathydoris* is a highly primitive Dorid possessing some characters that adapt it to a specialised habitat and mode of life, while those that are primitive connect it with the Tectibranchs, particularly the Pleurobranchids among existing forms. The derivation of the Dorids from Pleurobranchid ancestors is, however, no new proposition. GUIART, for example, has recently advocated their union into one group, and PELSENEER has derived all Nudibranchs from the Pleurobranchids with *Tritonia* as an intermediate link.

BERGH's advocacy of a special relationship between *Bathydoris* and *Tritonia* on the evidence of the buccal apparatus has already been criticised. PELSENEER's position, however, takes a wider outlook, but takes no cognisance of *Bathydoris* at all. He bases his contention of the Tritonid origin of all Nudibranchs on the possession by *Tritonia*, in common with the Pleurobranchids, of a large number of primitive Nudibranch characters which are not found together in any other Nudibranchs. These are:—a frontal veil, formed by the fusion of the oral tentacles of the Pleurobranchid, a wide foot, a ventricle turned to the right, a broad radula, a nervous system placed on the buccal bulb, an oesophageal crop, extensive salivary glands, a saccular, unramified kidney, a long reno-pericardial tube, pericardial glands on the auricle, male and female openings in a common vestibule, and a lateral anus. Of these, it will be noticed that

Bathydoris possesses all except the lateral anus. Further, it retains oral tentacles in a condition more strongly reminiscent of those of *Pleurobranchæa* than that of the oral veil of *Tritonia*, while the separate ganglia of the brain and the separate gonad of *Bathydoris* can certainly not be regarded as new and derived features in that genus. Thus, excluding the case of the lateral anus, which will be considered separately, *Bathydoris*, which is essentially Dorid in construction, exhibits all the primitive features of *Tritonia*, some indeed being more primitive than the corresponding ones in *Tritonia*, the supposed ancestor. At this *reductio ad absurdum* we arrive by considering only those primitive features selected by PELSENEER, without calling in the evidence of the blood and respiratory systems wherein *Tritonia*, with its symmetrical auricle receiving blood from symmetrical lateral sinuses, appears very modern indeed. It is in the complete avoidance of any comparison between vascular and respiratory systems in *Tritonia* and Pleurobranchids that the weakness of the Tritonid theory of Nudibranch descent lies, and it is significant that on the characters of these very systems is primarily based any discussion of gastropod and even molluscan affinities. Previous application of this criterion in the Opisthobranchs has resulted in their cleavage into Tectibranchs with a ctenidial gill and Nudibranchs with pallial outgrowths of varied form and distribution replacing the lost ctenidium. Of these neomorphic gills the lateral tufts of *Tritonia* have been regarded as an early type, but it is not clear whether the Dorid circlet was derived from them by concentration or by local specialisation round a posterior anus or was evolved independently. Nor is it clear why modern writers on the Opisthobranchs have always accepted the neomorphic nature of the Dorid circlet. It is true that a comparison of the highly specialised, multipinnate plumes placed in a pit in the tuberculate dorsum of some Dorids provides no suggestion of homology with the ctenidium of a Tectibranch; but it is not such a comparison of extremes that evinces homologies. In *Bathydoris*, however, the gill is in two portions only, joined by a crinkled ridge, it shows but the beginnings of pinnation, its lobes have the broad laminae running from the afferent to the efferent side seen in the ctenidium of the Tectibranch, and there is no suggestion of the circumanal ring in either the gill or the underlying vessels. From this point of view the extreme similarity of the condition of the auricle, the efferent branchial vessel, and the circular sinus in *Bathydoris* and the Pleurobranchids acquires a special significance. Evidence derived from the nature of the innervation is perhaps of doubtful value; but, so far as it goes, it is favourable to the present contention, since the Dorid gill is jointly innervated from pleural and visceral centres, while other Nudibranch gills receive no visceral nerves unless invaded by ramifications of the liver. The dorsal position of the Dorid gill should present little difficulty, since the pallial edge of the Dorids is undoubtedly a new formation of mechanical value which progressively increases in width within the group and is absent in many genera. In any case, the same difficulty would apply to the anus and renal pore, and there is no proposal to class them as new formations in the Dorids. The separation into two or more parts also forms no objection to the ctenidial nature of the Dorid

