

to find a shelter from the radiation by concealing themselves more completely among the rock-work or vegetation. *Anthea cereus* is also very sensitive to considerable variations of temperature, falling from its foot-hold to the bottom of the tank apparently dead.

Excess of heat and also strong sunlight are likewise to be as carefully guarded against, and I may state as an evidence of this, that on a particularly hot day during the summer of 1854, being absent from home, the servant omitted to screen a small case from the sun's rays during the hottest period of the day, and on my return I found every creature dead. It contained an *Anthea cereus*, *Actinia dianthus*, two specimens of *Athanas nitescens*, and several others.

Too much light has also the effect of rapidly propagating several of the minute animalcules of a green colour, as the *Euglena* and its congeners, which under this influence multiply so rapidly as to render the whole water of a grass-green hue; this will at times subside to the lower part of the tank as evening approaches and disappear in the shingle bottom, but immediately the morning light shines strong upon the aquarium it will rise like a thin green cloud and diffuse itself throughout the whole of the water. Although this animalcular growth is not unhealthy, yet it causes the aquarium to present a very unsightly appearance, and prevents all observation on the habits of the inmates. The want of light, I need hardly observe, causes the rapid decay of the vegetation, and the products arising from this change are highly poisonous to animal life, the whole contents of the aquarium becoming of a black colour, and very soon of an offensive odour.

Apothecaries' Hall, Sept. 11, 1855.

XXIX.—*On the Mechanism of Aquatic Respiration and on the Structure of the Organs of Breathing in Invertebrate Animals.*
By THOMAS WILLIAMS, M.D. Lond., F.L.S., Physician to the Swansea Infirmary.

[With a Plate.]

[Continued from vol. xiv. p. 262.]

Gasteropoda.

It is now proposed to inquire into the structure of the organs of breathing in that multitudinous group of mollusks which lies above the Lamellibranchiata, constituting literally a great sub-kingdom; it will be impossible within the limits of this memoir

to do more than to illustrate types and plans of structure by special reference to a few familiar examples. Little account will be rendered of those classes with reference to which no personal opportunities have occurred to the author for instituting original investigations.

The Pteropoda are thus first excluded.

In proceeding to the study of the respiratory system of the Gasteropod mollusks, there present themselves a few questions which must be preliminarily considered.

In the conchiferous orders of this class, the shell is not simply and exclusively intended to shield and protect from external violence the soft body of the animal: it is a means by which the animal maintains between itself and the surrounding medium a certain fixed and important relation. The soft parts are tied to the shell only at certain limited points (Pl. IX. fig. 2 *b*). The mode of connexion differs in different orders, but not in families and genera. The point or line of attachment (*b*) is the pivot upon which the motions of the body of the animal are performed. Locomotion, in which the animal as well as the shell effect a change of place, is accomplished by means of the foot. The movements of the animal within the shell, the latter being fixed, considered with respect to its immediate well-being, assume a far greater importance than that of progression. In all shelled Gasteropods, the shell, whatever be its figure, whether univalve or multivalve, spiral, tubular or conical, circumscribes a chamber which is larger in size than the body of the animal which it serves to lodge. The difference in sectional area in the case of the spiral Univalves between the solid coil of the contained body and the hollow coil (fig. 2 *a, a, a, a*) of the containing shell, indicates a space which in all instances is filled with water: it is water which occupies this space even in the land Helicidæ. In the Patelloid and Chitonoid families (fig. 1 *a, b*) a chamber corresponding to this space is bounded above by the hollow apex of the shell, below by the dorsal surface of the animal; it is closed behind and open anteriorly. When the occupant extrudes itself from this coned chamber, a spacious open cavity is generated at the apex of the shell, into which through an opening in the edge of the mantle (*b*), situated above the head of the animal, water or air rushes. In the Fissurellidæ, in which the apex of the shell is perforated, the surrounding element in part enters into, and escapes from, according as the inmate emerges from or retires into its shell, the space at this orifice, the edge of the mantle consequently being adherent nearly all round. This is a point of generic difference between the Patellidæ and Fissurellidæ. The layer of water intervening between the animal and the shell is in direct contact with that region of the body in which the