gill, since it is a progressive process in the group and is incipient in many Tectibranchs, including *Aplysia*. Moreover, at least one Dorid, *Trevelyana crocea*, has a single undivided laminate gill indistinguishable from a ctenidium. Furthermore, the three residual units of the pallial complex—namely, the kidney and its pore, the intestine with the anus, and the gill—occupy in the Dorids just those relative positions which they would occupy had they been turned over from the Tectibranch position into the median dorsal line. Here one is inclined to ask what is the nature of the great cavity, cut off from the underlying hæmocœle, which lies under the dorsal integument of the Dorid, but is absent in all other Nudibranchs. An exactly similar cavity in *Pleurobranchus* or *Oscamius* contains a shell-remnant, and is the shell-cavity. In the absence of any information regarding the metamorphosis of the veliger of either Dorids or Pleurobranchids, it is difficult to find any satisfactory reason for contradicting the homology of these two spaces.

It is on the above grounds proposed to define the Dorids as ctenidiate Opisthobranchs that have retained the shell-cavity and in which the elements of the pallial complex have moved dorsally into the median line. In this position the ctenidium has undergone progressive modification within the group, the retractile circlet being its highest development.

In *Tritonia*, on the other hand, the residual members of the pallial complex have remained in a more anterior position than they occupy in many Tectibranchs, and in that position the old molluscan gill has been lost. Whereas in the Dorids and Pleurobranchids the connection of the auricle with lateral integumentary sinuses is supplementary to the ctenidial connection, in *Tritonia* it is the sole remaining connection of the auricle with respiratory sinuses. As a primitive actenidiate animal, however, *Tritonia* retains many common features with the Dorids and Pleurobranchids, its nearest ctenidiate relatives.

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EXPLANATION OF PLATES XVII. AND XVIII.

Bathydoris brownii.

- Fig. 1. The animal seen from the dorsal side, natural size.
- Fig. 2. General view of the alimentary system from above. *b.m.*, buccal mass; *cr.*, cesophageal crop; *int.*, intestine; *l.*, liver; *æ.*, cesophagus; *p.m.*, lateral pads of the inner lips; *s.g.*, salivary glands.
- Fig. 3. Buccal cavity laid open from above. *J.*, jaws; *o.*, odontophore; *æ.*, cesophagus; *P.J.*, pads of the jaw; *p.m.*, pads of inner lips; *R.*, radula.
- Fig. 4. Portion of a half-row of the radula. *L.ⁱ-L.^v*, lateral teeth 1 to 5; *Rh.*, rhachidian tooth.
- Fig. 5. Stomach and adjacent parts of the alimentary canal laid open; the cut is continued into the posterior lobe of the liver. *b.o.*, bands on the wall of the crop; *l.*, liver; *int.*, intestine; *l.t.*, liver ducts; *s.r.*, gastric cæcum; *st.*, stomach.
- Fig. 6. Section across an cesophageal band. *b.c.*, brown cones; *ct.*, cuticle; *ep.*, epithelial layer; *m.*, muscle layers.
- Fig. 7. Nervous system. *b.co.*, buccal commissure; *c.g.*, cerebral ganglion; *gen.g.*, genital ganglion; *g.o.n.*, gastro-cesophageal nerves; *ped.g.*, pedal ganglion; *ped.com.*, pedal commissure; *p.ped.com.*, parapedal commissure; *pl.g.*, pleural ganglion; *s.g.l.*, buccal loop; *st.g.g.*, stomato-gastric or buccal ganglion; *v.l.*, *v.l.ⁱ*, visceral loop; *v.n.*, visceral nerve.
- Fig. 8. Kidney with thin dorsal wall removed. *a.c.*, aortic bulb; *b.g.ⁱ*, *b.g.ⁱⁱ*, lobes of the kidney to which the blood glands are attached; *c.art.*, cephalic artery; *h.g.*, hermaphrodite gonad; *int.*, intestine; *o.v.*, opening of aortic swelling into the ventricle; *r.d.*, renal tube to exterior; *r.p.d.*, reno-pericardial duct; *r.s.*, renal syrinx.
- Fig. 9. Arterial system. *a.c.*, aortic bulb; *b.g.ⁱ*, *b.g.ⁱⁱ*, blood glands; *c.art.*, cephalic artery; *cer.art.*, cerebral artery; *buc.art.*, buccal artery; *g.art.*, genital artery; *lab.art.*, labial arteries; *lac.*, lacuna under buccal mass; *ped.art.*, pedal artery; *sal.g.*, salivary gland; *v.art.*, visceral artery.
- Fig. 10. Diagram of the afferent and efferent vessels. *a.b.v.*, afferent branchial vein; *aur.*, auricle; *c.s.*, circular sinus; *e.b.v.*, efferent branchial vein; *h.v.*, hæmocœlic vessels; *m.s.*, median sinus.
- Fig. 11, *a* and *b*. Diagram showing the relation of the penis to its sheath in the retracted and protruded condition.
- Fig. 12. General view of the reproductive system. *a.l.*, atrial lips; *a.g.*, albumen gland; *amp.*, ampulla; *b.c.*, bursa copulatrix; *c.h.d.*, common hermaphrodite duct; *f.o.*, female opening; *h.g.*, gonad; *m.g.*, mucus gland; *o.d.*, oviduct; *p.*, pitted pad on penis; *p.s.*, penis sac; *v.d.*, vas deferens; *vg.*, vagina.

EVANS: NEW SPECIES OF BATHYDORIS.

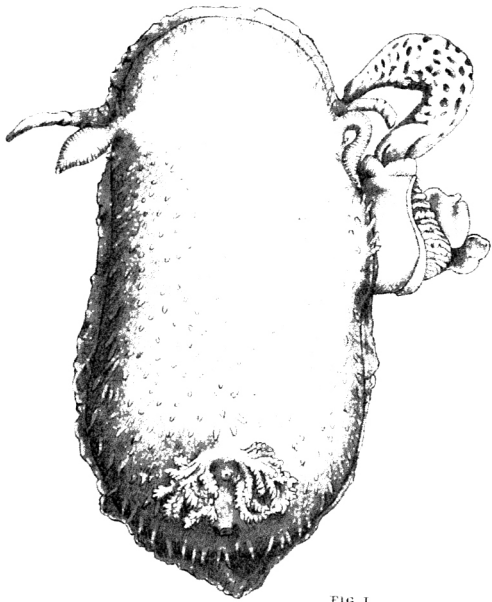


FIG. 1.

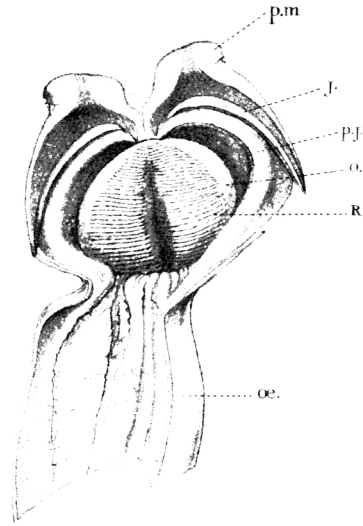


FIG. 3.

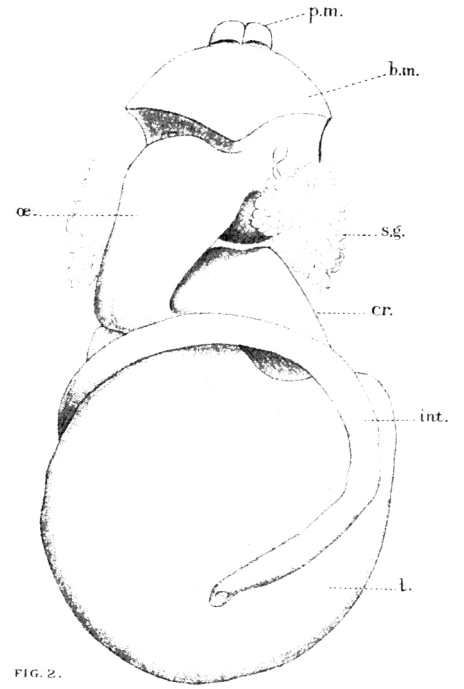


FIG. 2.