viscera are enclosed. The interior surface of the chamber of the shell is so nacreous and polished, and the corresponding portion of the animal is so serous and smooth, that every condition which can affect the facile motion of the one surface upon the other is thus secured. From this circumstance the mind is led forcibly to the idea, that this arrangement has really nothing more than this mechanical purpose for its object. It might be supposed, from the intimate contact thus effected between the external element and the visceral cavity, that the former might incidentally enter in considerable quantities by endosmosis into the latter, and thus replenish the diminishing volume of the nutritive fluids. In order to determine this latter point, and whether the water in the chamber of the shell (fig. 2 *a, a*) were capable of fulfilling an accessory part in the office of respiration, it became necessary to ascertain by actual observation two doubtful points of structure, viz. whether the membrane covering that portion of the body of the animal which is enclosed within the shell be ciliated, or otherwise favourably organized with a view to such an office; and secondly, whether the circulating fluids beneath this membrane were disposed conformably with such an intention.

The great bulk of the soft parts, the abdomen proper (fig. 6 *d, d*; fig. 4 *b, c*), by which the coil of the shell is filled, consists of the liver, a portion of the stomach and intestinal canal, and the reproductive organs. They are invested by a membrane which is the continuation of the mantle. The membrane here becomes thinner and smoother, assuming the characters of a serous structure; it is not adherent at any point to the shell. On the inferior aspect of the body it is drawn up into a *frenum*, in the layers of which are enclosed muscular fascicles. It is by means of this contrivance that the animal is enabled to coil itself firmly round and to grasp the columella (fig. 2 *c*). Although this coat has a serous aspect, it is the continuation of the fibrous mantle which forms the vault of the respiratory chamber (fig. 3 *A-a*, & fig. 3 *B-a*). If by a very careful dissection this covering be removed from the viscera underneath, the nature of its connexions with the latter will be readily seen. It nowhere leaves an open space between it and the solid organs which it invests. It is, on the contrary, so intimately united to them, that numerous fibrous threads and bands descend from its internal surface, penetrating into the substance of the viscera and becoming continuous with their stromatous fibrous structure. It is inseparably identified with the serous *tunica propria* of each viscus. The latter cannot be said to exist as an independent structure. In no single species of the Prosobranchiata (M.-Edw.), or the shelled Pulmonifera, is it provided with ciliary

epithelium. This is actually the case in the freshwater Limneids, the most highly ciliated of this order. In no single species is there discoverable a *space* of any description, or a layer of channels or vessels of any sort between it and the invested abdominal organs. It is therefore certain that the abdominal segment of the body in the conchiferous Gasteropods can lend no aid whatever in the function of breathing. The porcellaneous interior surface of the shell is totally devoid of all organic covering; its polished surface is well adapted for the ready motion of the soft abdomen, covered also by its finely polished membrane, in its coiled chamber. The nacreous internal layers of the shell answer another important end: they render the shell water-proof; that is, the water which is drawn into the abdominal cavity, through the space at the mouth of the shell between the thoracic chamber and the edge of the latter, cannot escape by exosmosis or evaporation through the texture of the shell. The aperture of the shell being closed, by the operculum and thoracic expansion of the mantle, the water in the spire cannot escape. It constitutes a permanent reservoir. In this position it answers important purposes. It prevents the drying of the delicate abdominal membrane. It preserves the vital organs underneath in the required condition of moistness. It obviates the exhaustion of the nutritive fluids by evaporation. But more than all, it is capable, by a slight movement backwards of the animal, of being pushed forward into the cavity of the anterior shell-coil, and thence it may be drawn into the branchial chamber. In the littoral families of Univalves this is not a useless function when they are left on the dry rock by the recession of the tide. In the land Helicidæ it subserves also a similar end. This fluid in the Cyclobranchiata is lodged in the hollow of the apex or vault of the shell (fig. 1 *a*) resting on the back of the animal. In this order the border of the mantle is deficient at the point (*b*), which corresponds with the back of the neck of the animal. It is by this orifice or passage that the water is drawn into the cavity (*a*). The character, the extreme dilatability and uses of this cavity may be advantageously studied in the common Patella. It is capable under certain circumstances of receiving and retaining a large volume of fluid. But the furthest limits (*c*) to which it may be distended without rupture are best shown by the injection of coloured size. By steadily continued force, the fluid thrown in will slowly thrust the mollusk out of its shell (*i*). It forms a fulcral point upon which the animal bears, in the act of fixing its shell to the rock. This dorsal chamber in the Chitonidæ is very small. In the Fissurellidæ the perforation at the apex of the shell opens into the cavity; the latter cannot therefore act on the mechanical principle above explained. But

since these mollusks are seldom out of the water, this mode of action can scarcely at any time be put in request. They fix themselves by the action of the foot alone. By the undulating motion of this organ, the water between it and the surface of the stone is pressed out. The soft parts within the shell are then subject to the uncounterbalanced pressure of the superincumbent column of water which operates through the orifice at the apex of the shell. In the case of the *Patella*, it is by the shell that the atmospheric pressure is borne. The vacuum is formed, not by the extrusion of the water from the roof of the shell, but by the adaptation of the foot to the surface of contact. Hydrostatic or atmospheric pressure, as the case may be, becomes thus a considerable assistant force, but it does not, as commonly supposed, constitute the only and exclusive mechanism by which these mollusks cling to the rock.

These observations therefore justify the total and unconditional exclusion of the abdominal region of the body in the Conchiferous Univalves from the office of aërating the fluids. Neither the investing membrane nor the distribution of the blood underneath sanctions this idea.

This conclusion is not opposed to the views first stated by Milne-Edwards, in his celebrated essay "*Sur la Circulation chez les Mollusques* *."

* *Annales des Sciences*, 3 Sér. tom. viii. 1847. Nowhere does this distinguished observer describe an *abdominal* cavity in the Mollusca. Nothing in this class in the adult state exists which can be compared to the free, undivided visceral cavity of the Echinoderms and Annelids. Here this space is occupied by an independent fluid, the chylaqueous. In Mollusca such a fluid does not exist. The cavity therefore is not required. Milne-Edwards chiefly insists upon the fact, that the *venous* system is deficient or imperfectly developed in this class. "*Dans tous les Mollusques dont la structure nous est connue, les vaisseaux sanguins manquent en partie, et une portion plus ou moins considérable du cercle circulatoire se trouve constituée par de simples lacunes.*" In another place he observes—"*Mais dans la tête, je voyais toujours l'injection s'extravaser et remplir une grande cavité où se trouvent logés le cerveau, les glandes salivaires, le pharynx, et tous les muscles de la bouche.*" Again, he speaks in *Halotis* of "*une communication libre et normale entre la grande artère du corps et la cavité céphalique où se trouvent logés les principaux centres nerveux et toute la portion antérieure de l'appareil digestif.*" He then states that this "*cavité céphalique*" is filled with arterial blood. In a still more definite manner he thus describes the *only* "*cavity*" for the reception of fluid which exists in the Molluscan organism:—"Effectivement, je me suis assuré que, chez ce grand Mollusque Gastéropode, l'artère aorte, parvenue au point où le canal digestif se recourbe pour descendre de la face supérieure du bulbe pharyngien dans la cavité abdominale, débouche directement dans une vaste lacune, dont les parois sont formées en partie par les téguments communs de la tête, et en partie par les muscles et les tuniques du pharynx jointes à des lames de tissu connectif étendues transversalement au devant de la cavité abdominale, lacune dont l'intérieur est occupé,

The spacious sinuses and lacunæ developed in the course of the venous half of the circulation are not said by this author to