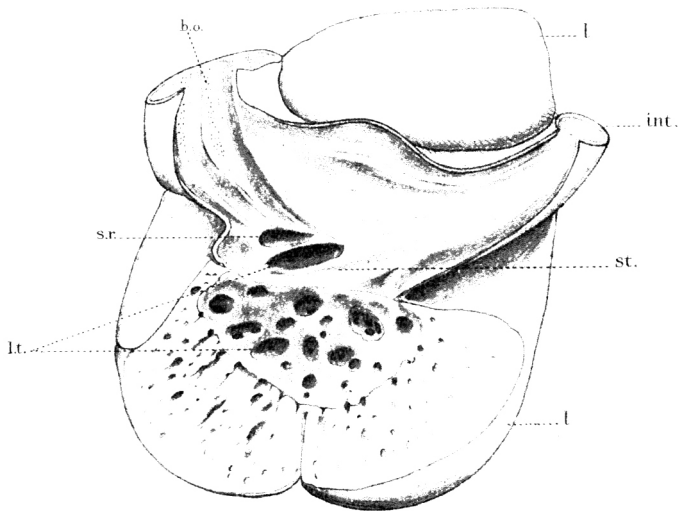


FIG. 5.

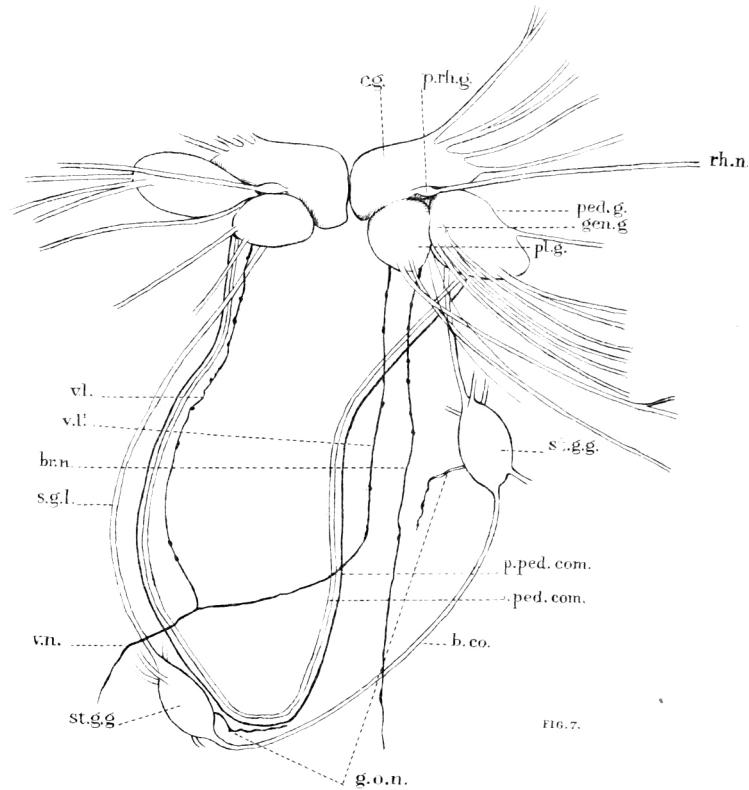


FIG. 7.

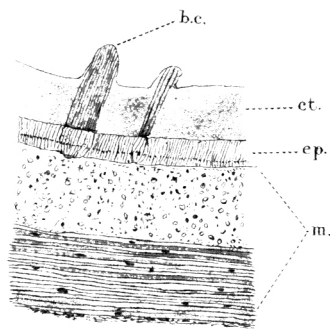


FIG. 6.