comme je l'ai déjà dit, par la masse charnue de la bouche, les glandes salivaires, les principaux ganglions du système nerveux, et un grand nombre de brides musculaires et fibreuses." "Mais un fait qui, au premier abord, paraîtra plus singulier encore, c'est que, tandis qu'une portion de la cavité générale vient compléter l'appareil vasculaire, l'artère aorte remplit des fonctions analogues à celles de la *cavité abdominale*, car elle loge dans son intérieur une portion de l'appareil digestif." It does not clearly appear from the observations of M. Quatrefages, in his memoir "Sur la Cavité générale du Corps des Invertébrés" (Ann. des Sci. 3 Sér. tom. xiv. 1850), that he has specially considered this point. He does indeed in one place positively state, that the "abdominal cavity in the Acephalan and Gasteropod Mollusks is a part or segment of the circulatory system":—"Chez les Mollusques Acéphales, proprement dit, l'existence de la cavité générale est encore plus complètement déguisée. Les Mollusques Gastéropodes présentent souvent quelque chose de semblable. Toutefois, chez ces derniers la cavité générale est presque toujours très reconnaissable, surtout dans la partie qui correspond au pied." Here no distinction is attempted between the true *peritoneal* cavity, such as it exists in the Radiated and Annulose classes, and those lacunæ or vascular dilatations such as Milne-Edwards first described in the structure of the Mollusca. This point is one of great zoological as well as homological interest. If in the Mollusca the circulatory system is peripherically nothing but a ramification of the *peritoneal* cavity, it is only a *chylaqueous* system plus a heart. But if it can be proved that the peritoneal space is obliterated in these mollusks, and that the venous lacunæ of Milne-Edwards are *parieted*, contractile, dilated vessels, that is, *segments* of the fluid system, situated in the interstices of the solid organs, every reason will have been overthrown for supposing that the apparatus of the circulation in the mollusks is *nothing but a ramified development of the peritoneal cavity*. In all animals below the Mollusca, the system of the perivisceral chamber is dedicated to a distinct and separate system of nutritive fluids. Its parietes in all cases are non-contractile—almost always ciliated at some point or other of its extent—while the fluid contents are invariably circulated by the action of externally situated muscles. These are peculiarities which appear to isolate this system almost completely from the circulatory apparatus of the Mollusca; in other words, they seem to prove that it partakes more fully of the characters which belong to the maturely developed circulation of the Vertebrated animal, than of those of the rudimentary chylaqueous system of the Radiate and Annulose classes. If the *arterial* half of the circulation of Mollusks be likened to the blood-proper system of Annelids, and the venous half of the former be taken as the representative of the perivisceral cavity in the latter, the homology of the molluscan fluid-system would be established! Siebold observes—"In Nudibranchs, Cyclobranchs, Scutibranchs, Tectibranchs, Pectinibranchs, and Pulmonata, &c., these venous canals are only lacunæ excavated in the *muscular* walls of the body, and are without proper walls, as Meckel has pretended is the case with those of *Aplysia*;" and Souleyet (Comptes Rendus, xx. p. 81, note 3) remarks, "que le système veineux des Mollusques n'est pas toujours formé par des vaisseaux distincts, mais qu'il se compose en grande partie de ces canaux creusés dans l'épaisseur ou dans l'interstice des organes." And it has been supposed by Prof. Owen and others, that the heart-like dilatations which occur at various points in the circulation of the Cephalopods, are lined

consist of the *abdominal cavity*, portioned off in order to aid in the circulation of the fluids. Whatever may be the embryonic significance of these roomy dilatations of the blood-channels in this class, it is quite certain that in very few instances are they situated external to and *around* the viscera (a position invariably occupied by the chylaqueous fluid), and therefore in the space bounded by the peritoneum and immediately underneath the external covering*. By the fact of their situation, these parts are then excluded from all participation in the office of breathing.

The preceding facts affect the present inquiry in the following manner:—They prove that the organization of the posterior or abdominal portion of the body in the Conchiferous Gasteropods, that part which is lodged within the shell, is not adapted for the admission of water into the interior of the animal, either for the supply of an aquiferous system or for the replenishing of the nutritive fluids. They prove, independently of other evidence, that the water with which the spire of the shell is filled, and in which floats the corresponding portion of the animal, cannot penetrate in any manner into the body; that it cannot be viewed as a reservoir whence is drawn the contents of a water-vascular system—if such a system has a real existence in these animals; that, in fact, it can only act in a mechanical sense by enabling the tenant to vary the specific weight of his house, to move

internally with a *mucous* membrane, like that which invests the branchial chamber. These and other facts drawn from the *adult* anatomy of the Mollusca, prove that, whatever argument may be drawn from embryonic development, that the open spaces, *lacunæ*, &c., which arise in the venous segment of the system, ought not too readily to be explained as merely cut-off portions of the perivisceral or peritoneal cavity.

If the spacious cephalic and pharyngeal *lacunæ*, first defined by Milne-Edwards, be not, in an embryonic sense, spaces cut off from the general cavity of the body, they must *ab origine* be parts of the vascular system. For the present this subject must remain an open question; that is, it cannot at present be confidently stated whether the circulating system of Mollusca form a distinct and independent system in the organism, or whether it be only a modified adaptation of the peritoneal cavity, or whether it be a fusion of both. To solve such doubts by an easy reference to the embryological relations of the parts were unsatisfactory. Two parts may have a common point of departure in the process of development, and yet they may stand very remotely apart in their ultimate structure and purpose. How little explanative it is, for instance, to remark, that the 'blood-proper' system of the Annelids and the tracheal system of Insects, being developments of the tegumentary, epidermal layer, are *therefore* homologous anatomically, and analogous in office! This, however, is not the occasion for the full discussion of this subject.

* It should be stated, however, that in the lowest Mollusca, as exemplified by *Frioloides* and *Atlanta*, the space between the integuments and the viscera is described by some observers as forming a constituent arc of the fluid-system.

readily to and fro in his chamber, and to shield the soft segment of the body from injury. It is not improbable that the layer of water thus placed between the body of the mollusk and the shell, may materially assist in the excretory process as described by Mr. Huxley, by which the latter is formed. It may add fluid to, or dissolve the excreted material furnished by the surface of the mantle, and adapt it to the internal surface of the shell. The limited ligament (fig. 2 *b*) by which the animal is *organically* united to its shell, places it beyond doubt that the latter can be formed by no other process.

By a few general observations, one department of the subject has been thus disposed of. No reference will hereafter be made to this subject, namely to the relation which subsists between the abdominal segment of the body in Gasteropods and external circumstances. It is extraordinary how in this class of mollusks the *most active* forces of life are developed and specialized in the thoracic region, and how comparatively passive are those parts which are bounded by the limits of the abdomen! Circulation and respiration are functions which belong to the former division. Large chylopoietic viscera are a resultant phenomenon. Thoracic development is a dynamic expression of an organic power. Without it, other results could not follow. It is the sign of power—without which the vegetative processes could not be sustained. Between the Acephala and Cephalophora there is this striking difference:—In the former the *mouth* is placed in the respiratory cavity, in the latter it is the anal orifice. In the former the alimentary and respiratory chambers are confounded, in the latter the breathing and the cloacal cavities are identified. This is a wide mark between the Lamellibranchs and the Gasteropoda.

The higher the animal in the scale of life, the more vigorous are the dynamic *active* powers. Thus, in the Gasteropod mollusks as compared with the Acephala, the physiologist expects an increment of vivifying force. How is it accomplished? By a more fully developed heart, impelled by the vital battery of a more highly organized cephalic ganglion, by a more actively endowed thoracic apparatus, by respiratory movements of a higher muscular character, and by branchial or pulmonary systems of incomparably more intricate workmanship.

In looking upwards along the line of the Cephalophora, it will be seen that the head as a detached member, as a distinct classificatory character, appears long before the respiratory organs—ex. Pteropoda, Heteropoda, Apneusta, and many Nudibranchs. Though the Encephala discover several marked signs of superiority as measured by the standard of the Acephala, it is well

determined that in the scale stretching between the Patellidæ and Cephalopods, the nervous and circulatory systems display few evidences of advancement.

In the lowest Gasteropod the heart is as perfect in structure as in the highest Cephalopod. When the branchial organ is symmetrically developed, the heart has two auricles. This is the case in *Chiton*, *Fissurella*, *Emarginula*, *Haliotis*, *Tethys* and *Janus*, and less completely in the Eolidæ. In all other Gasteropods the auricle is single. The position of the heart depends upon that of the respiratory organs. It is situated on the right side of the back in the Pulmonata, most Tectibranchiata, and the dextral Pectinibranchiata, and in all the Limacidæ; it is on the opposite side in the sinistral Gasteropods, *Ancylus* and *Haliotis*; it is to the left of the dorsal median line in *Carinaria*, *Clio*, *Hyalæa* and *Cleodora*; and near the hinder end of the body in *Firola* and *Atlanta*. In *Dentalium*, *Tritonia*, *Scyllæa*, *Phyllidea*, it is on the dorsal median line. The heart is furnished with a distinct pericardium in all Gasteropods, save the Apneusta, where it is not clearly defined. In all those genera whose branchial organs are symmetrical, the ventricle and aorta are directed forwards, but in the turbinated genera they are directed backwards.

Between the heart and respiratory organs in this class two relationships are discernible. In the first the heart is placed between the head and the branchiæ—Prosobranchiata (M.-Edw.); in the latter, between the tail and the branchiæ—Opisthobranchiata.