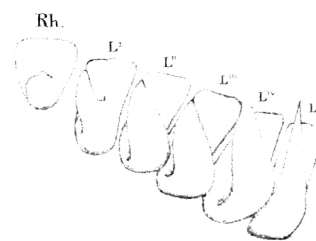


FIG. 4.

EVANS: NEW SPECIES OF BATHYDORIS.

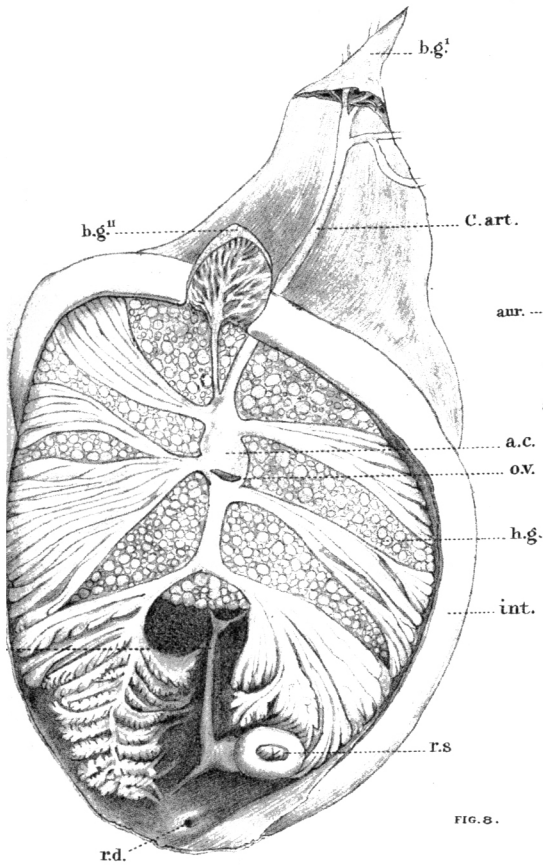


FIG. 8.

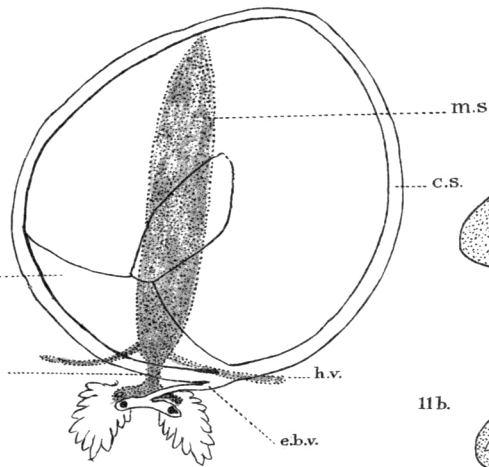


FIG. 10.

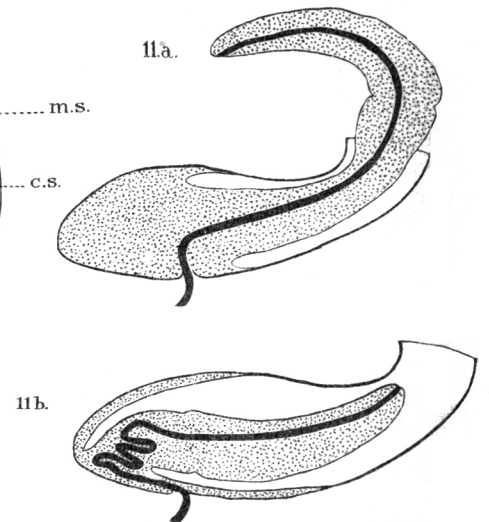


FIG. 11.