In all, there is between the branchiæ and the heart a most intimate juxtaposition. In all families the heart is *systemic*. In no single species is it pulmonic or branchial. In all, the auricle or auricles receive the blood immediately from the respiratory organ. The heart in the testaceous Gasteropods, spiral and otherwise, is always placed at the posterior end of the branchial cavity, or in other words, is fixed at that extremity of the branchiæ *farthest* from the entry of the aërating fluid. In *Dentalium* this rule is not broken, because here the water enters at the posterior instead of at the anterior orifice of the mantle.

The same general observations apply to the nervous system. Souleyet first explained that the parts which by their constancy and fixity constitute the essential centre of this system in the Mollusca, are always grouped around the œsophagus. The others should only be regarded as different degrees of development of these central portions, and this is proved by their degradation or disappearance in proportion as we descend in animals

of this series*. The primary ganglia always exist; many of the local parieto-splanchnic may be absent. The latter in size bear relation to the organ or part to which they furnish nerves. Those connected with the branchiæ vary with the latter organs. In the Mollusca, therefore, a part of the peripheric structures may acquire increased development, while the central systems remain unchanged.

Physics of the Respiratory Chamber in the Cephalophora.

In the Cephalophora the organs of respiration assume variable positions as regards the rest of the body. They lack the topographical constancy of these organs in the Lamellibranchs. As in the latter class, in the Cephalophora they consist essentially of developments of the tegumentary system. They are elaborated productions of the mantle. Although they may vary in structure and position, this relationship to the mantle is never radically affected. A brief review of the space or chamber in which the branchiæ are enclosed, will enable us to enter more detailedly into the regional anatomy of these organs.

The respiratory chamber (fig. 1 *f*) in the Cyclobranchiata is but imperfectly defined. It is for the most part a grooved circular fossa between the edge of the foot and the border of the mantle (fig. 1 *h*); but the branchiæ are not the less a development of this structure. If in the Patelloid and Chitonoid forms the edge of the mantle were prolonged and introverted, a channel would be defined in which the branchiæ would be enclosed. Wherever these organs are placed, some provision, such as a groove, is made for the efficient play of the *physics* of the branchial process.

The direction of the main aërating currents is from before backwards, and transversely on the branchial leaflets. The cavity which circumscribes the branchiæ in the Fissurellidæ commences at the neck and extends some distance backwards along the sides. It receives water though the vertical fissure, placed between the pedicles of the branchiæ; it escapes expiratorily at the lower and posterior border. In *Emarginula* the respiratory cavity of the mantle is situated at the back of the neck. In the Haliotidæ this cavity is similarly formed. *Patella*, *Acmaea*, *Pileopsis* and *Calyptræa* are the cervico-branchiate patelloid forms with a single non-symmetrical branchia. *Fissurella*, *Emarginula*, *Puncturella* and *Haliotis* are in the same cervico-branchiate category, but having two branchial leaves. (Clark.)

Thus in the same family how striking are the generic varia-

* Comptes Rendus, 1843.

tions in this one particular! The structure of the organs contained in these variously located chambers will be found to differ no less remarkably.

In the Pleurobranchiata the furrow for the branchia is situated between the foot and the lateral free border of the mantle. It differs in no essential respect in character and locality from that of the Patellidæ. This crypt or fossa has a higher position on the side in the Aplysiadæ. The *mechanics* of this cavity follow the same principle in all. The water-currents bear in an inward and backward direction under muscular and ciliary agency.

In the Pectinibranchiata (fig. 3 A, 3 B) a distinct and well-defined thoracic chamber exists (*a, a*). It is situated on the antero-dorsal region of the animal, and fills the anterior coil of the shell. It is overvaulted by the mantle. It does not form a closed cavity as in the Pulmonifera (figs. 4, 5, 6). It opens in front by a fissure extending from the right angle to the left. Behind, it is closed by the adhesion of the mantle to the edge of the diaphragm-like (fig. 4 *b*) partition between this chamber and the abdomen, thence the mantle is prolonged in a thinner form over the latter region. In this water-breathing order of mollusks this chamber is not exclusively specialized to the office of respiration. In every family it contains the termination of the intestine. It is thus at once respiratory and cloacal. In its walls, at a point differing in different families, is situated the heart, and a system of glands of complex formation. The branchiæ form only a small integral constituent. In the physics of this cavity one plan prevails throughout the Pectinibranchiate order. The branchiæ occupy a point in the chamber opposite to that taken up by the rectum. The former are to the left, the latter lies on the extreme right. It is on this side also that all the other excretory ducts terminate. The water-currents are excited and sustained by the muscular action of the parietes of the chamber. This force, which repeats itself in a regulated order, constrains the water to move in a fixed and determinate direction. It enters first at the left side, through the siphon (fig. 3 B, arrows), if this appendage be present—through the fissure directly, if it be absent. This *pure stream* impinges immediately upon the branchiæ. At this point, by means of an exquisite concert of muscular and ciliary forces, the mass of water thus received is divided into as many vertical sheets or secondary columns as there are spaces between the branchial leaflets. As the cartilaginous edges of these laminae are provided with muscles, and the flat surfaces of each are strewn with cilia (as will be afterwards described), the water is subdivided again into myriads of invisible streamlets. Issuing from the interlaminar spaces where its course is slow, the dispersed

columns reunite, assume a more rapid course, passing over the surface and between the folds of the "mucous glands," under the character of effete and deoxygenated water, and sweeping the termination of the intestine, and finally escape at the extreme right cleft (*b*) of the respiratory chamber, mechanically bearing on its current all the refuse products of the cavity. It will be anticipating, what will afterwards be studied more minutely, to enter further at this place into the details of this most beautiful arrangement.

The thoracic cavity of the aquatic and terrestrial Pulmonifera (figs. 4, 5 & 6) is mechanically arranged on the plan of that of the Pectinibranchiata. Though in some genera, as in *Parma-cella*, *Testacella* and *Onchidium*, it may assume a posterior position on the back, it is not changed in mechanism or in anatomical structure. In all other families of this order it occurs on the back near the head. In those species whose shell is sinistral the orifice is situated on the left side, in all others on the right. Under the former circumstances the respiratory movements of the parietes of the cavity are reversed. The pulmonary cavity of the air-breathing Gasteropods, relatively to the bulk of the body (fig. 4 *a*, *b*), is larger in dimensions than the branchial chamber of the Pectinibranchs. This difference is explained by the difference between air and water, but, as will hereafter be shown, it is due in reality to the comparatively rude and imperfect provision which has been made in the instance of the Pulmonata for the necessities of breathing. Here, the anterior fissure of the branchial cavity, so characteristic of this part in water-breathing Gasteropods, is accurately closed. The cavity communicates with the exterior by means only of a single orifice, which, for the most part, is situated on the right side. This orifice, in families of aquatic habits, is prolonged into an infundibulum (figs. 4 & 6 *a*, *a*).

The acts of inspiration and respiration are remarkably slowly performed. So spacious is this chamber in the Planorbidae (fig. 6 *c*), Limneadæ (fig. 4 *a*, *b*), and Helicidæ, that a supply of air capable of sustaining life for a considerable time under water, or in an irrespirable medium, can be stored.

The normal muscular movements of respiration are most satisfactorily studied in *Helix aspersa*, previously carefully, and without injury to the soft parts, removed from its shell. It will be seen that the volume of air drawn in by the inspiratory act is driven by the slow vermicular movement of the parietes (arrows in fig. 4) from right to left, chiefly along the roof. If the air is long retained, it repeats the same orbit. During the act of expiration the walls of the whole of the dorsal and lateral regions of the body simultaneously contract, and the breathing-chamber

collapses in a most remarkable manner. It is during the expiratory act that the faecal excreta are expelled, and this takes place through one and the same orifice. In this character the Pulmonata are strikingly distinguished from the Pectinibranchiata. In the latter, the pure current entering the breathing-chamber is scrupulously separated from that which is about to be expelled. When water and not air is the medium of respiration, this is a constant feature in the history of the Cephalophora.

This circumstance is still more beautifully and perfectly observed in the physics of breathing as exemplified in the Cephalopod mollusks (fig. 7). It has already been explained, that so completely and intimately is the body of every Invertebrate animal surrounded and *apparently penetrated* by the external element, that not only is it profusely admitted into the digestive and respiratory organs, but, as for example in tubicolous Worms and testaceous Cephalophora, its contact with the entire exterior of the body is secured by express provisions.

In the Cyclobranchiata, as formerly described, a water-reservoir occupies the concave apex of the shell: the abdominal coils of the shells of all Univalves constitute a similar receptacle. The same rule is recognized in the organization of the Cephalopods. In this class, in a given time, a considerable volume of water traverses the branchial chamber. The respiratory actions of the mantle and the funnel are rapid and powerful.