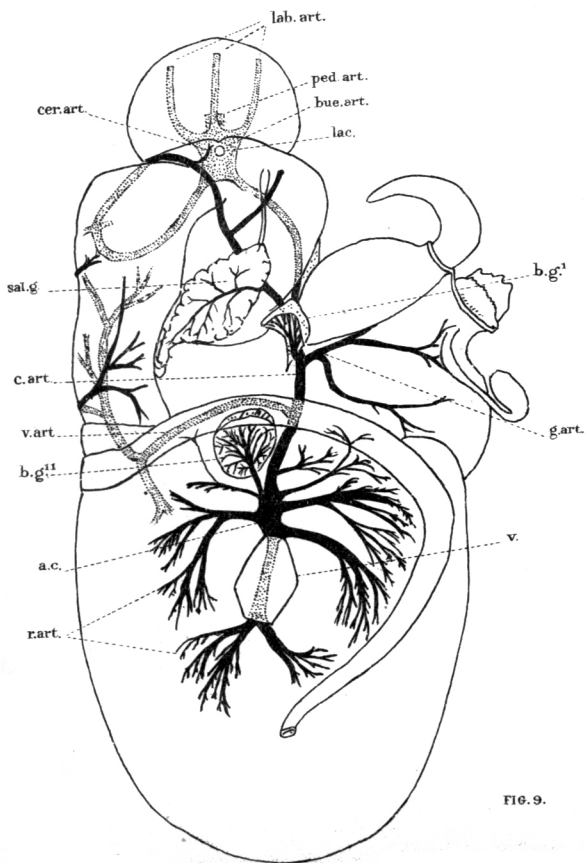


FIG. 9.

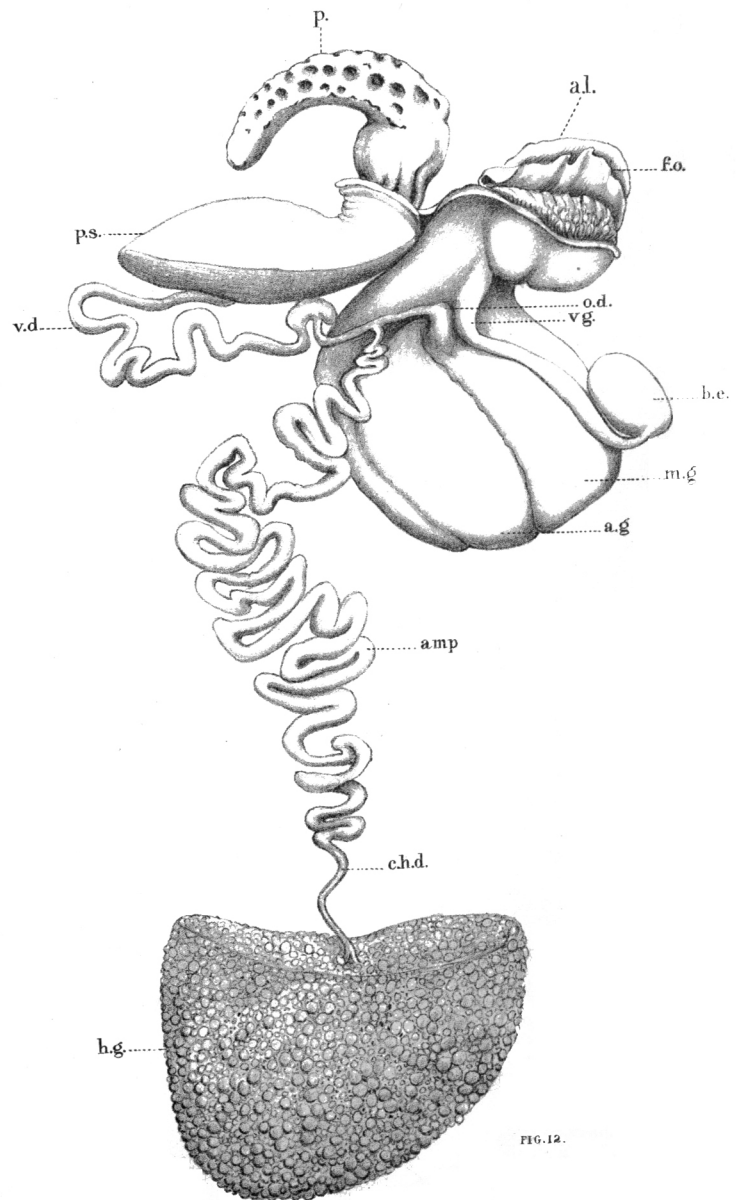


FIG. 12.