In the Nautilus, Ammonite, and other testaceous Cephalopods, the base of the branchial recess of the mantle is continuous with the siphuncle. In this manner the external element is admitted directly into the abdominal segments of the shell, therein chiefly to subserve mechanical purposes. If the respiratory chamber in the shelled Gasteropods were perforated at its posterior border, opening thus into the spiral spaces of the shell, the water occupying this portion in these families would stand in the same relation to that of the branchial cavity as it does in the case of the Nautilus.

In those orders, chiefly the Dibranchiata, which are devoid of an external shell, the respiratory chamber is larger and more prolonged into the spaces between the vital organs than in those in which this appendage is present. *Octopus*, *Loligo*, or *Sepia*, afford the best opportunity for witnessing the mechanical actions of breathing. The anterior edge of the mantle is separated from the side of the body by a broad open fissure (fig. 7 *b*, and incoming arrows). This fissure within the mantle assumes the character of a canal which leads back *along the floor* (*c*) of the branchial chamber as far as the attached or cardiac base of the gills (*d*). Along this canal up to this point the water enters as

a broad single column (fig. 7, arrows). It is then suddenly deflected forwards into the *interior of the gills* (e), which, in *Octopus* and *Sepia*, form *hollow conical organs*, in *Loligo* and the Calamary a hollow *semicylinder*. In the former during the moment of inspiration a copious column of water rushes up the hollow axis of the gill; in the latter families, along the inferior concavity. These currents are directed by a most complexly coordinated series of muscular actions. From the interior of the branchiæ the water is compressed by a muscular power resident in the branchiæ themselves. It issues in as many streams as there are perforations between the ultimate *pinnæ* of the organ. These streams regather themselves and flow backwards again in the direction of the base of the gills, leaving the branchial hearts and other large blood-channels situated in that region; then driven forwards by the expiratory collapse of the entire mantle, the water in form of a single column enters the base of the funnel (f), through which it finally leaves the cavity as an excretory and expiratory current (a).

The author will explain on another occasion how much that is old and how much that is new is contained in these observations. In succeeding papers they will be supported by a large mass of anatomical details of great interest, and hitherto, he believes, unknown to naturalists.

EXPLANATION OF PLATE IX.

Fig. 1. An imaginary vertical section through the shell and body of *Patella athletica*. a, water-cavity in the roof of the shell, capable of being enlarged to the dimensions of b and c. e, gills; f, fringed edge of the mantle; g, g, edge of shell; i, foot; j, anus, terminating in the chamber above the mouth.

Fig. 2. A longitudinal section of the shell of *Buccinum undatum*, showing the abdominal spires, a, a, a, a, which are filled with water and with the abdomen of the animal. b. denotes the ligament by which the animal is attached to the columella, c.

Fig. 3 A. Male animal of *Buccinum undatum* taken out of its shell. At b, is shown the mode in which the penis is carried in the branchial chamber a.

Fig. 3 B. The same animal with the penis withdrawn from the branchial chamber. On the left is the siphon through which, as indicated by the arrows, the water enters the chamber (a), describing therein a circuit marked by the arrows; it escapes at the right cleft b.

Fig. 4. The animal of *Lymneus stagnalis* taken out of its shell. The arrows define the pulmonary chamber and the circulation performed by the air under the vermicular action of the walls. b. is the posterior limit of the thoracic chamber; c. marks the solid abdominal portion of the body, and a. the respiratory and defecatory siphon.

Fig. 5. *Limax maximus* in outline. a. denotes the respiratory and defe-





Williams, Thomas. 1855. "XXIX.—On the mechanism of aquatic respiration and on the structure of the organs of breathing in invertebrate animals." *The Annals and magazine of natural history; zoology, botany, and geology* 16, 315–329. <https://doi.org/10.1080/037454809496411>.

View This Item Online: <https://www.biodiversitylibrary.org/item/19432>

DOI: <https://doi.org/10.1080/037454809496411>

Permalink: <https://www.biodiversitylibrary.org/partpdf/30109>

Holding Institution

Natural History Museum Library, London

Sponsored by

Natural History Museum Library, London

Copyright & Reuse

Copyright Status: Public domain. The BHL considers that this work is no longer under copyright protection.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.